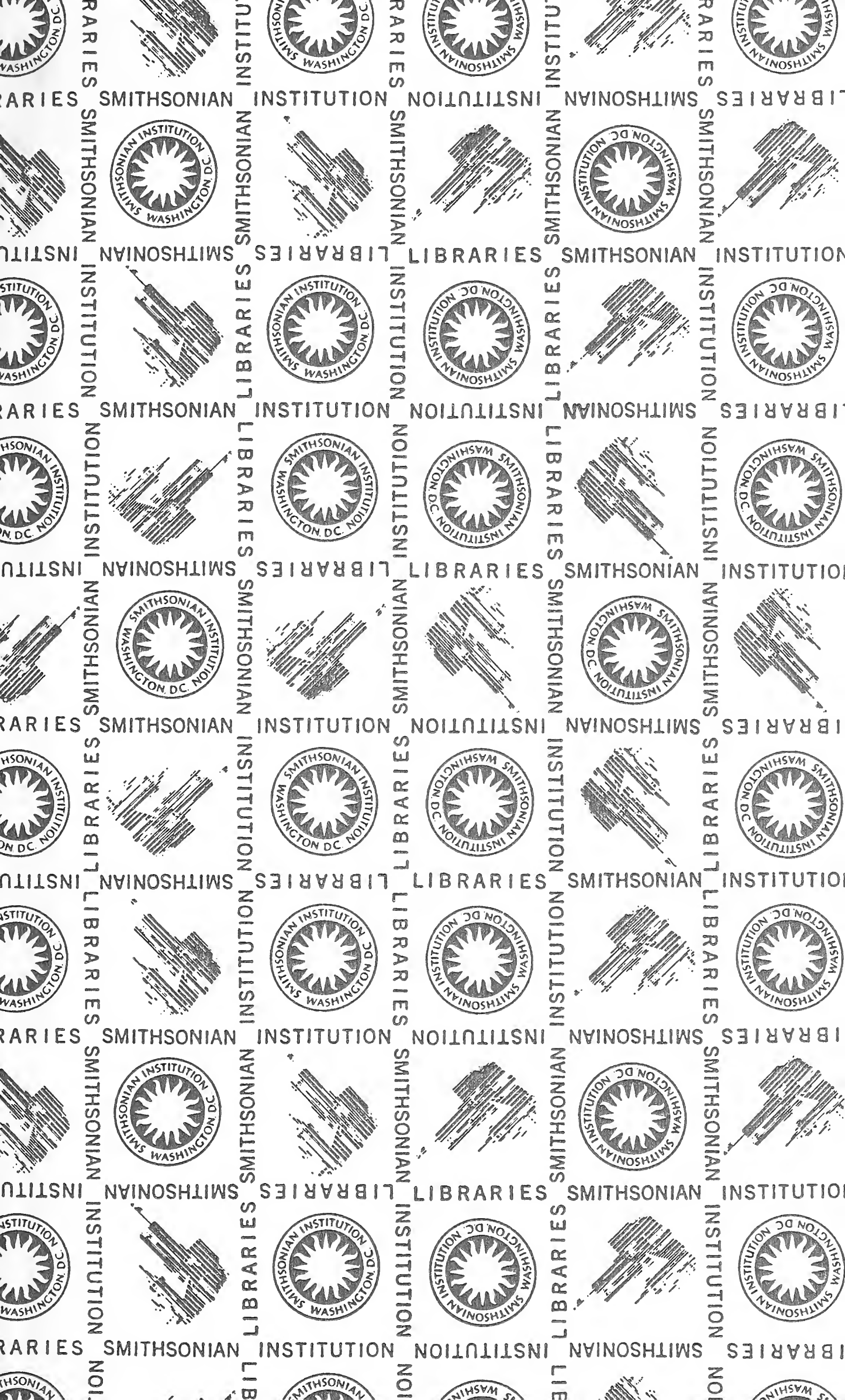
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PSYCHE

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STUDIES ON UPPER CARBONIFEROUS INSECTS: 1. THE GERARIDAE (ORDER PROTORTHOPTERA)

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INTRODUCTION

Despite the importance of the order Protorthoptera,[1] little is known about its evolutionary history. While recent workers have emphasized morphological and taxonomic diversity in the group (Carpenter, 1971, 1977; Wootton, 1981), no one has undertaken serious revisionary study at the family level. As a consequence, our understanding of relationships within the order, as well as relationships of the Protorthoptera to other Paleozoic insects, is rudimentary at best. Clearly, revisionary studies on this group are badly needed.

We know that the Protorthoptera first appear in the fossil record at the base of the Upper Carboniferous (Namurian Stage) and apparently flourished for 80 million years before becoming extinct at the end of the Permian. We also know that they were remarkably

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[1] It was one of the dominant orders of the Paleozoic (exceeding all other insects both in number of species and in number of individuals), and is considered by many to be ancestral to the Endopterygota (the group to which 90% of all living insects belong).

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*Present address.

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diverse morphologically, and that diversity in the group (*sensu lato*) far exceeded that of any other Paleozoic order (Carpenter, 1977). Structural modifications normally associated with more recent insects, including brightly patterned wings, raptorial fore legs, and thoracic extensions of various kinds, are found throughout the group.

Despite this fascinating array of characters, Carboniferous Protorthoptera have generated little interest among systematists. This is due, in part, to problems common to all paleoentomological study: an overall lack of material (rarely is a species based on a large series of specimens); preservational quality that ranges from excellent to very poor; and a taxonomy that is highly subjective.

In addition, there are problems unique to the Protorthoptera which make their study particularly difficult. First, they are neopterous, and as a consequence, are most frequently found with their wings superimposed on one another. Interpretation of the venation under these circumstances is not only difficult, but prone to error. Second, the vast majority of Carboniferous Protorthoptera are known from only two localities: Commentry in France, and Mazon Creek in the United States, and were studied primarily by turn-of-the-century workers.[2] As new material has become available for study in recent years, the accuracy of much of this earlier work has been questioned.

Finally, there is the problem of variation. Distinguishing species-level differences from intraspecific variation in fossils that have such a limited array of characters is not easily resolved. How, for instance, does one recognize sexual dimorphism in a fossil species when there are no genitalia or secondary sexual characters to serve as guidelines? It is not surprising under the circumstances that paleotaxonomy rests largely on subjective reasoning. But this, unfortunately, has its pitfalls.

Previous work on the Geraridae is a case in point. Anton Handlirsch, responsible for most of the earlier work on the family, described a new species of gerarid for every specimen he examined,

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[2] The Permian Protorthoptera are generally much better known than their Carboniferous relatives. This is attributable to the fact that there are more than eight major Permian deposits (including two in the U.S.) at which Protorthoptera have been found. Furthermore, intensive studies on these insects have attracted the attention of such well-known recent workers as Carpenter, Kukalová, and Sharov.

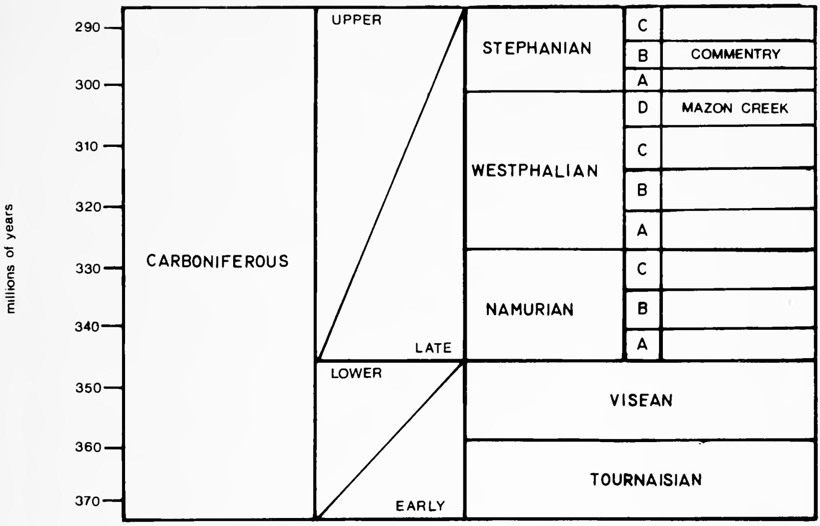

Fig. 1. Geological Time Table of the Carboniferous. Note the different ages of the Commentry and Mazon Creek localities.

basing his taxonomic decisions on small differences in wing venation (Handlirsch, 1906b, 1911, 1922). This approach, while rendering the decision making easier, is nevertheless open to criticism. Studies on intraspecific variation in some Permian Protorthoptera have shown, for instance, that two fore wings belonging to the same specimen will exhibit noticeable differences in venation (Carpenter, 1966). From these findings we can conclude that intraspecific variation in the Protorthoptera was high, and that the variation Handlirsch saw was no greater than that seen in a single specimen. Further evidence that suggests Handlirsch was unrealistic in his representation of species diversity comes from the low probability of finding only one individual per species (for all species collected) in a random sample of living insects. Similarly, we cannot reasonably expect to find only one specimen per species in a paleontological sample, particularly when fossilization was catastrophic (and hence random) as is true for the Mazon Creek biota.

Nevertheless, in spite of these drawbacks to the study of fossil insects, the field can be immensely rewarding. This is because it provides us with concrete evidence (in the form of fossils) of what early insect life was like. Without such proof, we would be guided only by our imagination, and having this proof provides a base on which insect phylogeny and early insect evolution can be reconstructed.

Clearly, revisionary studies on Paleozoic insects are important. Fortunately, recent revisional work by Carpenter has greatly increased our knowledge of certain Paleozoic orders (i.e., the Paleodictyoptera, Megasecoptera, Diaphanopterodea, Protodonata, and Caloneurodea), but much work on the Protorthoptera remains. This revision of the family Geraridae is, at least, a beginning and is intended to be the first in a series of family-level studies on Upper Carboniferous Protorthoptera.

Selection of the Geraridae as a starting point was influenced, ultimately, by two factors: 1) it is typical of many of the families in the Protorthoptera, having last been studied in the early part of this century (despite the discovery since then of new material assignable to the family); and 2) the Geraridae are morphologically most unusual insects. They were large (up to 75 mm in body length), and had as their single most distinctive attribute, a prothorax that was elongate, flask-shaped, and adorned with long, numerous spines. These spines gave them the appearance of walking pincushions, and presumably provided some defense against vertebrate predators.

The systematic importance of the family plus the impact this work has on current classifications of the Protorthoptera will be discussed in subsequent pages. The remaining sections of this paper cover (in the following order): the systematics of the Geraridae; paleoecological differences between the two localities at which gerarids have been found (Mazon Creek and Commentry); and the significance of this study relative to phylogenetic relationships within the Protorthoptera.

SYSTEMATICS

MATERIALS AND METHODS

The fossils examined for this study occur mostly as impressions (imprints in a sedimentary matrix devoid of organic matter) but some occur as compressions (in these, organic matter is present, but usually coalified). Both types of fossils were prepared by degagement,[3] i.e., an uncovering of the fossil by removal of the overlying rock matrix. This is generally done using a fine pneumatic drill and

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[3] From the French verb *dégager* meaning to disengage, extricate, or get clear.

compressed air gun. The technique is particularly effective at revealing regions of an insect's body (wing tips, legs, etc.) that are found beneath the bedding plane. Following degagement, specimens were studied under a Wild M-5 stereo microscope and photographed with a Zeiss 4″ by 5″ format camera.

Drawings were made of each fossil by tracing a general outline from a photographic enlargement. Verification of detail was made by referring back to the specimens and examining them frequently under the microscope. The most complete reconstructions (e.g., fig. 2 of *G. danielsi*) were possible for those species that consist of a large series of specimens. This is because one fossil rarely displays all characters equally well, and, therefore, the larger the number of specimens, the greater the likelihood of multiple character preservation.

Type specimens, including the holotypes, for all taxa considered in this revisionary study were borrowed and examined using the above methods. Pre-existing taxa were synonymized whenever possible, a decision based on the assumption that (for reasons cited earlier) intraspecific variation in the Protorthoptera is great. Characters of greatest taxonomic importance were venation and body size and shape, particularly with respect to the prothorax. In situations where clearcut characters were lacking, as is true for several of the Mazon Creek gerarids, I relied solely on size as a criterion for specific assignment. While this may result in the recognition of some dubious species, it seems preferable to relegating certain specimens to *incertae sedis* status.

Since wing venation is such an important taxonomic tool both in paleoentomological and extant systematic study, it is surprising that until recently no standardized wing terminology has been adopted. This is particularly unfortunate for the Protorthoptera, 80% of which have been described on the basis of wings alone. Inroads have recently been made into this problem primarily by the efforts of Carpenter in the United States and Wootton in Great Britain. Both have stressed (Carpenter, 1966; Wootton, 1979, 1981) the importance of a standardized venational nomenclature and Wootton (1979) has proposed a terminology modified slightly from the one used previously by Lameere (1922) and Martynov (1924, 1938).

Wootton proposes that the following nine major longitudinal veins be recognized: Costa (C); Subcosta (SC); Radius (R); Radial Sector (RS); Anterior Media (MA); Posterior Media (MP); Anterior Cubitus (CUA); Posterior Cubitus (CUP), and Anals. In light of the historical basis for the nomenclature (used extensively in the paleoentomological literature) and its conservatism (it may be used to homologize the wing venation of all insects) I enthusiastically concur with Wootton's recommendations and will employ his system here and in future systematic work.

A total of 58 specimens were made available for study through the loans of various institutions and individuals. These are listed here with their abbreviations:

Field Museum of Natural History (FMNH), Chicago, Illinois, U.S.A. (This includes specimens collected by Jerry Herdina and subsequently acquired by the Field Museum).

Institut de Paléontologie, Muséum National d'Histoire Naturelle (IP), Paris, France.

Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts, U.S.A.

United States National Museum (USNM), Washington, D.C., U.S.A.

Yale Peabody Museum (YPM), New Haven, Connecticut, U.S.A.

Daniel Damrow, of Mosinee, Wisconsin. Private collection. (DMRW) (Includes specimens previously in the collection of Walter Dabasinskas).

David Douglass, of Yachats, Oregon. Private collection. (DGLS)

Francis and Terri Wolff, of Port Charlotte, Florida. Private collection (Wolff).

ORDER PROTORTHOPTERA HANDLIRSCH

Family Geraridae Scudder, 1885

[*Nom. correct.* Handlirsch, 1906a (*ex* Gerarina Scudder, 1885)]

Gerarina Scudder 1885:342. Type: *Gerarus* Scudder.

Geraridae Handlirsch 1906a:146, 1906b:701, 1911:312, 1920:151.

Sthenaropodidae Handlirsch 1906a:141, 1919:37, 1920:150; Sharov 1968:19. Type: *Sthenaropoda* Brongniart. NEW SYNONYMY.

Genopterygidae Richardson 1956:41. Type: *Genopteryx* Scudder. NEW SYNONYMY.

Description

Fore and hind wings similar in size and shape, but markedly different in venation.

Fore wing: length 35–55 mm, and apparently not coriaceous; costal area broad in basal region, SC simple, terminating in C; R parallel to SC, terminating at wing apex; RS originating from base of R near midpoint of wing; M either anastomosing with RS for a short distance or connecting to it by a cross-vein; CUA strongly developed, arising from base of M; CUP forked, arising independently from wing base.

Hind wing: length 30–48 mm; costal area not as broad as in fore wing; SC simple, terminating in C; R parallel to SC, terminating at wing apex; RS pectinate, arising from R near wing base; M forked, arising near base of RS; CUA and CUP simple and parallel to one another; CUA arising from base of RS near M, CUP arising independently from wing base; anal area unusually reduced; cross veins abundant in both fore and hind wings.

Body: prothorax elongate, flask-shaped, and distinctively spinose; abdomen cylindrical; antennae filamentous; head small and probably mobile; legs cursorial, tarsi five-segmented.

Diagnosis

In many ways the Geraridae are typical Orthopteroidea, having mandibulate mouthparts, hypognathous heads, and filamentous antennae. But they differ from other orthopteroids in two important characters: their well-developed prothorax which is armed with spines (the latter reach a length of 10 mm in *G. danielsi*), and their distinctive fore and hind wing venation. While gerarids can be readily recognized on the basis of the prothorax alone, wing venation is generally a better diagnostic character. Particularly distinctive are the RS-M veins in the fore wing, and the R-RS veins in the hind wing. In the fore wing RS is reduced and M is expanded with 5 to 6 branches. The apical branch of M either anastomoses with RS for a short distance or is connected to it by a short cross vein. In the hind wing, the opposite is true: M is greatly reduced and RS expanded into 5 to 6 branches.

It is worth noting that the anal fan in the hind wing, if present, was very small (see fig. 17). This suggests that in gerarids the fore and hind wings may have functioned equally well in flight, unlike in extant Orthoptera, which rely primarily on expanded hind wings for flight propulsion. The abdomen is essentially unknown for the family, but was probably shorter than the wings, a claim based on the comparison of wing length to legs, thorax, and head. No cerci are preserved, but because the Geraridae are orthopteroid, it may be assumed that they were present.

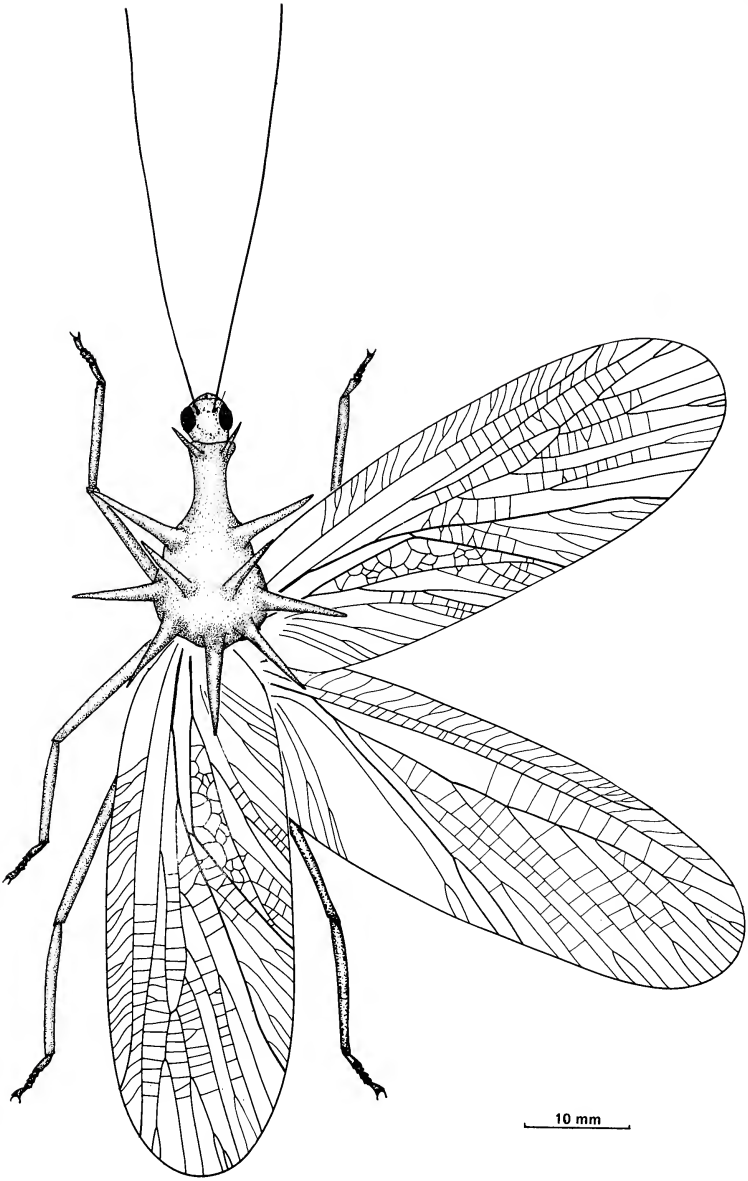

Fig. 2. *Gerarus danielsi*, composite drawing, based primarily on specimens FMNH PE 5276, 31973, 32027, 32029; and USNM 31973.

Remarks

The family Geraridae was first established by Scudder (1885) for several fossil insects from Mazon Creek noted for their slender bodies, which tapered "greatly anteriorly" (Scudder, 1885:344), and for the distinctive branching pattern of RS in the hind wing. Scudder placed the family in the order Paleodictyoptera, section Neuropteroidea, where it remained until 1906 when Handlirsch erected the order Protorthoptera and transferred the Geraridae to it.[4] Most of the subsequent work on the family was carried out by Handlirsch who added a total of two new genera and nine new species to it (Handlirsch, 1906a, 1906b, 1911, 1920).

This revision is the first systematic work carried out on the family since then, and rectifies many of the taxonomic errors made by these earlier workers. To a large extent, the mistakes made by Scudder and Handlirsch may be attributed to the limited availability of material at their disposal, and the preservation of most gerarids with all four wings lying over one another. Nevertheless, their errors were of grave consequence. To begin with, neither worker apparently recognized the extent to which intraspecific variation occurs in the family, and therefore each named only monotypic species. But, more importantly, owing to the difficulties of wing overlap, neither Scudder nor Handlirsch correctly interpreted the wing venation of *Gerarus*; both managed to interpret the venation of one wing (the hind wing) and then assumed that fore and hind wings were identical, although neither actually saw the fore wing.

The advantage of having more material at my disposal made it possible for me to overcome the problems that faced these workers. Certain well-preserved specimens (especially FMNH-PE 5276, 31973, 32027; IP 5, 23) were instrumental in demonstrating the complete venational differences between fore and hind wings. A comparison of figs. 6a and 6b shows how strikingly different the fore wing actually is from the hind wing. This, in itself, was quite a revelation. But it was only later, when searching through the literature looking for venational similarities with other groups, that the

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[4] Prior to this, all Carboniferous insects were included in the one order Paleodictyoptera in accordance with Scudder's beliefs that ordinal differentiation had not taken place in the Insecta as early as the Carboniferous. We know, of course, that this was incorrect; a total of 11 orders are now recognized from that Period (Carpenter, 1977; Wootton, 1981).

full significance of the discovery emerged. It became immediately apparent, based on fore wing characters, that the type genus (*Sthenaropoda*) for the family Sthenaropodidae[5] is inseparable from *Gerarus*. The consequences of this are twofold: 1) it extends the geographic range of the Geraridae from North America to Europe, strongly suggesting that the family was once large and successful; and 2) the synonymy casts serious doubts on current classifications of Paleozoic orthopteroids such as those proposed by Sharov (1968) and Rasnitsyn (1980). The implications of this are addressed in the discussion section at the end of this paper.

GEOLOGICAL RANGE: Carboniferous—Westphalian D to Stephanian. OCCURRENCE: Mazon Creek, Illinois, U.S.A.; Commentry, France. TYPE GENUS: *Gerarus*.

Synonymies

The families Genopterygidae and Sthenaropodidae are synonymized here with the Geraridae, since I find no unique characters by which to recognize them as independent taxa. All major veins and body characters are in complete agreement with the definition of the Geraridae. Although the Genopterygidae are described from the hind wing alone, and this synonymy may therefore change as additional material is found, the venational similarities between *Genopteryx* and *Gerarus* are striking (see fig. 7). This, in my mind, is sufficient reason at this time to synonymize these families. The synonymy of the Sthenaropodidae with the Geraridae is based not only on the venation of both wings, but also on the prothorax (complete with spines) and body size. The two families are so similar in character that synonymy at the species level could almost be justified were it not for their separation both geologically and geographically.

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[5] The Sthenaropodidae, like the Geraridae, were the focus of taxonomic work largely at the turn of the century. Brongniart first described *Sthenaropoda* (based on *S. fischeri*) in 1885 and placed it with a series of other Carboniferous Protorthoptera in the family Paleoacridiodea. Eight years later he synonymized *Sthenaropoda* with *Oedischia* (now recognized as belonging to the Orthoptera), believing their differences too slight to warrant generic separation. In 1906 Handlirsch restored the genus *Sthenaropoda* and placed it in its own family. His decision was later defended by both Lameere (1917) and Sharov (1968), who felt that the oedischiids, by virtue of their saltatorial legs, were true Orthoptera, and that the sthenaropodids, which lacked well-developed jumping legs, were clearly members of the Protorthoptera. The ramifications of this are discussed in the concluding pages of this paper.

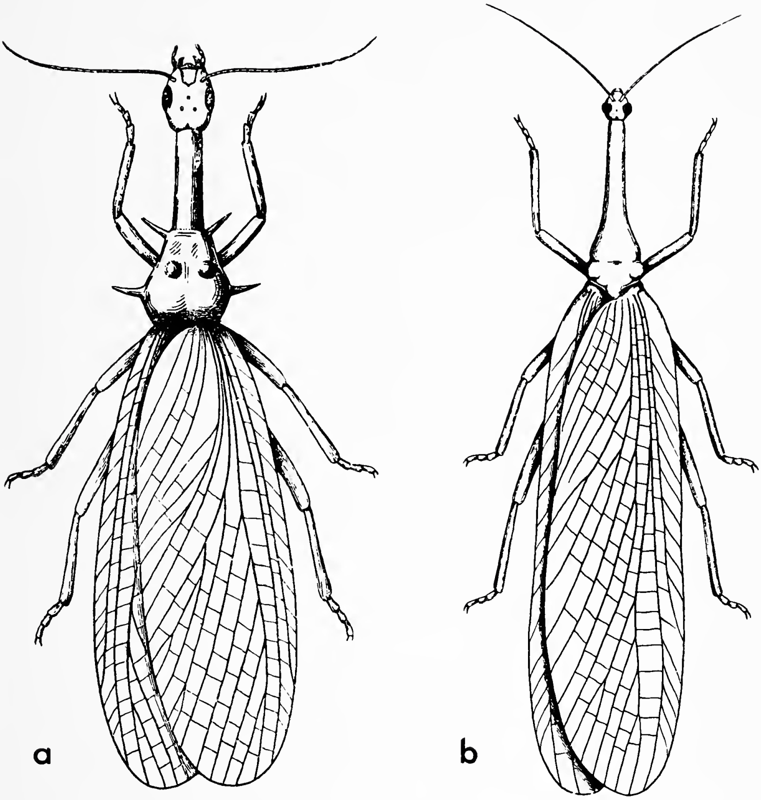

Fig. 3. Handlirsch's reconstructions of two species of *Gerarus*. a. *G. danielsi*; b. *G. collaris* (=*longicollis*). (From Handlirsch, 1920:152,153).

Genus *Gerarus*

Gerarus Scudder 1885:344; Handlirsch 1906a:147, 1906b:702, 1911: 313, 1919:38. Type: *Gerarus vetus* Scudder (original designation).

Sthenaropoda Brongniart 1885:59; Handlirsch 1906a:148, 1906b: 704, 1919:30. Type: *Sthenaropoda fischeri* (original designation). NEW SYNONYMY.[6]

Genopteryx Scudder 1885:327; Handlirsch 1906a:148, 1906b:704, 1919:30. Type: *Genopteryx constricta* (original designation). NEW SYNONYMY.[7]

Archaeacridites Meunier 1909a:39, 1909c:145; Handlirsch 1919:39. Type: *Archaeacridites bruesi* (original designation). NEW SYNONYMY.

Rossites Richardson 1956:44. Type: *Rossites inopinus* (original designation). NEW SYNONYMY.

Description

Fore wing: membranous, larger than hind wing, rounded at apex; SC long, weakly turning anteriorly to fuse with C at point three-fourths to two-thirds the length of the wing; R parallel to SC, terminating in C slightly anteriorad to wing apex. Fore wings differ from hind wings in the following veins: in the fore wing, RS branches from R in the basal third of the wing, and bifurcates two or three times. M four- or five-branched, either connecting to RS by a cross vein or fusing with it; CUA coalesces with M for short distance at wing base and may be weakly branched; CUP simple, elbowed towards CUA; network of anal veins present.

Hind wing: RS has three to six distinct pectinate branches and does not fuse with M; M multiply branched, arising from RS; CUA

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[6] Some doubt exists concerning the date of publication of this paper with respect to Scudder's 1885 article, but I have concluded for the following reasons that Scudder had priority of publication: 1) Although we do not know the month of publication for Brongniart's paper, we do know that Scudder's was published early in April, 1885. Unfortunately, attempts to obtain the exact date of publication for Brongniart's article from the Muséum d'Histoire Naturelle de Rouen and the Societé des Amis des Sciences Naturelles de Rouen have met with no response. 2) Citations of these two papers (e.g., Handlirsch, 1906a, 1922) have consistently listed Scudder's paper before Brongniart's. 3) Scudder's 1885 account of *Gerarus* includes a full description, figures, and designation of a type species (*G. vetus*), whereas Brongniart's paper only mentions *Sthenaropoda* and gives no formal description.

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[7] *Gerarus* and *Genopteryx* were named and described by Scudder in the same paper (1885). In accordance with the I.C.Z.N. procedures, and as the first reviser, I have treated *Genopteryx* as the junior synonym of *Gerarus*, the better known and larger genus.

simple or with one bifurcation; CUP simple and parallel to CUA; anal area slightly expanded, but unusually reduced for the Orthopteroidea. See fig. 17.

Diagnosis

Gerarus may be distinguished from the other genera in the Geraridae (*Nacekomia, Progenentomum, Genentomum* and *Gerarulus*) by size (members of this genus are large, fore wing is 40 mm to 55 mm in length); and the nature of the RS and M veins in the fore wing. In *Gerarus* RS branches two or three times; in *Progenentomum*, it branches at least four times. M in *Gerarus* is four- or five-branched, and either coalesces with RS for a short distance or is connected to it by a well-developed cross vein. In contrast, M in *Nacekomia* is distinct from RS, and in *Genentomum,* M is only three-branched and these branches are distinctly parallel to one another. Other characters such as the shape of the thorax and number of prothoracic spines may ultimately prove important in distinguishing these genera from one another, but as yet, we lack the well-preserved specimens necessary for separating all four genera in the family on the basis of such additional characters.

Remarks

Handlirsch (1911:313) characterized *Gerarus* by its prothorax, described as "a broad base, either provided with tubercles or smooth, but in every case, produced into a long neck-like part bearing the head." While he was correct about the nature of the "neck," he was incorrect in his assessment of the "tubercles," which were presumably present in all adult gerarids as fully produced spines, not tubercles. He was also slightly inaccurate in describing the prothorax as "a broad base." This study has shown the width of the prothorax to vary from 5 mm to 13 mm depending on the species. A better description for the genus is one based on wing venation.

GEOLOGICAL RANGE: Upper Carboniferous—Westphalian D to Stephanian. OCCURRENCE: Mazon Creek, Illinois, U.S.A.; Commentry, France. TYPE SPECIES: *Gerarus vetus.*

Synonymies

As indicated in previous pages, clarification of the venation of both fore and hind wings has led to several important synonymies. A comparison of *Sthenaropoda* with *Gerarus* reveals that the venational differences lie largely in the number of branches of M and this, in my opinion, does not justify distinction above the species level. Similarly, *Archaeacridites*, lacking distinct venational characters, cannot be separated from *Gerarus*.

I am also synonymizing two genera from the order Caloneurodea with *Gerarus: Genopteryx* and *Rossites*, for which Richardson (1956) erected the family Genopterygidae. *Genopteryx*, originally described by Scudder (1885), and placed in the family Homothetidae, was transferred subsequently to the Geraridae by Handlirsch (1906a). Richardson (1956:41) removed *Genopteryx* from the Geraridae and placed it in the order Caloneurodea. He did so on the basis of its "heavy cross veins and the close straight parallel CUA and CUP" these being the "two characters regarded by Carpenter (1943) as prescribing inclusion in the order Caloneurodea." Richardson then states that "*Rossites* has delicate cross veins and its CUA deviates from strict parallelism with CUP, yet the venation is nearly identical with that of *Genopteryx*," and for that reason placed the two genera in the same family. While these genera do seem to belong together, I see no reason to include them in the Caloneurodea. One result of the present study was the discovery that CUA and CUP are typically parallel in the hind wing of the gerarids, and that placement and number of the cross veins is variable. Therefore, with the disappearance of the supposed diagnostic venational characters that Richardson used to justify their inclusion in the Caloneurodea and the discovery of synapomorphies by which they may be linked to *Gerarus*, I feel that there is every reason to include these species in the Geraridae. It is interesting to note, however, that the parallel positions of CUA and CUP, characteristic of this family, may ultimately indicate a closer relationship with the Caloneurodea than previously recognized.

Gerarus vetus
Figures 4 and 5

Gerarus vetus Scudder 1885:344, 1890:308; Handlirsch 1906a:147, 1906b:702, 1919:30.

Description

Fore wing: length 45–55 mm, width 13 mm; RS two- to three-branched, fusing with M for short distance at point where M elbows towards RS; M three-branched; CUA simple, CUP forked.

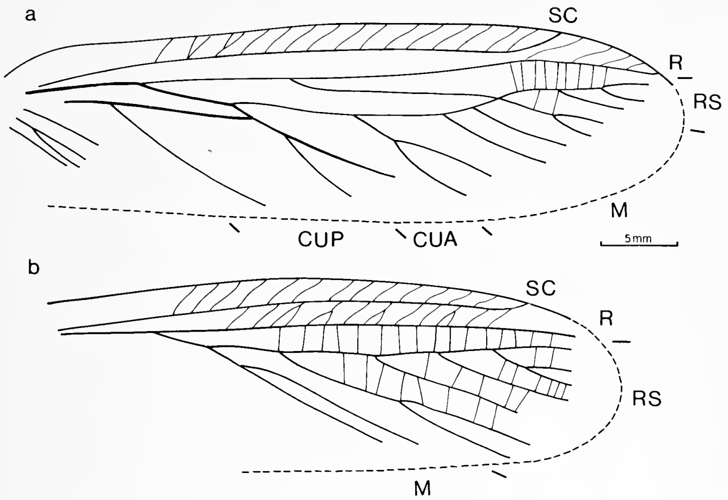

Fig. 4. *Gerarus vetus*, a. composite drawing of the fore wing, based on DGLS 1 and USNM 38136. b. composite drawing of the hind wing, based on DGLS 1 and USNM 38136.

Hind wing: length 42–50 mm, width 11–12 mm; RS at least four-branched; M forked; CUA and CUP not known.

Body: prothorax much smaller in this species than in *G. danielsi*. Width about 5 mm at its widest point, length 10–15 mm. Largest measurable spine 7 mm. Unfortunately, the arrangement and number of spines in this species is uncertain, but nine are expected in keeping with the genus. Head small, 4–5 mm in length. Coxae possibly enlarged; tibiae and femora long and slender.

Diagnosis

This species is distinguished from *G. danielsi* on the basis of its long and slender appearance, its diminutive prothorax and narrow wings. Unfortunately, the venation is not sufficiently preserved in any of the specimens assigned to this species to be useful as a diagnostic character. Although body length is intermediate between that of *G. danielsi* and *G. collaris*, this species is clearly more slender than the other species in the genus. Compare fig. 5 with figs. 9 and 13.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A.

Fig. 5. *Gerarus vetus*, photograph of specimen FMNH PE 32024. Note the narrow prothorax, and head, on which a compound eye is visible. Length of wing, 52 mm. e = eye; s = spine.

HOLOTYPE: USNM 38136. Specimen examined. This specimen consists of a prothorax, including spines, and the hindwings which overlap one another. Unfortunately, details of the venation are incomplete.

New material

FMNH PE 32022. Obverse and reverse halves. The prothorax and five spines are preserved in this specimen but unfortunately, due to overlap, venational details are obscured.

FMNH PE 32024. Obverse and reverse halves. The head is well preserved, and complete with a compound eye, clypeus, one mandible, and a spine base. Parts of all three legs are also preserved. The enlarged prothoracic femur is probably an artifact of preservation, the result of lateral compression during burial.

DGLS 1. Obverse and reverse halves. This is a somewhat distorted specimen with the prothorax pushed into the mesothorax. Fore and hind wings on the right side are slightly splayed apart and reveal most of the venation of the hind wing.

Wolff 301. Obverse and reverse halves. Only a fragmentary specimen with a poorly preserved prothorax and spine bases.

DMRW 2 (Dabasinskas 2). Obverse and reverse halves. An excellent specimen showing posterior part of the head, complete prothorax (although the spines are broken), mesothorax, metathorax, and wings, which unfortunately overlap. Its long and slender appearance and slim prothorax place it in this species.

Gerarus danielsi

Figures 2, 3, 6, 7, 8, 9, 10 and 11

Gerarus danielsi Handlirsch 1906a:147, 1906b:703, 1919:30.
Gerarus longus Handlirsch 1906a:147, 1906b:702, 1919:30. NEW SYNONYMY.
Gerarus angustus Handlirsch 1906a:148, 1906b:703, 1919:30. NEW SYNONYMY.
Gerarus latus Handlirsch 1911:313, 1919:30. NEW SYNONYMY.
Gerarus reductus Handlirsch 1911:314, 1919:30. NEW SYNONYMY.
Genopteryx constricta Scudder 1885:327; Handlirsch 1906a:148, 1906b:704, 1919:30. NEW SYNONYMY.
Rossites inopinus Richardson 1956:44. NEW SYNONYMY.

Description

Fore wing: length 53–55 mm, width 17–19 mm; SC unbranched, parallel to C, connecting to latter by multiple cross veins; R simple, parallel to SC, terminating at wing apex; RS pectinate with 2 to 3 branches, originating from R in basal third of the wing; CUP simple, originating from very base of R, connecting to RS by a short cross vein; M four-branched, fusing for approximately 9 mm at its base with CUA; CUA also four-branched; CUP simple, arising independently of CUA at the wing base. CUP elbows towards CUA, connecting to it by short cross vein. Anal veins slender and bifurcating. Well-developed reticulation present in anal area.

Hind wing: length 40–48 mm, width 14–16 mm; SC and R same as in fore wing; RS pectinate with five branches, arising from R near wing base; M arising from near base of RS and deeply cleft with two or more terminal bifurcations; CUA and CUP parallel and independent at wing base. Anal area not well preserved, only slightly expanded, and with reticulated venation.

Prothorax: distinctly large and swollen posteriorly. There are nine prominent spines symmetrically arranged in the swollen region (see fig. 8). Width at widest point 10–13 mm, length 20–22 mm; spines 7–10 mm in length. One, possibly two, vertical spines extend from the anterior of prothorax, posterior to head.

Body: large, ranging from 70 mm to 75 mm (tip of wing to anterior tip of prothorax). Legs long and thin.

Diagnosis

This species may be distinguished from the other species in the genus by the large prothorax and well-developed spines (longer in this species than in any other); and the overall body size which is distinctly larger than that of either *G. vetus* or *G. collaris* from Mazon Creek. Although venational characters do vary intraspecifically, it should be noted that in the fore wing M connects to RS by a small cross vein, and that the anterior branch of CUP connects to CUA also by a small cross vein. This contrasts with the other species in the genus in which one finds an actual anastomosis of these veins.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A.

HOLOTYPE: USNM 35574. Specimen examined. Reverse half only.[8] The bulbous region and spines of the prothorax are well preserved in this specimen. Only the costal margins of the fore wings are present, but venation of the hind wings is clear, except in the anal area. All evidence of the head and anterior region of the prothorax has been lost.

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[8] The obverse half was originally in the Daniels collection, the location of which is not known (see Carpenter, 1965, for further details on this collection).

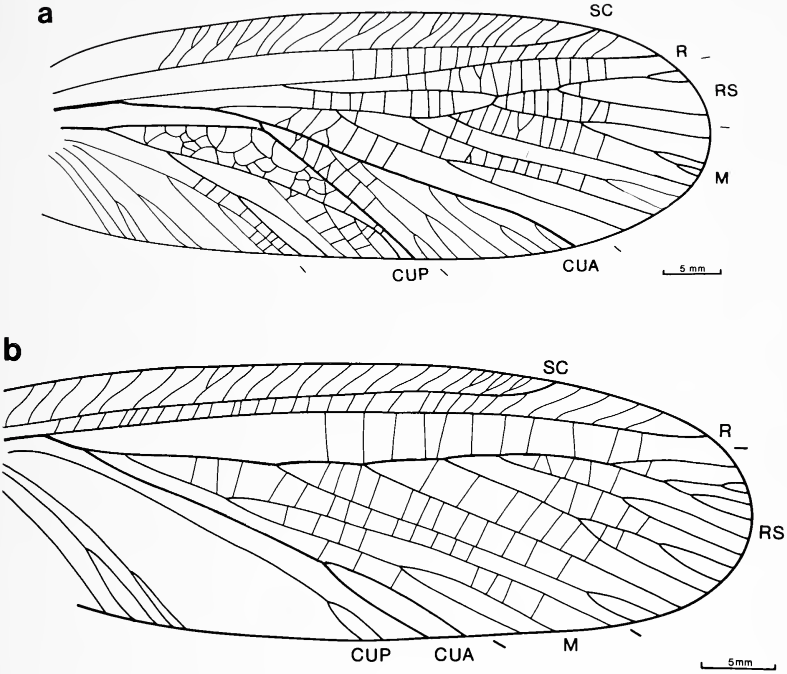

Fig. 6. *Gerarus danielsi*, a. composite drawing of the fore wing, based primarily on FMNH PE 5276, 31973; and DMRW 1. b. composite drawing of the hind wing, based primarily on USNM 35574, FMNH PE 32031, and MCZ 222.

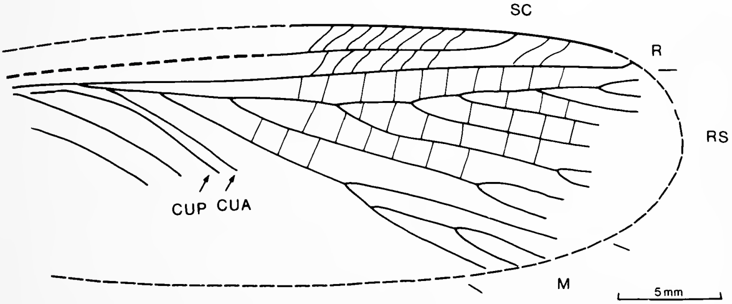

Fig. 7. *Gerarus danielsi*, originally *Genopteryx constricta*. Drawing of hind wing, based on USNM 38148. Compare this with the hind wing in Fig. 6b.

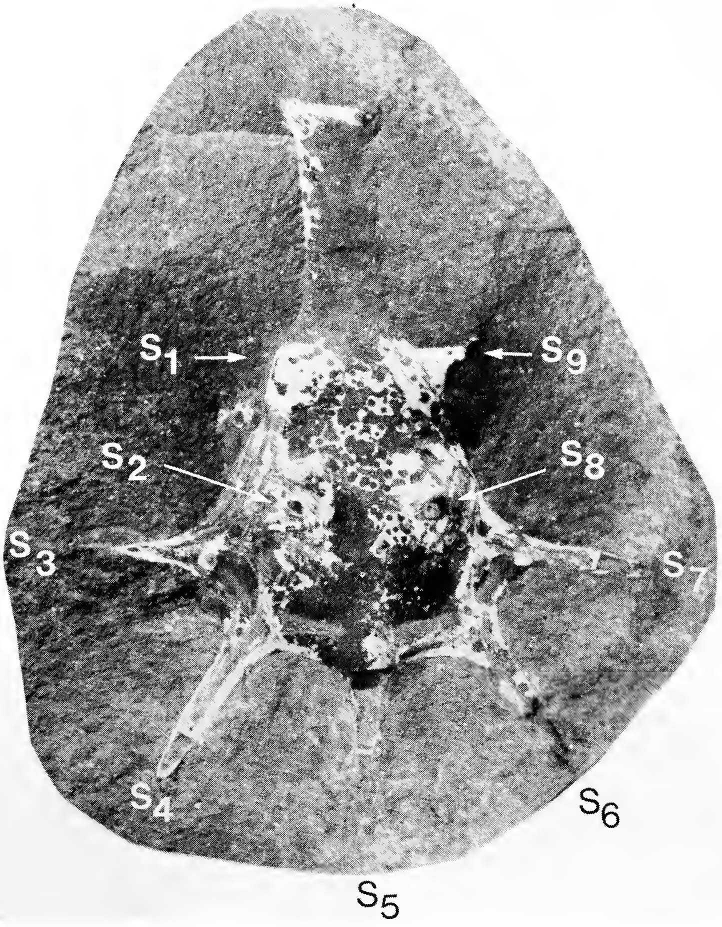

Fig. 8. *Gerarus danielsi*, photograph of the prothorax, PE 32029. Total length of prothorax, not including spines, 21 mm, s = spine.

Synonymies

Gerarus latus YPM 33. Specimen examined. Obverse and reverse halves. This species is synonymized here with *G. danielsi* by virtue of its size (hind wing as preserved is 45 mm long, but is short several millimeters at its apex) and the shape of its prothorax. The latter, despite some distortion, clearly has spines of the same length and pattern as *G. danielsi.* A single spine base is present at the anterior

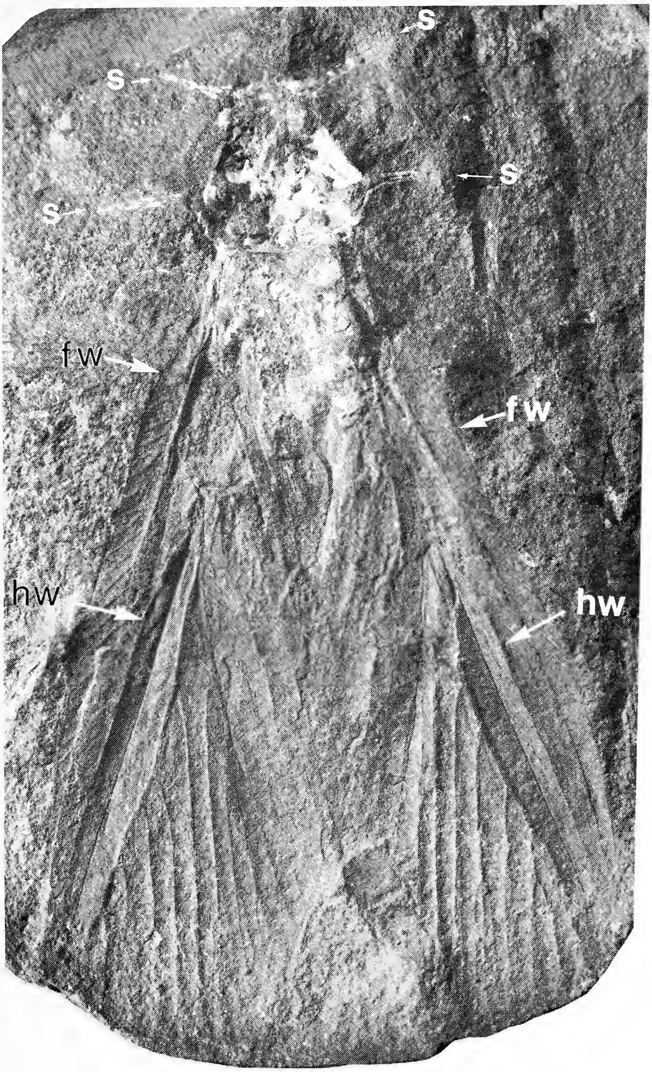

Fig. 9. *Gerarus danielsi*, photograph of the holotype, USNM 35574. Length of fore wing 42 mm, as preserved. fw = fore wing; hw = hind wing; s = spine.

tip of the prothorax. Fore and hind wings overlap. Only the costal area of the fore wing is visible, but most of the hind wing venation is visible under close scrutiny.

Gerarus reductus YPM 35. Specimen examined. Obverse and reverse halves. This is an unusual specimen in that two wings are preserved in the same concretion, but nothing suggests that they necessarily belong to the same specimen—or even to the same species. The specimen is badly fractured into four distinct pieces, and the two wings appear to be in different bedding planes. Handlirsch (1911) described the two wings as fore and hind wings of the same species, but expressed reservations concerning their generic assignment. I am convinced that these wings do not belong to the same specimen but believe instead that they are both hind wings belonging to different species. The specimen that Handlirsch (1911:315, fig. 20) considered to be a fore wing is here designated the lectotype of *G. reductus* and it is herein synonymized with *G. danielsi.* The specimen that he interpreted as the hind wing of *G. reductus* (1911:314, fig. 19) undoubtedly *is* a hind wing, but not sufficiently well preserved to warrant family determination and it is placed here in Protorthoptera *incertae sedis.*

Gerarus longus USNM 38822. Specimen examined. Obverse and reverse halves. Fore and hind wings overlap but the venation is very similar to that of the holotype of *G. danielsi*: RS is pectinate, with five branches, and M is deeply cleft. Also the prothorax, although badly preserved, does have spines, two of which are visible on the left side. This, plus the size of the specimen (fore wing measures approximately 55 mm, hind wing 44 mm) warrants synonymy of *G. longus* with *G. danielsi.*

Gerarus angustus USNM 38811. Specimen examined. Obverse half only. This is a poor specimen: all four wings overlap, and the fossil has been weathered so the venation is only barely visible. Nevertheless, in my opinion, the overall size of the specimen (fore wing length is 55–57 mm) and the swollen prothorax justify its synonymy with *G. danielsi.* Certainly it displays no unique characters by which it may be distinguished as a separate species.

Genopteryx constricta USNM 38148. Specimen examined. This species was originally assigned to the Geraridae by Scudder (1885), but later transferred by Richardson (1956) along with *Rossites inopinus* (see below) to the Caloneurodea. Having examined both type specimens, I find no characters by which to separate either genus from *Gerarus*. Because there are no significant differences in venation between *R. inopinus, G. constricta* and *G. danielsi* (compare fig. 6 with fig. 7), synonymy at this point seems justified.

Rossites inopinus FMNH PE 3304. Specimen examined. Obverse and reverse halves. Only the basal half of the hind wing is preserved, but it shows CUA and CUP very clearly. Length of the wing as preserved measures 29 mm; actual length is estimated as 40 mm.

New material

FMNH PE 5276. Obverse and reverse halves. This specimen is, without doubt, the most spectacular of all specimens examined for this study. Both halves are excellent, and the obverse half gives a particularly good three-dimensional effect (see fig. 11). The latter also shows the entire prothorax and part of the head. The base of the vertical spine at the anterior end of the prothorax may be seen in the reverse half. Parts of all three legs are visible in the specimen and unequivocally demonstrate the gracile nature of the femora.

FMNH PE 31973. Obverse and reverse halves. An almost perfect specimen of a single *G. danielsi* fore wing. The apex of the wing is missing, but the anal area is remarkably well preserved in this specimen.

FMNH PE 31988. Obverse and reverse halves. This is a poor specimen: fore and hind wings overlap, and are only partially present. However, venation and size both place it in *G. danielsi.*

FMNH PE 32023. Obverse and reverse halves. This is not a well-preserved specimen, but venation and size both conform to the species description.

FMNH PE 32027. Obverse half. The prothorax, pterothorax, and basal areas of the right hind wing and left fore wing are evident. The prothorax bears the characteristic arrangement of nine spines and also has a tiny lateral spine projecting from its anterior left side. Although smaller than the other specimens in this species (width of fore wing is 12 mm) it is included in *G. danielsi* because it is, in all other respects, identical to the holotype.

FMNH PE 32029. Obverse and reverse halves. This specimen, which has an impressive array of spines on the prothorax, and a vertical spine at its anterior tip, is magnificent. Hind wings are preserved, but overlap.

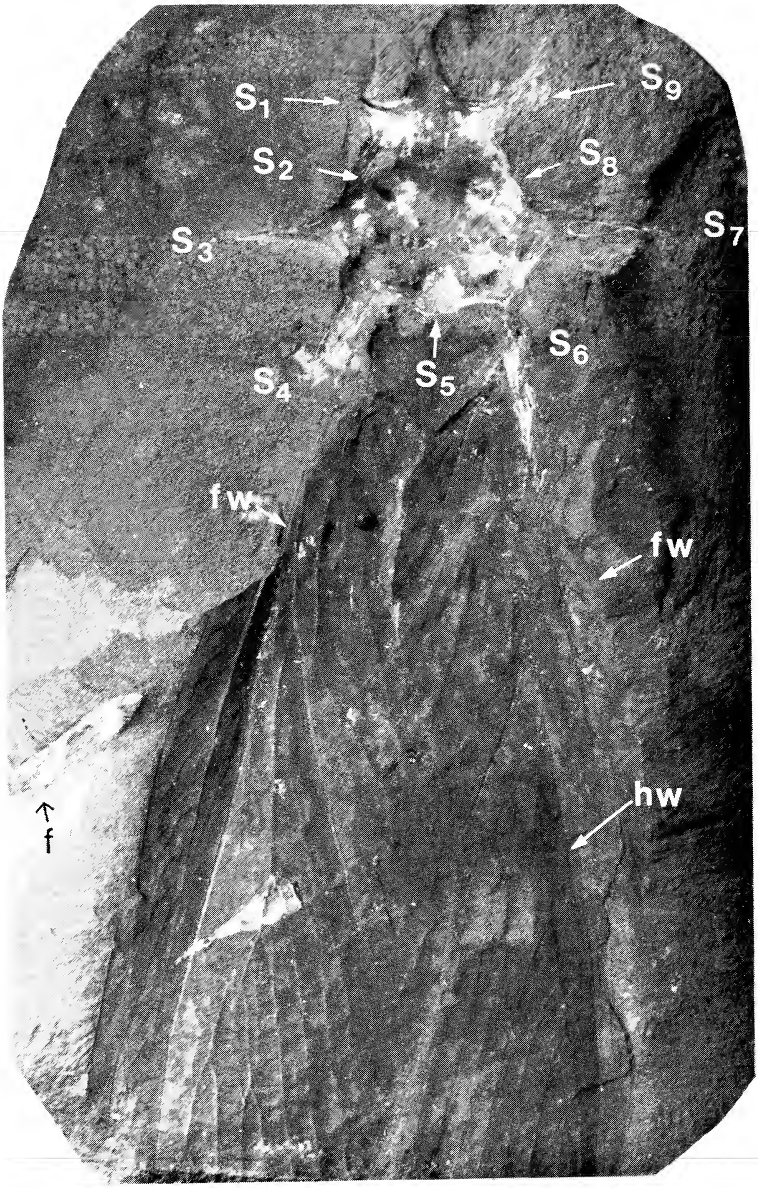

Fig. 10. *Gerarus danielsi*, photograph of FMNH PE 5276, obverse half. Length of fore wing 50 mm, as preserved. s = spine; fw = fore wing; hw = hind wing.

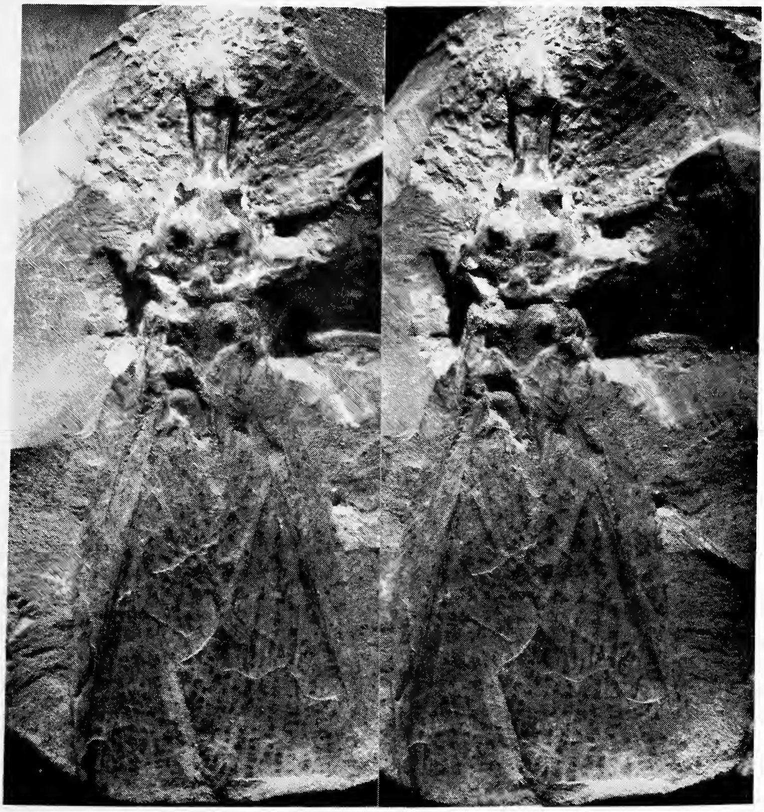

Fig. 11. *Gerarus danielsi*, stereophotograph of FMNH PE 5276, reverse half. Total length = 77 mm. Photograph by F. M. Carpenter.

FMNH PE 32031. Obverse and reverse halves. This is an excellent specimen that shows the venation of the hind wing, and an outline of the prothorax, complete with spines.

DMRW 1 (Dabasinskas 1). Obverse and reverse halves. This is a beautifully preserved specimen, showing almost the entire fore wing, and two-thirds of the hind wing. It differs from the holotype in the nature of M, which has only three major branches, but is otherwise consistent with *G. danielsi*. Recognition of DMRW 1 as a new species merely on the basis of M, given that nothing is known of the body, does not seem warranted at this time.

Wolff 491. This specimen consists of head, thorax, and the basal area of two wings, but nothing can be made of the venation. The prothorax is large and bears at least seven spine bases. The head is preserved at a slight angle to the prothorax. Labrum is visible, as are one antenna and both eyes.

MCZ 222. Reverse half. Costal margin of the fore wings and most of the hind wings preserved. This insect is small for the species (hind wing measures 45 mm long, 14 mm wide) but the venation is indistinguishable from that of the holotype.

Gerarus collaris
Figures 12 and 13

Gerarus collaris Handlirsch 1911:314, 1919:30.
Gerarus longicollis Handlirsch 1911:315, 1919:30. NEW SYNONYMY.

Description

Fore wing: length 45–50 mm, width not known. Venation of fore wing obscured in all specimens.

Hind wing: length 40–45 mm, width 10–12 mm; RS apparently five-branched, M deeply forked; CUA and CUP parallel.

Prothorax: small, 11 mm in length and narrow (approximately 6 mm wide). Posterior, or bulbous region, 7–8 mm long. Broken spines are present on all *G. collaris* specimens examined, but no more than six can be seen on any one specimen.

Diagnosis

This is the smallest of the *Gerarus* species. Unfortunately, the venation in all known specimens is not clear enough to serve as a species level character. *G. collaris* is, therefore, best recognized by its prothorax, which tapers gradually from the anterior to the posterior end, and is much narrower and shorter than in other species of *Gerarus*. The distinctive nature of the prothorax, and its usefulness as a species-specific character, can be seen by comparing figs. 5, 11 and 13.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A.

HOLOTYPE: *Gerarus collaris* YPM 34. Specimen examined. Obverse half. Fore and hind wings overlap in this specimen, only the costal margin of the fore wing is well preserved. The prothorax is intact and several spine bases are visible, but the overall preservation is mediocre.

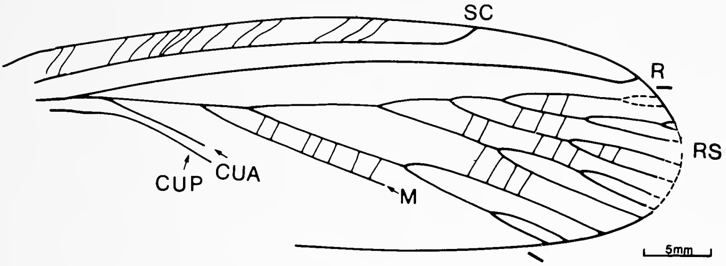

Fig. 12. *Gerarus collaris*, drawing of hind wing, based on holotype YPM 34.

Synonymy

G. longicollis YPM 36. Specimen examined. Obverse half. A fragmentary specimen. Wings are poorly preserved, and only RS and CUA/CUP in the hind wing are visible. This species is synonymized here with *G. collaris* on the basis of its prothorax, which is small and tapers gradually from the posterior to the anterior end, as it does in all known members of *G. collaris*.

New Material

USNM 38835. Obverse half. Only the base of the wings and the prothorax are preserved in this small specimen. The prothorax, which bears at least six spine bases, is clearly narrow and elongate, and is the reason for including this specimen in *G. collaris*.

Gerarus fischeri

Figures 14, 15, 16 and 17

Sthenaropoda fischeri Brongniart 1885:59; Handlirsch 1906a:142, 1919:38.
Oedischia fischeri Brongniart 1894:559.
Sthenaropoda lerichei Lameere 1917:178. NEW SYNONYMY.
Sthenaropoda agnusi Lameere 1917:178. NEW SYNONYMY.

Description

Fore wing: length 40–50 mm, width 14–15 mm; SC parallel to C turning upward to fuse with it at point that is two-thirds length of wing; R parallel to C, terminating at wing apex; both SC and R connecting to C and SC respectively by numerous sigmoidal cross veins; RS diverging from R at midpoint of wing and branching twice; M originating at base of R, anastomosing with RS basally before branching off and forking once; CUP forked, originating

Fig. 13. *Gerarus collaris*, photograph of holotype, YPM 34. Length of fore wing 48 mm. fw = fore wing; hw = hind wing.

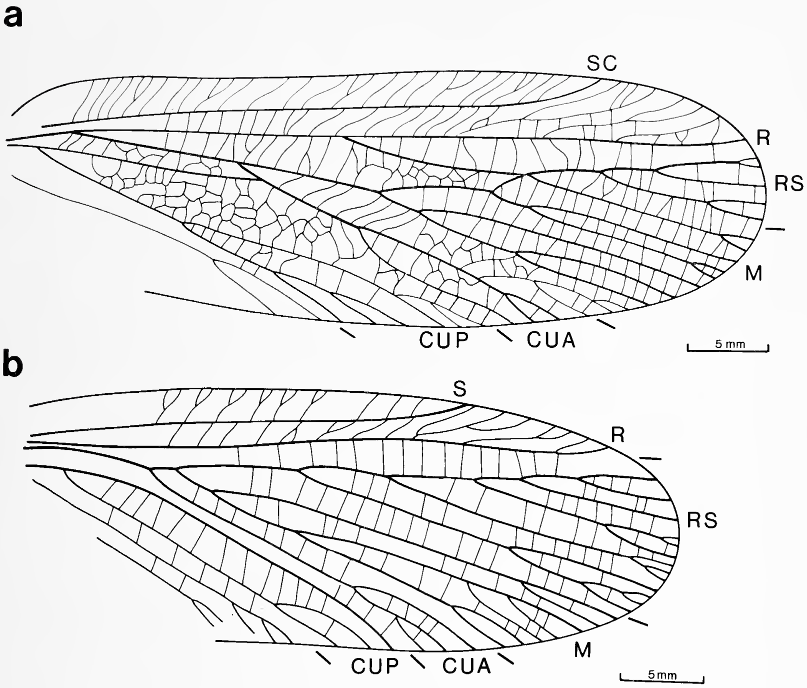

Fig. 14. *Gerarus fischeri*, a. drawing of fore wing, based on specimens IP 4, 5, 7, and 23. b. drawing of hind wing based on specimens IP 5, 7, and 10.

separately from CUA at wing base; anterior branch of CUP fusing with CUA for approximately 9 mm before weakly breaking away; multiple veins and well-developed reticulation present in anal area.

Hind wing: length 39–47 mm, width 13–14 mm; SC and R same as in fore wing; RS parallel to R and pectinate, with number of branches varying from four to five; spacing of these branches relative to one another also variable (in one specimen IP 2 the first branch of RS is connected to the main stem of RS by a strengthened cross vein, forming a small oval in the middle of the wing); M deeply cleft with one or two branches; CUA and CUP parallel. The anal area of hind wing not known for this species, but appears to be slightly expanded, judging by overall wing shape. See fig. 17.

Diagnosis

G. fischeri is remarkably similar to *G. danielsi* in many respects: prothorax, size, venation (compare fore and hind wings of each in figs. 6 and 14). The only obvious difference lies in the nature of CUA and CUP in the fore wing. In *fischeri* CUA forks only once (in *danielsi* it has many small branches) and the anterior branch of CUP fuses with CUA for a distance of 9 mm. In *danielsi* the two are connected by a small cross vein.

Remarks

G. fischeri was first described by Brongniart for a series of orthopteroid insects recovered from the Commentry Coal Basin. The series is remarkable not only because it contains a large number of individuals, but because most of these individuals are exceptionally well preserved. Under these circumstances it is somewhat odd that affinities between the Commentry species and the Mazon Creek species went unrecognized for so long. Many of the Commentry specimens (especially IP 5, IP 7, and IP 23) have most of the body, including the prothorax, preserved and demonstrate the same arrangement of spine bases seen in the Mazon Creek material. Moreover, venation of the fore and hind wings in these specimens is unequivocally clear. Handlirsch might have recognized the similarities between *Sthenaropoda* and *Gerarus* had he examined the Commentry material himself, but this is debatable since the fore wing for *Gerarus* was unknown at the time. The similarities between *G. fischeri* and *G. danielsi*, given above in the diagnosis, are extraordinary. While separation of the two species on such minor morphological differences might be subject to debate, I have chosen to recognize the two species as distinct from one another on geographical and geological grounds. *G. danielsi* comes from Mazon Creek in North America (Westphalian in age) and *G. fischeri* from Commentry in France (Stephanian in age).

GEOLOGICAL RANGE: Stephanian. OCCURRENCE: Commentry, France.

HOLOTYPE: *Gerarus fischeri*. IP 5. Specimen examined. Obverse half only. This is probably the most spectacular of all the Commentry gerarids and of great taxonomic significance because the wings are splayed apart and venation of both fore and hind wings is readily visible. The insect is preserved dorso-laterally and the three legs

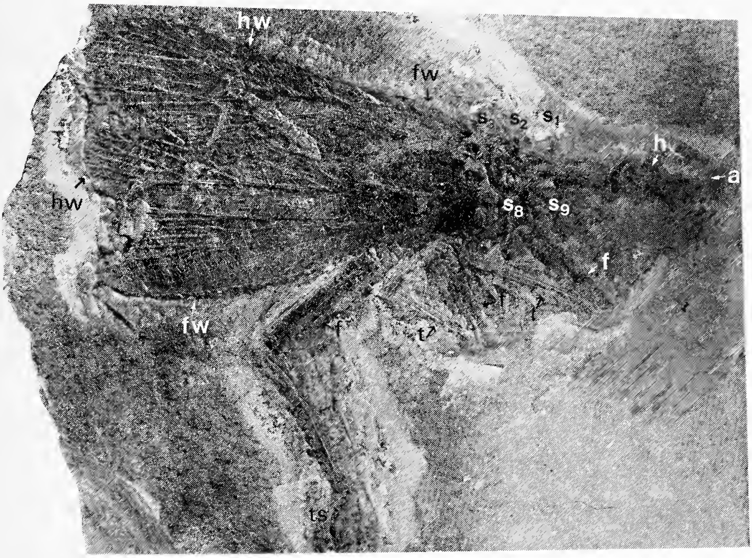

Fig. 15. *Gerarus fischeri*, photograph of holotype, IP 5. Total length = 75 mm. s = spine; h = head; a = antenna, f = femur; t = tibia; ts = tarsomere; fw = fore wing; hw = hind wing.

on the right side are preserved, as are the thorax and head. Spine bases are present on the bulbous region of the prothorax, although the spines themselves have broken off (see fig. 15).

Synonymies

S. lerichei. Holotype. IP 23. Specimen examined. Obverse half.

S. agnusi. Holotype. IP 19/21. Specimen examined. Obverse and reverse halves.

I am synonymizing these species with *G. fischeri* as there are no obvious specific level differences by which they may be recognized.

The specimen of *S. lerichei* is a well-preserved, dorsal compression of almost the entire insect. Because the wings are separated, it is possible to interpret the venation of both fore and hind wings, and especially that of the fore wing. The venation, the prothorax (including spine bases) and the size of this insect are perfectly compatible with *G. fisheri.*

The specimen of *S. agnusi* is a single fore wing, superbly preserved. Although the apex of the wing is missing, the basal area,

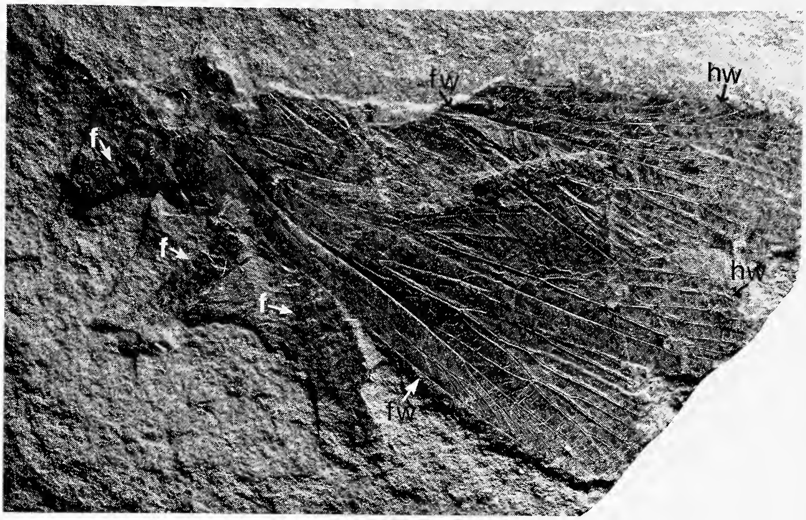

Fig. 16. *Gerarus fischeri*, photograph of IP 7. Length of fore wing = 50 mm. f = femur; fw = fore wing; hw = hind wing.

including cross-veins, is extraordinarily well-preserved, as are all major veins. I cannot find sufficient differences between this specimen and the others already included in *S. fischeri* to warrant separate species status.

Several species previously included in *Sthenaropoda* are transferred here to family, genus *indet.* These are *S. elegantissima* Meunier and *Sthenaropoda minor* Handlirsch, the types of which I have examined, and I do not believe are similar enough to *Gerarus* to warrant inclusion in the family.

New Material

IP 7. Reverse half. This specimen, although fragmentary, does show venation of fore and hind wings. The specimen is preserved dorso-laterally; three femora on the left side are visible, but the rest of the body including the thorax and head is missing. See fig. 16.

IP 8. Obverse half. This insect has both fore wings, a prothorax, complete with spine bases, a head bearing moniliform antennae, and parts of all six legs present. The hind femora are not enlarged and demonstrate unequivocally their cursorial nature.

IP 6. Reverse half. This specimen is not particularly well preserved due to apparent post-burial distortion of the insect. The pro- and mesothoracic legs on the left side are detached from the body, and the antennae, although present, are detached from the head. Fore and hind wings on the left side overlap, but the venation of the fore wing is preserved, and nothing of the hind wing. The prothorax is largely intact and shows the spine bases.

IP 4. Reverse half. The fore and hind wings on the left side are separated, and the venation of the left fore wing is clear. Unfortunately, little can be seen of the remaining three wings.

IP 2. Obverse half. A single well-preserved hind wing. Anal area is missing but may be folded under the wing. This wing differs from most other gerarid hind wings because the first branch of RS connects to the main stem of RS by a strengthened cross vein, forming a small triangle in the center of the wing (see fig. 17c).

IP 3. Reverse half. This is a partially preserved insect and shows most of the right hind wing but only a fraction of the other three wings. It is interesting, however, for one feature: the right hind wing shows an anastomosis of the first branch of RS with the main stem of RS as seen in IP 2. Because the anastomosis in this specimen is smaller than in IP 2, and present in only one of the hind wings, it may be assumed that it is a form of intraspecific variation, and not significant at a higher level.

IP 9. Obverse half. Although the venation is virtually obscured, this specimen is important because the insect has been compressed laterally and all six legs are spread apart. The fore legs are only partially preserved, but the meso- and metathoracic legs on both sides are magnificent. This is the only specimen from Commentry in which one can count tarsal segments. There are five tarsomeres, and a pair of tarsal claws. The prothorax and its spine bases are also present in the fossil.

IP 10. Reverse half. This is a single hind wing and well preserved except at the apex and in the anal area, which is folded over.

IP 11. Reverse half. The specimen is a single hind wing, and so poorly preserved that the specimen is almost useless.

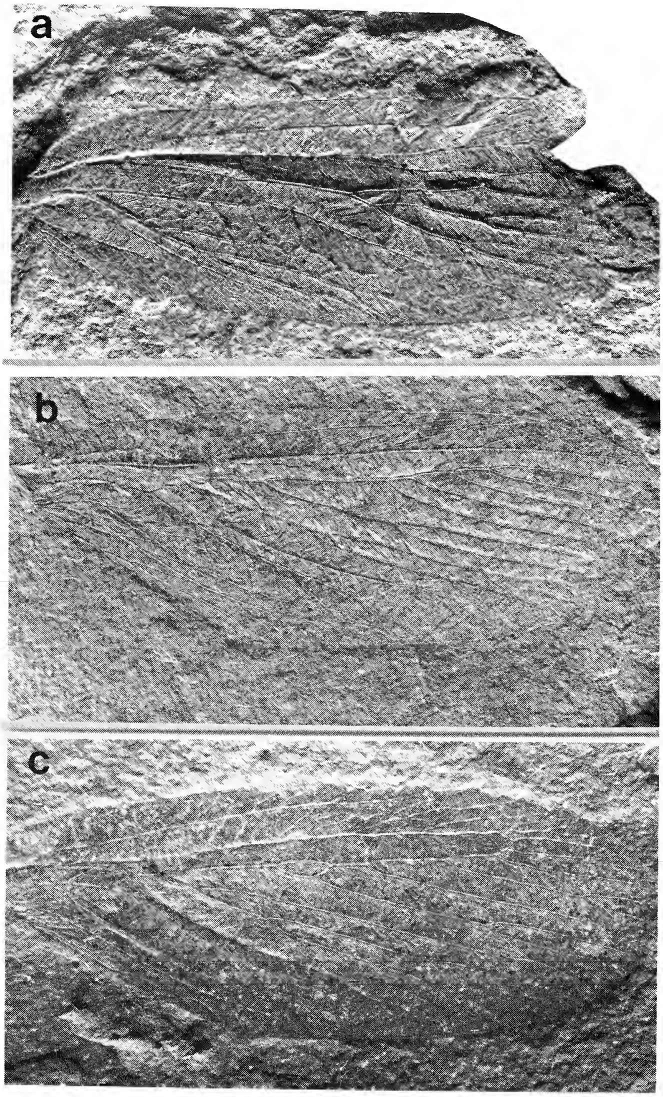

Fig. 17. *Gerarus fischeri*, a. photograph of fore wing, specimen IP 19. Length 42 mm, as preserved. b. photograph of hind wing, specimen IP 10. Length 40 mm, as preserved. c. photograph of hind wing, specimen IP 2. Length 40 mm, as preserved. Note the small triangle formed by the anastomosis of one branch of RS with the main stem of RS.

Gerarus bruesi
Figures 18 and 19

Archaeacridites bruesi Meunier 1909a:39.
Sthenaropoda bruesi Handlirsch 1919:39.

Description

Fore wing: length 45 mm (as preserved, estimated as 48 mm), width 15 mm; SC terminating in apical third of wing, at C; R parallel to C, connecting to it apically by several cross veins; RS branching twice, each branch forking once distally; M expanded, with five main branches; CUA four-branched, fusing with M at its base; CUP elbowed towards CUA, connecting to the latter by a strong cross vein; anal veins present; well-developed reticulation present in area basal to CUA.

Hind wing: unknown.

Diagnosis

This species is based on a single, but almost perfectly preserved, fore wing from Commentry. Meunier originally described *bruesi* and assigned it to the genus *Archaeacridites* because he felt that this species was in some way ancestral to the extant Acrididae (order Orthoptera). While the relationships of the Protorthoptera (including the Geraridae) to the true Orthoptera have yet to be resolved, I do believe that synonymy of *Archaeacridites* with *Gerarus* is warranted. I have studied the holotype, and can find no characters to justify separate generic status for this species. However, I do think that species separation is warranted on the basis of CUA which connects to M only by a cross vein and does not anastomose with it as in *G. fischeri*. The nature of CUA in *G. bruesi* is much more reminiscent

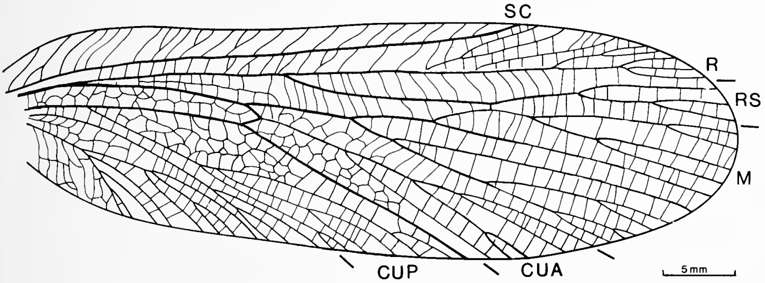

Fig. 18. *Gerarus bruesi*, drawing of fore wing, based on holotype no. IP 20.

of *G. danielsi*, where CUA also connects with M by a short cross vein. M, however, is more expanded (more branched) in *G. bruesi* than in *G. danielsi*.

GEOLOGICAL RANGE: Stephanian. OCCURRENCE: Commentry, France.

HOLOTYPE: *Gerarus bruesi*. IP 20. Specimen examined. This specimen is a single fore wing only, but beautifully preserved. All veins except those at the very apex of the wing are clear and can be interpreted without difficulty (see fig. 19).

Genus *Genentomum*

Genentomum Scudder 1885:329; Handlirsch 1906a:144, 1906b:700.

Description

Fore wing: SC and R parallel to C; RS branched, originating from R in basal third of wing; M distinctive with 3 to 4 branches, all parallel; CUA parallel to first branch of M; CUP elbowed towards CUA; anal area with several veins.

Hind wing: SC and R parallel to C; RS multi-branched, arising from R near wing base; M, CUA, CUP, and anal veins not known.

Diagnosis

This genus may be distinguished from the other genera in the family on the basis of M, which in the fore wing has the unique branching pattern described above, and the strong topography of the major longitudinal veins displayed by the two species assigned here to this genus.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A. TYPE SPECIES: *Genentomum validum* Scudder.

Genentomum validum

Figures 20 and 21

Genentomum validum Scudder 1885:329; Handlirsch 1906a:145, 1906b:700, 1919:40.
Genentomum carri Cockerell 1917:81. NEW SYNONYMY.

Description.

Fore wing: length 45 mm (estimated), width 14 mm; SC parallel to C, connecting to it by a series of cross veins; costal margin narrow; R parallel to C; RS at least two-branched, originating from R in basal third of wing; M three-branched, and distinctive for the genus; CUA parallel to first branch of M; CUP elbowed towards CUA; anal area with several fine longitudinal veins.

Fig. 19. *Gerarus bruesi*, photograph of holotype no. IP 20. Length of fore wing 45 mm, as preserved.

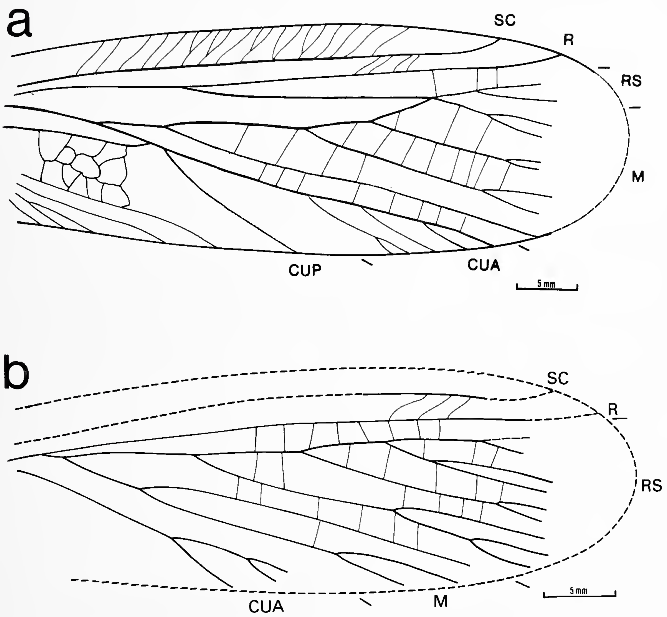

Fig. 20. *Genentomum validum*, drawings based on holotype no. USNM 38135. a. fore wing. b. hind wing.

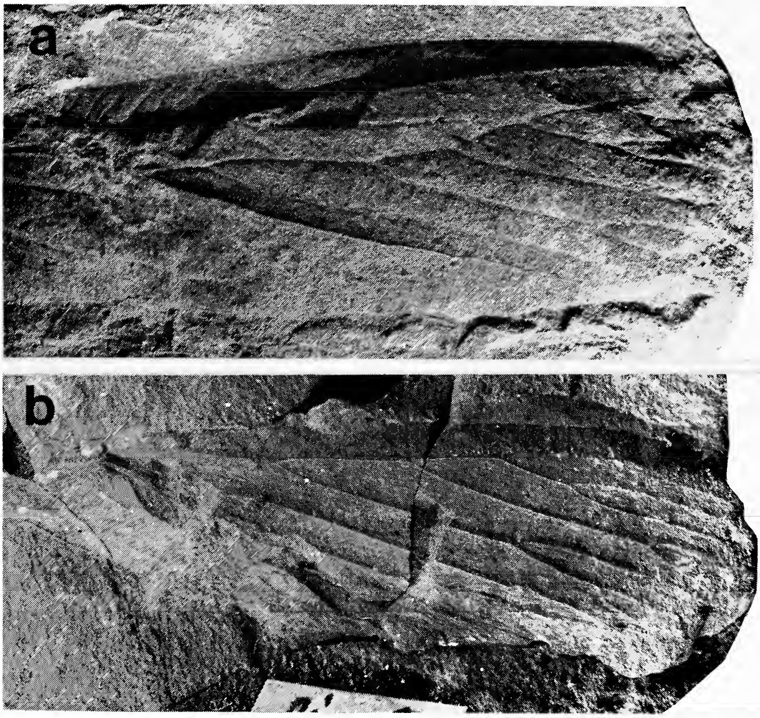

Fig. 21. *Genentomum validum*, photographs of holotype no. USNM 38135. a. fore wing. Length 42 mm, as preserved. b. hind wing. Length 40 mm, as preserved.

Hind wing: length 40 mm, width 14 mm; SC and R as in fore wing; RS four-branched, originating from R near wing base.

Remarks

Originally described by Scudder as a member of the Homothetidae (Neuroptera), this species was subsequently transferred to the family Oedischiidae by Handlirsch (1906b) on the basis of M, which anastomoses with RS in the fore wing. Of course Handlirsch had no idea that this character is also found throughout the Geraridae. My inclusion of *Genentomum* in the Geraridae is based on the study of all major veins and these are completely consistent for the family.

Geological range: Westphalian D. Occurrence: Mazon Creek, Illinois, U.S.A.

Holotype: USNM 38135. Specimen examined. Obverse and reverse halves. Both fore and hind wings are preserved, although the apex of the fore wing extended beyond the edge of the concretion and was therefore lost. Base and anal area of the hind wing also missing. Wings are separated and almost at right angles to one another.

Synonymies

Genentomum carri USNM 65023. Obverse half. This insect is an impression of the wings only. Although the wings do overlap, the fore wing on the right side and the hind wing on the left side are visible.

I am synonymizing *Genentomum carri* with *Genentomum validum*. Cockerell (1917) described this specimen as a new species on the basis of R which he figured with a single anterior branch. After close examination of the holotype, I find that he was incorrect in his interpretation of this vein as a branch of R. Either it is a very weak cross vein, or a wrinkle in the wing membrane. Branching pattern of RS in both fore and hind wings is similar to *G. validum*, and M is virtually identical in both.

The following genera and species are described from single specimens (most from single wings). Their descriptions are therefore somewhat approximate. There seems to be no justification for removing any of these taxa from the Geraridae at this point, although the discovery of more nearly complete specimens may provide characters that will alter this arrangement.

Genus *Progenentomum*

Progenentomum Handlirsch 1906a:145, 1906b:701, 1919:40.

Description

Fore wing: SC terminates in C at point two-thirds distance from wing base to apex; R parallel to anterior margin of wing, fusing with margin just before wing apex; RS pectinate with several branches; M more branched than RS and elbowed distally, touching RS at that point; branches of RS and M close to one another and parallel; numerous cross veins present; CUA, CUP, and anal region not known.

Hind wing: unknown.

Diagnosis

Progenentomum is close to *Gerarus* but separated from it by RS, which has at least four branches in the fore wing. Compare with *Genentomum*.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A. TYPE SPECIES: *Progenentomum carbonis.*

Progenentomum carbonis
Figures 22 and 23

Progenentomum carbonis Handlirsch 1906a:145, 1906b:701, 1919:40.

Description

Fore wing: length 30 mm preserved (estimated as 50 mm), width 15 mm; RS pectinate with four branches; distal branch of M elbows up to touch RS. A distinct cross vein connects branches two and three of M, and probably acted as a brace vein.

Diagnosis

This species differs from all others in the family in having a linear series of punctations between R and RS. These may or may not have been pigmented, but because this specimen is only an impression, no organic material remains.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A.

HOLOTYPE: USNM 35580. Specimen examined. Obverse half.

Genus *Nacekomia*

Nacekomia Richardson 1956:33.

Description

Fore wing: SC terminates in C two-thirds from wing base; R parallel to SC; RS two-branched; M four-branched; CUA and CUP simple.

Hind wing: unknown.

Diagnosis

Nacekomia differs from *Gerarus* only in the nature of M, which is separate from RS, and not connected to it except by several very small cross veins. This, in my opinion, warrants separate generic status but not separate family status.

Remarks

This monotypic genus was originally included in the family Cacurgidae (order Protorthoptera), but is here transferred to the Geraridae on the basis of its fore wing venation. While one cannot

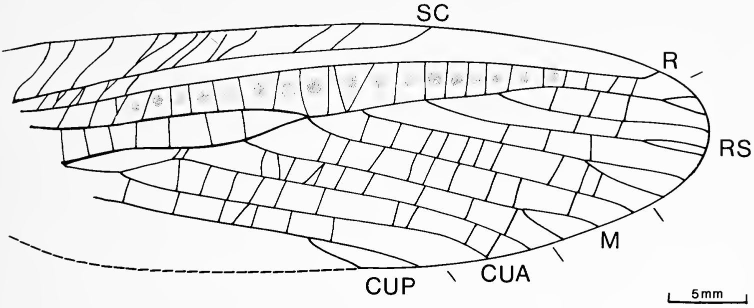

Fig. 22. *Progenentomum carbonis*, drawing of fore wing based on holotype no. USNM 35580.

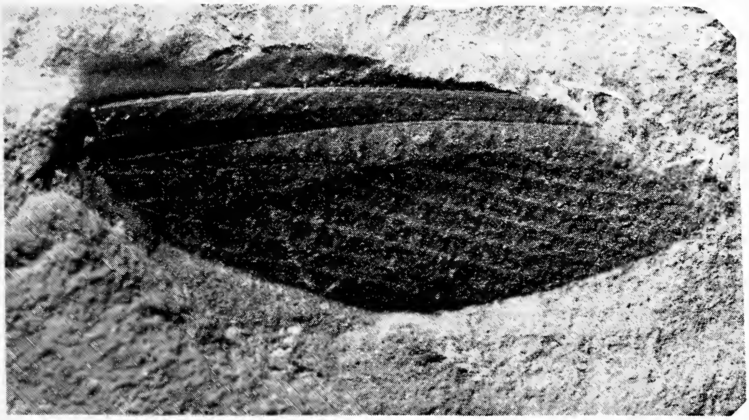

Fig. 23. *Progenentomum carbonis*, photograph of fore wing, based on holotype no. USNM 35580. Length 30 mm, as preserved.

be certain that this genus belongs in the Geraridae until a more nearly complete specimen is found, the fore wing is so similar to that of *Gerarus* that I do not hesitate to include it in the family. I certainly can see no justification for the inclusion of *Nacekomia* in the Cacurgidae, where it was placed by Richardson (1956). The venation of *Nacekomia* differs considerably from that of *Cacurgus*. In the latter, R is branched, RS simple, M is reduced, CUA simple, and CUP many branched. In the former, R is simple, RS branched, M has many branches, and CUA and CUP are simple.

Geological range: Westphalian D. Occurrence: Mazon Creek, Illinois, U.S.A. Type species: *Nacekomia rossae*.

Nacekomia rossae
Figures 24 and 25

Nacekomia rossae Richardson 1956:34.

Description

Fore wing: length 43 mm, but apex is missing; SC terminates in C, two-thirds distance from wing base; R parallel to SC, terminating at wing apex; RS two-branched, diverging from R at midpoint of wing; M with four well-developed branches; CUA strongly convex and fused at base with M, nature of CUP uncertain.

Hind wing: unknown.

Diagnosis

It is impossible to designate specific characters when the genus is based on a single specimen, but in all probability the nature of RS (with only two branches) may be important.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A.

HOLOTYPE: *Nacekomia rossae* FMNH PE 791. Specimen examined. Obverse half.

Genus *Gerarulus*

Gerarulus Handlirsch 1911:318, 1919:30.

Description

Fore wing: SC parallel to C, terminating on it; R simple, RS branched; M with multiple branches, anastomosing briefly with RS; CUA simple, CUP elbows towards CUA.

Hind wing: SC and R same as fore wing; RS pectinate; M simple; CUA and CUP independent from one another and parallel.

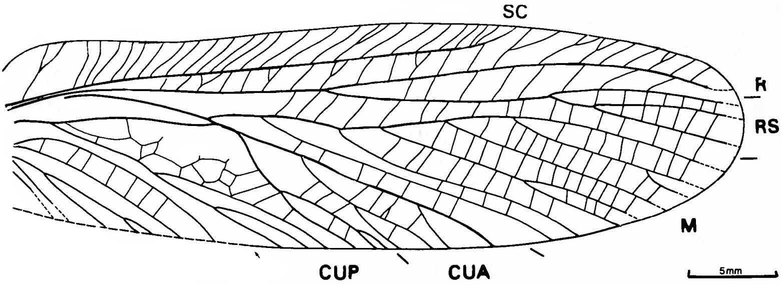

Fig. 24. *Nacekomia rossae*, drawing of fore wing based on holotype no. FMNH PE 791.

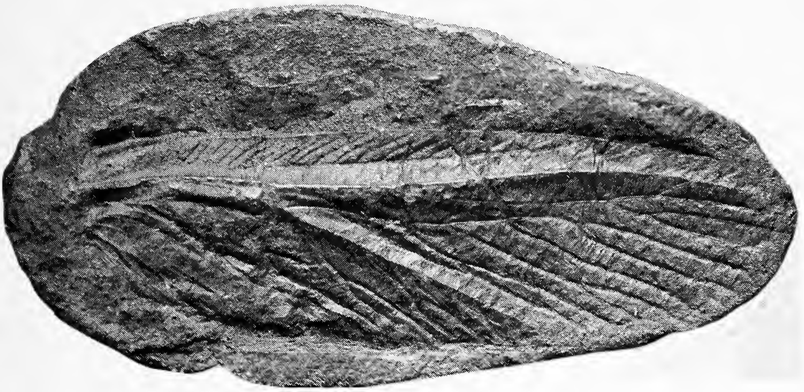

Fig. 25. *Nacekomia rossae*, photograph of fore wing of holotype no. FMNH PE 791. Length 43 mm.

Diagnosis

Although the prothorax is unknown, venation of fore and hind wings is typical for the family. I have retained this as a distinct genus only on the basis of the diminutive size of its one species, and this may change as more material is found.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A. TYPE SPECIES: *Gerarulus radialis.*

Gerarulus radialis

Figures 26 and 27

Gerarulus radialis Handlirsch 1911:316, 1919:30.

Description

Fore wing: length 25 mm as preserved (estimated as 35 mm), width 11 mm; SC parallel to C, terminating on it; R simple, RS branched (at least two or three times); M anastomosing briefly with RS, appearing to be four-branched; CUA simple, CUP elbowed towards CUA; two anal veins visible, each forking once.

Hind wing: length 21 mm as preserved (estimated as 30 mm), width 10 mm; SC and R simple and parallel to C; RS pectinate, although the number of branches is unknown; CUA and CUP independent from one another and parallel; anal area slightly enlarged; abdomen, although indistinctly preserved, appears to be rather slender; prothorax missing.

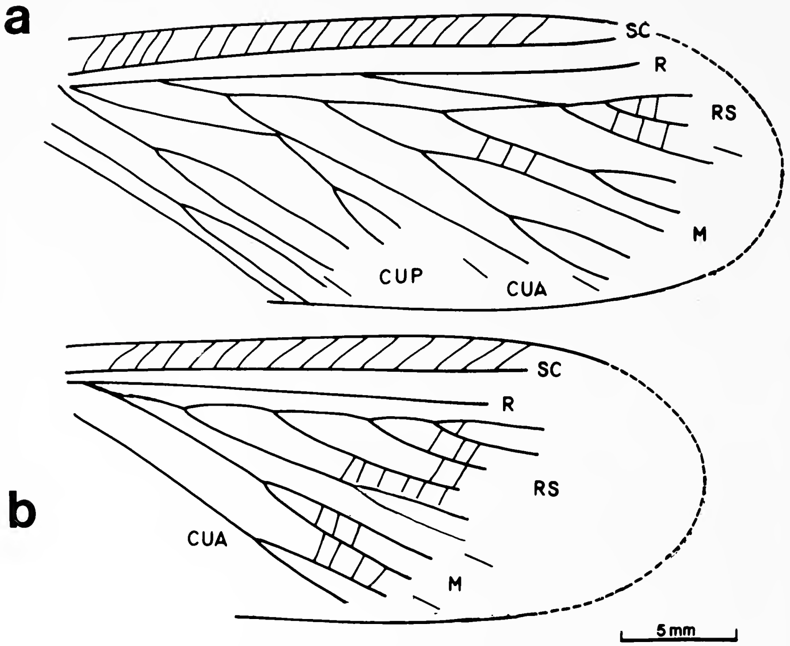

Fig. 26. *Gerarulus radialis*, drawings based on holotype no. YPM 37. a. fore wing. b. hind wing.

Diagnosis

This is the smallest of all the gerarids and its size seems, at present, to be the most distinguishing feature of this species.

Geological range: Westphalian D. Occurrence: Mazon Creek, Illinois, U.S.A.

Holotype: YPM 37. Specimen examined. Obverse and reverse halves. This specimen is somewhat unusual in that both fore and hind wings are stretched out on one side of the body and do not overlap at all. The abdomen appears to be rather slender. The prothorax is missing.

Genus *Anepitedius*

Anepitedius Handlirsch 1911:318, 1919:30.

Description

Owing to the poor state of preservation of the type specimen, it is impossible to describe diagnostic characters for this genus.

Remarks

It is clear that this genus belongs in the family Geraridae: the prothorax is distinctively shaped, and the limited venational characters are in accordance with the family. Unfortunately, since this is a monotypic genus and based on a single, poorly preserved specimen, it is impossible to assess its relationship to other taxa in the family.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A. TYPE SPECIES: *Anepitedius giraffa.*

Anepitedius giraffa

Anepitedius giraffa Handlirsch 1911:318, 1919:30.

Description

Fore wing: length 40 mm, width 10 mm; M converges with RS, connecting to it by a short cross vein before diverging.

Hind wing: apical half of wing missing and only costal margin visible.

Remarks

This species deviates from the other species in the family by having a combination of narrow wings and a robust prothorax. Unfor-

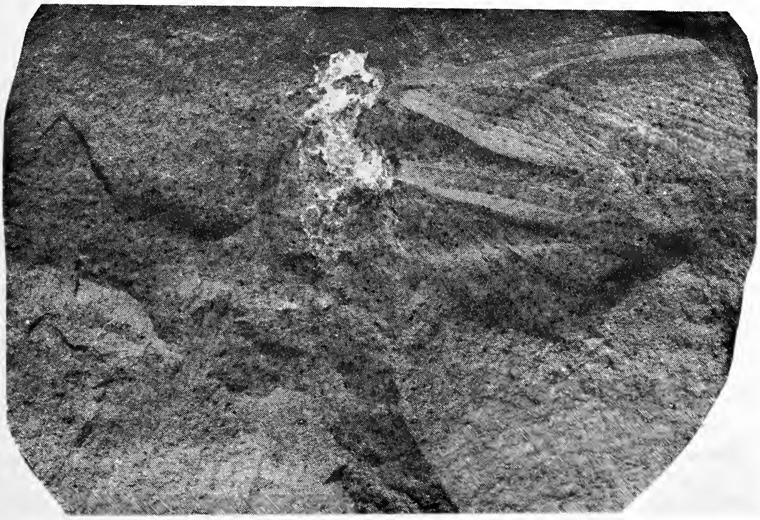

Fig. 27. *Gerarulus radialis*, photograph of holotype no. YPM 37. Length of fore wing 25 mm, as preserved.

tunately, the poor preservation of the one specimen known precludes a more detailed species description.

GEOLOGICAL RANGE: Westphalian D. OCCURRENCE: Mazon Creek, Illinois, U.S.A.

HOLOTYPE: YPM 38. Specimen examined. Obverse and reverse halves.

DEPOSITIONAL ENVIRONMENT

For most of this century, Mazon Creek and Commentry have reigned as the two major localities of Upper Carboniferous insects (a third locality has just been added to this list; see Burnham, 1981). Both have provided large numbers of superbly preserved specimens and have contributed greatly to our understanding of early insect evolution. Because the family under consideration is represented at both places, a comparison of their geological history is warranted.

Roughly three hundred million years ago, in the Stephanian Stage of the Upper Carboniferous, the Commentry Coal Basin was a shallow lake—9.6 km long, 3.2 km wide, and encircled by mountains (Fayol, 1887; Stevenson, 1909). Two principal streams descended from the surrounding mountains into the lake, where deltaic swamps formed from the deposition of fine-grained sediments. These were, in many respects, typical coal swamps, characterized by *Cordaites,* and, in lesser numbers, other coal swamp flora such as *Lepidodendron* and *Stigmaria.* Fossilization at the site was almost instantaneous, the result of flooding that deposited massive amounts of sediment in the lake and bordering swamp. The remarkable preservation of the Commentry insects would not have been possible without their immediate burial under these catastrophic conditions, and it is assumed that they were buried with minimal post-mortem transportation.

The first fossils at Commentry were discovered in the mid-nineteenth century as a result of extensive coal exploration in the central region of France, and were made accessible to collectors only because of intense mining activity in the area. Once the coal supply began to diminish, about 1915, the mines were closed down and filled in, and further fossil collecting prohibited. For an historical account of the Commentry collections and a review of the literature on Commentry insects, see Carpenter (1943).

Mazon Creek, in contrast, was once part of a major delta on the edge of the Illinois Basin Sea. Periodic floodings in this area resulted in the burial and preservation of a wide diversity of organisms, both plant and animal. Two assemblages are recognized: the Essex fauna (mostly marine organisms); and the Braidwood assemblage (freshwater to brackish flora and fauna). According to Richardson (1956:11–12) the Braidwood fossils "represent the fauna that lived on an aggrading plain, [just] above sea-level" and consisted of "more than 200 species of small animals, including insects, arachnids, mussels, and amphibians." Over 140 species of insects have so far been described from this locality (Richardson, pers. comm.) and many of the specimens show exceptionally fine detail.

Unlike the Commentry fossils, which are preserved in shale, Mazon Creek fossils are found primarily in iron carbonate or siderite concretions. These concretions (also called nodules) form due to decay of the organism contained within them, but will do so only under the right conditions (iron-rich sediments, high pH, rapid burial). They are characteristic of certain Upper Carboniferous coal-bearing strata and have been recorded from localities in the United States, France, England, and Germany. Nodules are shaped roughly according to the dimensions of the organism they contain and can be split along the bedding plane to reveal their fossilized contents. Preservation is generally good, although appendages (particularly legs) are frequently lost due to insufficient chemical reaction in the extremities. For a more detailed account of concretion formation see Woodland and Stenstrom (1979).

The Mazon Creek biota has been known since the middle of the nineteenth century (Nitecki, 1979), but their initial discovery (unlike Commentry) was due to the erosion of fossil-bearing strata by stream action rather than by mining exploration. Concretions washed out by the stream (Mazon Creek) accumulated along its banks, and were found there by local collectors. Eventually the area became the focus of extensive mining exploration and several pit mines were dug in an effort to obtain coal. This was enormously beneficial to paleontologists because it exposed great numbers of concretions that then became available for study. Although most of the mining has now ceased, at least one mine remains open (pit eleven) from which fossils are still being collected, primarily by an avid corps of amateur collectors, many of whom have made their finds available for scientific study.

The presence of the Geraridae at both Mazon Creek and at Commentry may seem somewhat surprising.[9] The Mazon Creek locality is roughly 5 to 10 million years older than that at Commentry and the two formed under quite different circumstances. How can the presence of *Gerarus* at both be explained?

To find an answer, one must look at land mass movements during the Carboniferous, and at their influence on climatic patterns and continental distributions (see fig. 28). The collision of the continents Gondwana and Laurasia during this period had two major consequences. These were 1) the formation of the Allegheny Mountain range in North America; and 2) the alignment of eastern North America and western Europe so that they were contiguous at zero latititude. The significance of these events for the family Geraridae is twofold. One, the separate land masses were fused into a single continent, and two, their new position along the equator resulted in the formation of extensive coal swamps throughout North America and Europe. These events made dispersal of insects from one region to the other relatively easy. Although the creation of the Allegheny Mountain chain may have acted as a barrier to dispersal for some insects (and other animal and plant species), this was probably not so for those that were strong fliers. It is likely, therefore, that the Geraridae were able to cross the barrier, and in so doing, passed from one coal swamp habitat to another. It is assumed, being orthopteroids, that they were herbivores, and probably restricted in their feeding habits to plants found in these swamps. It is not surprising, then, that they should have been so widespread and successful during the Upper Carboniferous. For the same reason, it is not surprising that they died out by the end of the Carboniferous when climatic changes led to the drying up of the great coal swamps and the concomitant extinction of the coal swamp fauna and flora.

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[9] Three other genera common to both these localities have previously been reported. They are *Homaloneura* (Carpenter, 1964) and *Spilaptera* (Carpenter and Richardson, 1971) in the order Paleodictyoptera, and *Mischoptera* (Carpenter and Richardson, 1968) in the order Megasecoptera.

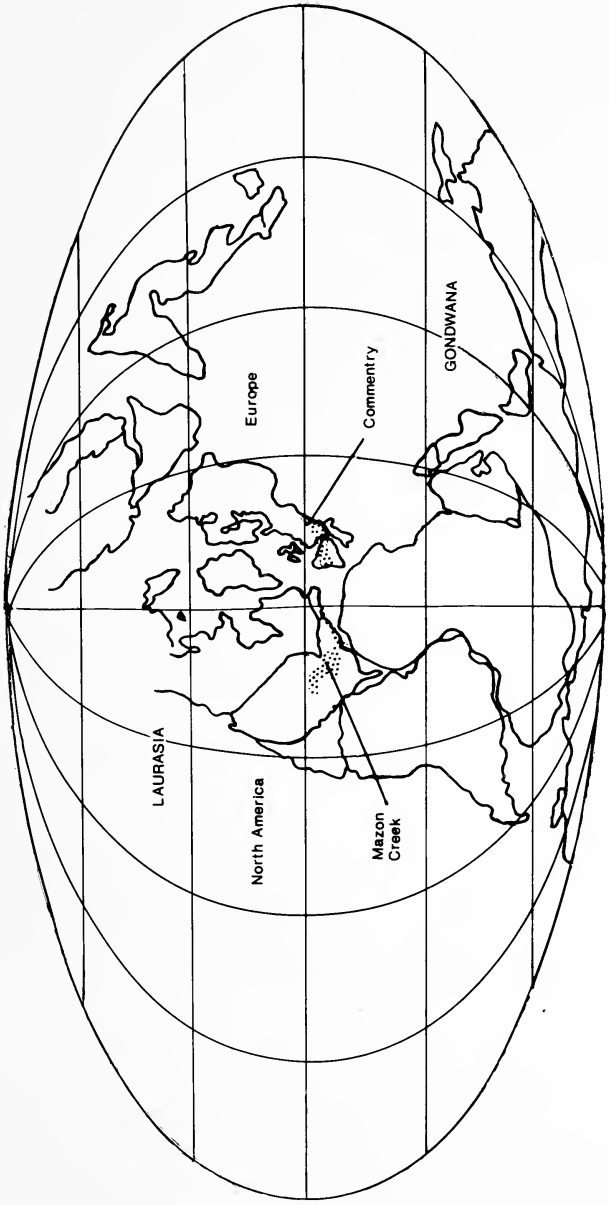

Fig. 28. Geographic map of the Upper Carboniferous. Stippled areas represent coal swamps. Note location of Mazon Creek relative to Commentry. (After Bambach, *et al*, 1980).

DISCUSSION

Recognition of the Protorthoptera has had a varied and unsettled history. Despite the unquestioned importance of the order in the evolution of the higher Insecta (as ancestors to extant Orthoptera and possibly to the Holometabola) there is as yet little agreement about affinities within the group. Our understanding of relationships within the order is still rudimentary. This is well documented by the present study in which the families Sthenaropodidae and Geraridae (previously assigned to two distinct orders) are synonymized. Many attempts have been made to separate the Paleozoic Orthopteroidea into more "natural lineages," but it is currently proposed (Carpenter, 1966) that recognition of one order Protorthoptera (*sensu lato*) is preferable until a better understanding of the group's true phylogeny emerges. While this forces acknowledgement of the Protorthoptera as a "taxonomic wastebasket" and the group "as thus constituted is almost certainly polyphyletic" (Carpenter, 1966), adoption of a presumably phylogenetic classification would, at this time, only misrepresent the actual evolutionary relationships of these insects. I believe that previous work on the Protorthoptera (particularly the Sthenaropodidae) is a good example of how such misrepresentation can occur as the result of inadequate study of a given fossil group.

The Protorthoptera were first recognized in 1906 when Handlirsch split the Paleozoic orthopteroids into three orders: the Protorthoptera, Protoblattodea, and Protorthoptera vel Protoblattodea (for species that seemed to merge the characteristics of the first two). In 1938 the Soviet scholar Martynov made an alternative suggestion: that the fossil Orthopteroidea be divided into the two orders Protorthoptera and Paraplecoptera according to whether they possessed saltatorial legs, as in the Protorthoptera, or cursorial ones, as in the Paraplecoptera. The Geraridae were placed at this time in the Paraplecoptera, and Martynov considered them, on the basis of size and cursorial legs, to be typical representatives of that order. Sharov (1960, 1962) originally suggested that these orders be reorganized into the Protorthoptera, Paraplecoptera, and Protoblattodea, but later (1968) expressed agreement with Carpenter that the Paraplecoptera and Protoblattodea cannot be recognized as distinct orders.

Convinced that the Protorthoptera should reflect direct relationship to the Orthoptera, Sharov narrowed the order to include only a single family, the Sthenaropodidae, synonymized here with the Geraridae. Unfortunately, not having had the opportunity to examine the Commentry types, he erroneously believed that the family consisted entirely of saltatorial forms and used this to justify its placement in the Protorthoptera. The various families previously assigned to the Protorthoptera were placed in the Paraplecoptera (containing the Geraridae), and the true Orthoptera. More complete accounts of these various classifications are given by Carpenter (1966, 1977) and Sharov (1968).

The most recent classification of Orthopteroidea was proposed by Rasnitsyn (1980) in his work entitled *The Historical Development of the Insecta.* Here he distributes the Paleozoic orthopteroids among ten separate orders and proposes a new order Gerarida for which Geraridae is the type family. The order Gerarida includes six Mid to Late Upper Carboniferous families (previously assigned to the Protoblattodea and Paraplecoptera), which Rasnitsyn considered related to one another on the basis of their elongate prothoraces and free, highly mobile heads. He includes in this order the Eucaenidae, Spanioderidae, Dieconeuridae, Ischnoneuridae, Cnemidolestidae, and Geraridae.

Rasnitsyn (1980:165) admits that recognition of the Gerarida and its division into these families is "extremely provisional owing to insufficient study of its members." Inasmuch as this revision of the Geraridae has shown the degree to which detailed study of a particular taxon can affect higher levels of paleoentomological classification, it would seem premature to accept Rasnitsyn's ordinal classification at this time. In my opinion, it is preferable to continue to recognize the Protorthoptera *sensu lato* until we have valid synapomorphies by which the true monophyletic groups in the Protorthoptera can be recognized.

The relationship of the Geraridae to other Carboniferous Protorthoptera must consequently remain unresolved. Nevertheless, there are several interesting possibilities to consider. The first of these is that Rasnitsyn may be correct in grouping together those families with elongate prothoracic segments. It is perfectly possible that they represent a monophyletic offshoot of the Insecta that left no descendants.[10]

Other possible relationships, however, may be construed on the basis of venational characters, particularly the nature of M in the fore wing. This vein is distinctive in that it either anastomoses with RS for a short distance, or is connected to it by a cross vein. Because a similar trend is seen in other groups of Protorthoptera, it may suggest common descent. Families, aside from the Geraridae, known to possess this anastomosis between M and RS are the Streptocladidae, Oedischiidae, Nugioneuridae, and Tococladidae. While many of these families (particularly the Streptocladidae) have a much more complex venation than the Geraridae, it may be that they represent an earlier stage in the evolution of the group—one that led eventually to the saltatorial forms represented by the oedischiids. Because the oedischiids were clearly saltatorial as far back as the Carboniferous, it is reasonable to speculate that the gerarids fall into a proto-saltatorial complex of Upper Carboniferous Protorthoptera and may represent a line of evolution quite distinct from that of the cursorial orthopteroids living today.

SUMMARY

The family Geraridae, previously thought restricted to North America, and known only from Mazon Creek, was apparently a widespread and fairly successful group in the Upper Carboniferous. Careful examination of Commentry Protorthoptera has resulted in the synonymy of *Sthenaropoda* with *Gerarus* from Mazon Creek and illuminates the problems inherent in the classifications proposed by several recent authors. Recognition of the family Sthenaropodidae as the sole family of the order Protorthoptera and the Geraridae as members of the order Paraplecoptera or Gerarida is no longer tenable.

While further study is required to determine whether the Geraridae are more closely related to the Mazon Creek families considered

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[10] Rasnitsyn is not the first to propose that the elongate prothorax is a synapomorphic character. Others, especially Handlirsch, have already suggested that the Geraridae are close relatives of the Spanioderidae on this basis. An argument against this relationship, however, is the fact that they have distinctly different patterns of venation. (In the Spanioderidae CUA is multiply branched and R branches only once. Neither character is true for the Geraridae.)

by Rasnitsyn as belonging to the "Gerarida," or to the oedischiid complex of true Orthoptera, at least monophyly for the family is now established. What remains is the task of clarifying the relationships of these other families; not only in terms of their relationships to each other, but to their extant descendants as well.

TABLE 1. Past and Present Classifications of the Geraridae.

Classification proposed by previous workers	Classification proposed by Burnham in this article
Order Paraplecoptera	Order Protorthoptera
Family Geraridae	Family Geraridae (= Genopterygidae, Sthenaropodidae)
Gerarus	
vetus	*Gerarus* (= *Sthenaropoda, Rossites, Genopteryx, Archaeacridites*)
danielsi	
longicollis	*vetus*
longus	*danielsi* (= *latus, reductus, longus, angustus, constrictus, inopinus*)
angustus	
latus	
reductus	*collaris* (= *longicollis*)
collaris	*fischeri* (= *lerichei, agnusi*)
mazonus	*bruesi*
Genopteryx	*Genentomum*
constricta	*validum* (=*carri*)
Gerarulus	*Progenentomum*
radialis	*carbonis*
Anepitedius	*Nacekomia*
giraffa	*rossae*
	Gerarulus
Order Protorthoptera	*radialis*
Family Sthenaropodidae	*Anepitedius*
Sthenaropoda	*giraffa*
fischeri	
elegantissima	
bruesi	
minor	
agnusi	
lerichei	
Order Orthoptera	
Family Oedischiidae	
Genentomum	
validum	
carri	
Progenentomum	
carbonis	

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TESTING VISUAL SPECIES RECOGNITION IN *PRECIS* (LEPIDOPTERA: NYMPHALIDAE) USING A COLD-SHOCK PHENOCOPY

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There have been many studies of the role of color and pattern in mating and species recognition in butterflies. For example, Crane (1955) manipulated the bold color pattern of *Heliconius* spp. (Heliconiidae), affecting mating success; Burns (1966) claimed on the basis of spermatophore counts that differential attractiveness of female morphs helped to maintain a mimetic polymorphism in *Papilio glaucus* L. (Papilionidae); and Silberglied, Aiello, and Lamas (1980) found that modifying the pattern of *Anartia* (Nymphalidae) affected mating success but not survivorship.

Recently Hafernik (1983) demonstrated that the conspicuous pale dorsal forewing band serves as a visual species-recognition character, contributing to reproductive isolation between the partly sympatric buckeye butterflies *Precis* (=*Junonia*) *coenia* Hubner and *P. nigrosuffusa* (Barnes & McDunnough). In hybridization experiments these entities are quite compatible genetically and developmentally; Hafernik concluded that differences between them "are probably not associated with major genomic reorganization, but are rather the result of allelic differences at a few loci," including presumably those that control the presence or absence of the forewing band.

The experiments done by Hafernik to test the hypothesis of visual reproductive isolation were modeled on the work of Scott (1972), involving presentation of reared virgin females to wild patrolling males afield. There were four sets of experiments (i) actual combinations of *nigrosuffusa* and *coenia*; (ii) *coenia* painted to resemble *nigrosuffusa*; (iii) "wing transplants" (wings of one type glued onto the wings of a living animal of the other; (iv) paper models. All of these tended to indicate that *coenia* males discriminate against

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bandless females, and that species-specific pheromones need not be invoked to account for reproductive isolation. None of Hafernik's females actually mated, but Scott (1972) showed that darkening the wings of male *coenia* does not lower their courting success with conspecifics, as it does when females are darkened.

Despite the consistency of these results, there are possibly confounded variables whenever one tests using entire genomes (as in i above, in which pheromonal and subtle behavioral cues cannot be controlled for), or altered phenotypes (as in ii and iii, where the "similarity" to the other species is questionable, and wing loading and odor may be altered by glues or paints). However, another test is available, not exploited by Hafernik: pure *coenia* genomes can be induced to produce *nigrosuffusa*-like phenotypes, which may then be presented to *coenia* males afield. This situation arises from the sensitivity of *coenia* to temperature shocks applied shortly after pupation.

A named aberration of *coenia, "schraderi,"* figured in color by Comstock (1927, plate 43), resembles *nigrosuffusa* in lacking the band. Other characters, including the hindwing ocelli, are in the *coenia* rather than the *nigrosuffusa* state. Schrader's specimen was reared, but similar individuals do occur in nature. One shown in fig. 1f has the hindwing ocelli and distal pattern obsolescent; others are normal for these pattern elements. The actual frequency of bandless buckeyes is unknown. I have taken two at the same locality in eleven years, during which time I must have seen hundreds of thousands of individuals. No clear-cut genetic basis for bandlessness has been established, but the same phenotypes are readily inducible by subjecting wild California pupae to sustained low temperatures. Fig. 2 shows chilled individuals from three different families. The extensive variation in individual response to treatment is characteristic of such experiments. The involvement of the ocelli and distal pattern is partly controllable by age of the pupa at onset of chilling, but even very precise timing can only reduce, not eliminate, the variation. Such indeterminacy was characterized as early as 1913 in Pictet's "law of melanization and albinization of parts," which is a statement of the partial independence of different pattern-determining processes during wing development.

Several broods of pure *coenia* from Solano County, California were reared and subjected to a potent cold-shock treatment (3 weeks

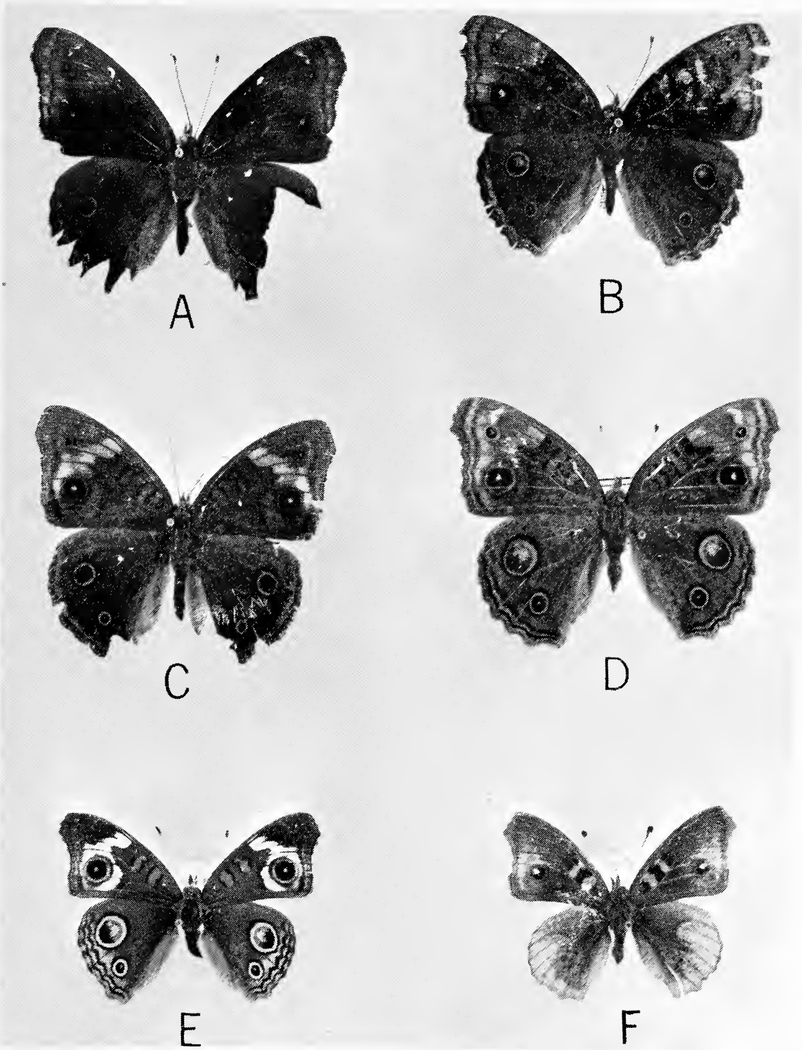

Fig. 1. Phenotypes of wild-collected *Precis*. A,C, male, B,D, female *P. nigrosuffusa* from Arizona, USA and Sinaloa, Mexico. E, normal female *P. coenia*, Solano Co., California. F. "*schraderi*", Suisun Marsh, Solano Co., CA. viii.28.1978.

at 3°C beginning 8 hr after pupation). The usual spectrum of phenotypic response was observed. About one-third of the animals which eclosed were seriously crippled and unusable for mating tests. The remainder—46 females *in toto*—were classified into three more or less arbitrary phenotypic categories: (i) essentially unaltered (fig. 2e), (ii) bandless but with ocelli unaltered (figs. 2a-d), and (iii) bandless and with ocelli obsolete (fig. 2f). These were used in experiments modeled on Scott's and Hafernik's, carried out on a total of 9 days at Suisun City, Solano County, and Rancho Cordova, Sacramento County, in urban vacant lots and annual grassland from late September to early November 1982. Wild male *coenia* were common throughout this period.

My methodology differed from Hafernik's in a few points. Virgin females were held, unfed and unflown, in the dark at 3°C for 3 to 11 days before use. This treatment did not diminish their attractiveness relative to Hafernik's females. They were transported in a cooler in the dark to the study sites and allowed to warm in the sun (air temperatures 14–24°C). After a test they were usually recaptured, rechilled for at least 15 min, and re-used. A few were lost, and about one-fourth mated successfully and were not re-used. As in Hafernik's work, only releases in which the male at least investigated the female were scored. Females were considered to have elicited a courtship if the male either attempted to copulate or remained oriented toward the female for at least 20 sec. The durations of about a third of the courtships were recorded.

The percentages courted were overall higher than seen by Hafernik. For Point Richmond, California female *coenia* × male *coenia* at Point Richmond, Hafernik had 64% courtship. When female *nigrosuffusa* from Texas were used, this dropped to 10%. My corresponding figures (table 1) are 74% and (pooled classes ii and iii) 49%. The difference remains highly significant, however, and the discrepancy in frequency may be due to differences in weather conditions or to the torpidity of my females. For timed courtships, bandless females elicited less persistence than banded ones, but the difference was not statistically significant. Most of the actual copulations were essentially instantaneous, regardless of phenotype.

This experiment does not rule out pheromones in *Precis* courtship, but as in previous work indicates that visual cues are impor-

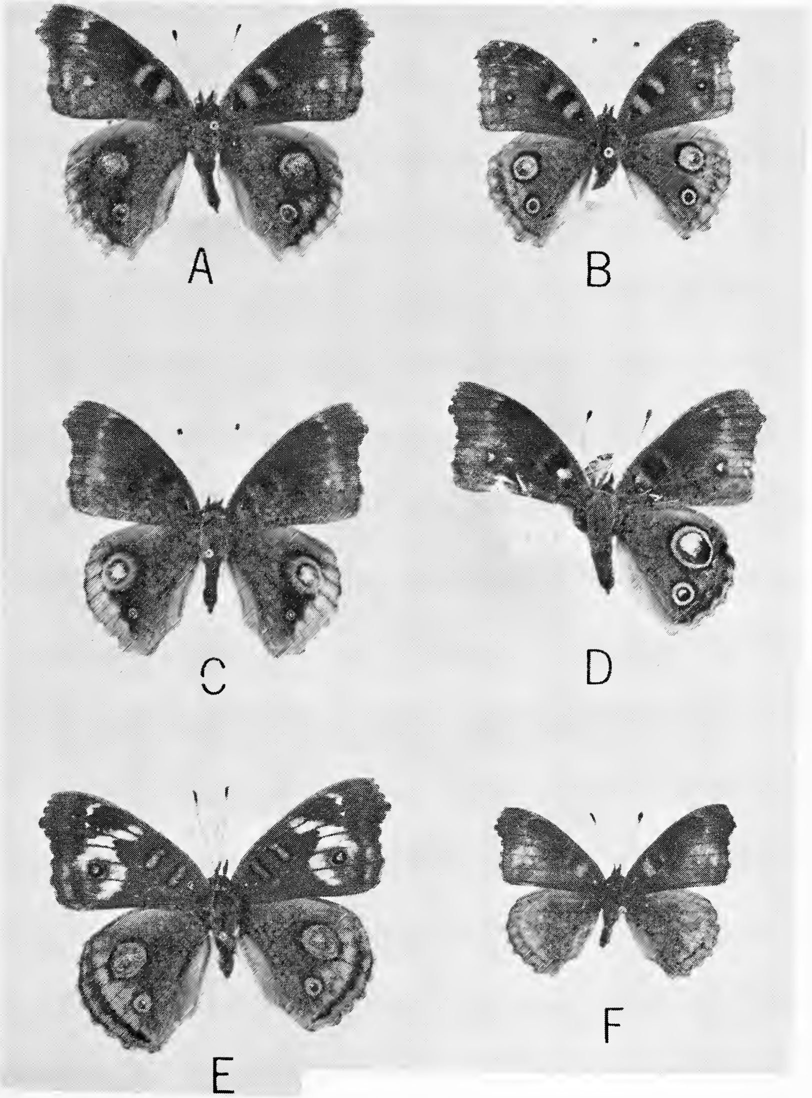

Fig. 2. Phenotypes of female *P. coenia* from northern California, induced by chilling the young pupa. A—D, grade ii (bandless, ocelli unaltered). E, grade i (essentially unaltered). F, grade iii (bandless, ocelli obsolete).

tant and possibly adequate to account for reproductive isolation. (It is conceivable that pheromones could be physiologically coupled to phenotypes such that the most phenotypically deviant females would also be pheromonally abnormal.)

The control of pattern in *Precis* has been studied by Nijhout (1980a, b), who has shown that all of the wing pigments in *P. coenia* are melanins and that the ocelli are determined by well-defined foci in the early pupal wing. His work does not permit a causal analysis of how pupal chilling phenocopies the normal phenotype of *nigrosuffusa,* though the phenocopy "straw" has been linked functionally to its genocopy in *Drosophila* (Seybold, Meltzer, and Mitchell, 1975). In Shapiro's (1981) model of the evolution of phenotypic plasticity, a genetic basis for bandlessness could be established by selection of modifiers bringing the latent "*schraderi*" response to the surface under normal developmental temperatures. The derivative character of bandlessness is shown clearly by its variable penetrance (especially in females) in pure *nigrosuffusa* populations. But how did it become virtually fixed? Discrimination by male *coenia* against bandless females, even genotypicaly normal ones with intact wings, should lead to selection against any bandless allele, however originated. Under the conventional model for enhancement of prezygotic reproductive isolating mechanisms in secondary sympatry, one could rationalize bandlessness as a device protecting the gene pool of *nigrosuffusa.* This, however, presupposes a disadvantage to

Table 1. Success of cold-shocked female *Precis coenia* in attracting courtships by wild males in field tests in northern California.

Type of female	Number of ♀♀	Total releases	Number of ♀♀ mated	Number of courtships
(i) essentially unaltered phenotype	18	42	6	*31*
(ii) bandless, ocelli unaltered	20	55	5	*27*
(iii) bandless, ocelli obsolete	8	17	0	*8*
Totals	46	114	11	*66*

z-test for courtship proportions, (i) *vs.* (ii + iii): $z = 2.7845$ (significant at 0.01) hybridization which outweighs the discrimination against bandless females, and no such disadvantage has been found. Bandlessness may be quite incidental to hybridization, but that still leaves the question of why it persists.

ACKNOWLEDGEMENTS

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DEFENSIVE ADAPTATIONS AND NATURAL ENEMIES OF A CASE-BEARING BEETLE, *EXEMA CANADENSIS* (COLEOPTERA: CHRYSOMELIDAE)

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Introduction

The larval habit of constructing and carrying a portable case has evolved many times in the Holometabola. It is a widespread trait of the Trichoptera and Lepidoptera (e.g. the Coleophoridae and Psychidae). Among the Coleoptera, casebearing is found in four related subfamilies of the Chrysomelidae, the so-called camptosomates: Clytrinae, Cryptocephalinae, Chlamisinae, and Lamprosomatinae (Böving and Craighead 1931). The larval case of many insects is thought to function primarily in defense by providing armor or camouflage (Otto and Svensson 1980). Here we describe the uses of the case and other defenses in a chlamisine beetle, *Exema canadensis* Pierce, and speculate briefly on the evolution and consequences of the case-bearing habit.

The genus *Exema* Lacordaire contains nine species in North America (Karren 1966). All of the species appear to be univoltine and to feed on a fairly restricted range of herbaceous or shrubby genera in the Asteraceae (Jenks 1940; Karren 1966, 1972). In central New York *E. canadensis* is commonly found on goldenrods (*Solidago* spp.) and asters (*Aster* spp.). Its life cycle was summarized by Messina and Root (1980). Le Sage (1982) recently described the immature stages.

Methods

We observed the life history and natural enemies of *E. canadensis* during 1979 and 1980 at Whipple Farm, 8 km N.E. of Ithaca, New

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York. Field-collected larvae and pupae were reared to measure the incidence of parasitoids. Voucher specimens of *E. canadensis* and its enemies were placed in the Cornell University Insect Collection (Lot no. 1068).

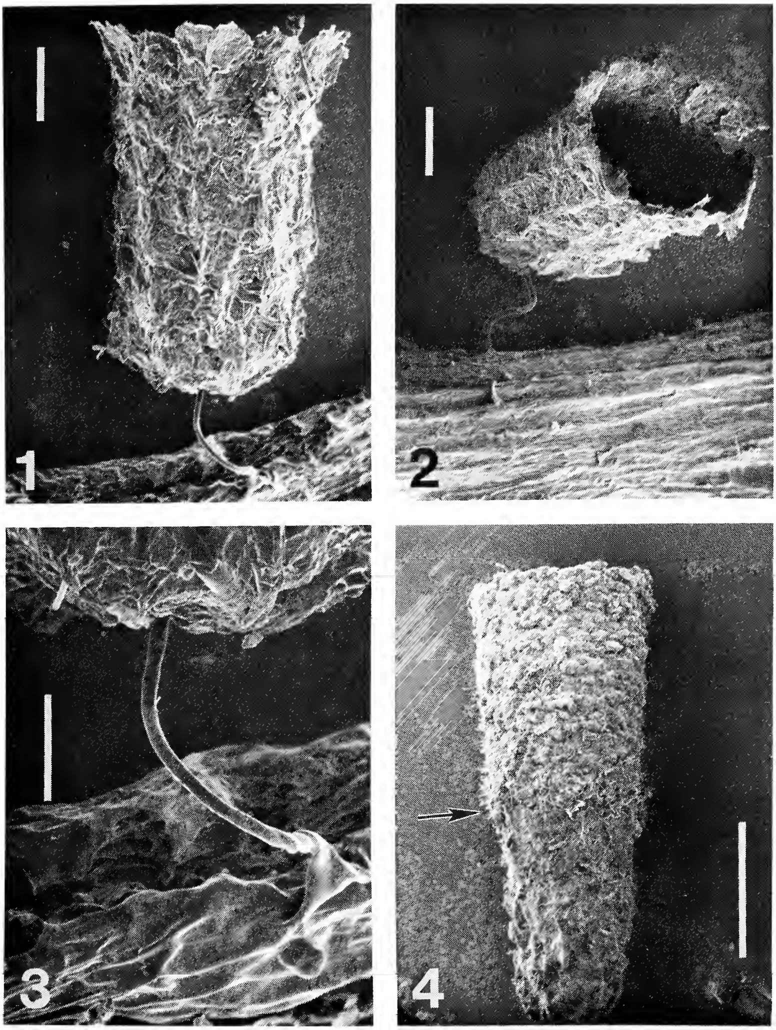
The morphology of *E. canadensis* was examined with the scanning electron microscope. Larval cases and adults were air-dried and mounted on metal stubs with double-sided tape. Larvae and pupae were dehydrated in an ethanol series and critical-point dried with CO_2 before mounting. All specimens were sputter-coated with gold-palladium (ca. 200A). Measurements of larvae and cases were made with an ocular micrometer.

We did experiments on the protective functions of the case by exposing beetles to three predaceous insects: *Podisus maculiventris* (Say) (Pentatomidae), *Nabicula subcoleoptrata* (Kirby) (Nabidae), and *Hippodamia glacialis* (F.) (Coccinellidae). For these experiments we carefully extracted 4th-instar larvae from their cases; this procedure did not appear to harm the larvae. "Exposed" and untreated ("encased") larvae were placed in petri dishes containing moist filter paper and a few goldenrod leaves. In trials using *P. maculiventris*, two 5th-instar nymphs were taken from a vigorous lab culture and added to dishes containing three exposed and three encased *E. canadensis* larvae (a choice situation). We recorded the number of each prey type that were consumed by the stink bugs after 6 and 24 h. In trials using *N. subcoleoptrata* and *H. glacialis,* field-collected adults were starved for 24, 48, or 72 h before being added to dishes containing either exposed or encased *E. canadensis* larvae (a no-choice situation). Each dish held three predators and five prey. We recorded prey consumption hourly for up to 5 h.

RESULTS

The larval case and adaptations associated with its use

In chlamisine beetles the female parent provides the initial larval case in the form of an egg case or "scatoshell" (Hinton 1981). The female deposits a single yellow egg that is attached to the plant on a smooth, yellowish stalk (Figs. 1-3) that appears to be continuous with the egg chorion. The attachment is shaped into the contours of the leaf or stem surface (Fig. 3), suggesting that the base of the stalk is extruded in a plastic state. The female then systematically surrounds the egg with strips of green fecal material. She starts around



Figs. 1–4: Cases of *E. canadensis*. 1, Egg case with egg stalk attached to stem. 2, View from top of case before cap has been added (egg was removed). 3, Close-up of egg stalk and base. 4, Case of 1st instar larva. Arrow indicates juncture between original egg case and larval additions. Scale bars = 500 (Fig. 4), 200 (Figs. 1–2), or 100 (Fig. 3) μm.

the stalk and periodically twists the egg with her hind legs as she builds up the sides until the egg is enclosed in a cuplike case with a flared ridge (Figs. 1–2). A flat top is then added to seal the egg in the case. The flexible egg stalk often remains twisted beneath the case (Fig. 3). The entire deposition process takes 20–30 min in the laboratory. The egg case turns a drab brown color as it dries.

The larva emerges by chewing through the flat top of the case. It then flips the case over, presumably after severing the connection with the egg stalk (Karren 1972). Inside the inverted egg case, the larva assumes the characteristic folded posture of the camptosomates with the mouth and anus both adjacent to the single case opening.

The larva begins to feed and gradually enlarges the case by adding its own fecal material to the rim around the opening. The juncture between the contributions of the mother and the larva remains distinct (Figs. 4–5), and the original egg case eventually appears as a small nipple projecting from the tail of the larval case. A larva passes through four stadia, always molting within the enlarging case (Le Sage 1982). Case length is a moderately good predictor of larval instar, as determined by the width of the head-capsule (Table 1).

Larvae of *E. canadensis* possess several morphological features that are probably related to the case-bearing habit. The legs are unusually long; each coxa is movable and so elongated that it exceeds the length of the femur (Fig. 6). The legs can extend laterally beyond the rim of the case when the larva is walking. If disturbed, the larva retracts its legs and pulls the case down so that the rim is appressed to the foliage (Wallace 1970). The strongly recurved tarsal claws (Fig. 7) may facilitate this maneuver by providing a firmer grip on the substrate. The larval cuticle, which is normally covered, is sclerotized in only a few areas (Le Sage 1982). Setae (usually tricoid sensillae) are sparse, but spiny or rounded protuberances are scattered over much of the surface. These protuberances serve may to increase traction between the larval cuticle and the case. The larval spiracles are uniforous and annular (Fig. 8). The requirements for spiracular closure and moisture retention may be reduced in a case-bearer; Karren (1964) reports that artificially exposed *Exema* larvae are highly vulnerable to desiccation.

The prepupa seals the case rim to a leaf or stem with a layer of frass. It then reorients itself so that the posterior end is against the

Table 1: Head capsule widths and case lengths (in mm) of the immature stages of *E. canadensis.*

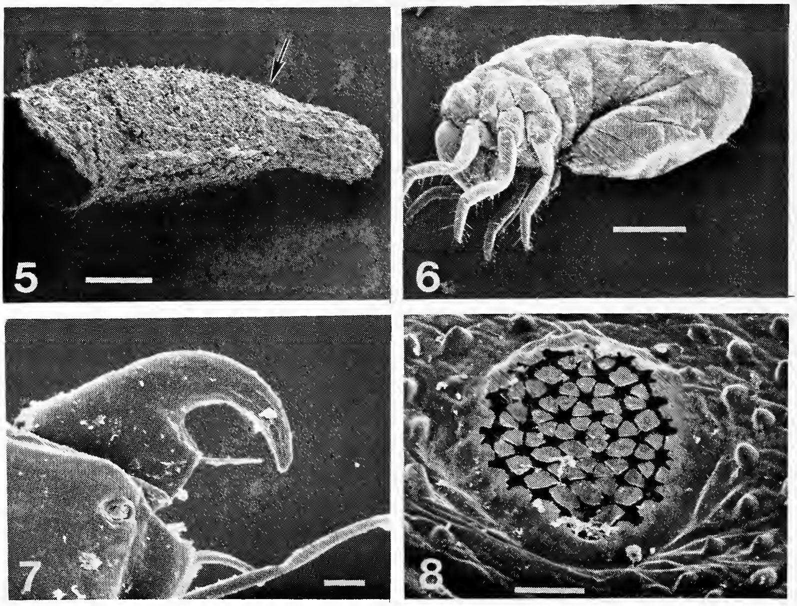
	Egg	I	II	III	IV
Head width					
x̄(SE)		0.29(±.01)	0.37(±.02)	0.50(±.02)	0.67(±.02)
N		7	7	7	9
Case length[1]					
x̄(SE)	1.05(±.05)	1.62(±.38)	2.69(±.33)	3.55(±.32)	4.34(±.26)
Range	0.96–1.12	1.04–2.32	2.16–3.36	2.80–4.08	3.84–4.80
N	12	23	18	32	45

[1] As measured from case opening to tip of original egg case.

substrate and the anterior end faces the nipple at the tail. Fully sclerotized adults cut a circular cap in the tail of the case with their mandibles; this cap is pushed off as the beetles emerge. The barrel-shaped, tuberculate adults (Figs. 9–10) can be easily mistaken for caterpillar frass by humans (Jenks 1940; Karren 1964; and our personal experiences). It may be that vertebrate predators overlook them in the same way. The adults exhibit the widespread chrysomelid trait of quickly withdrawing the legs and dropping off the substrate when they are disturbed. This escape mechanism is elaborated in *Exema*; the deep sternal grooves (Fig. 10) allow the adult to retract its appendages so completely that the falling beetle bounces and rolls off the foliage. The compact adults also slide deeply into the litter beneath the plant and often come to rest in a deep recess where they are extremely difficult to find.

Natural enemies

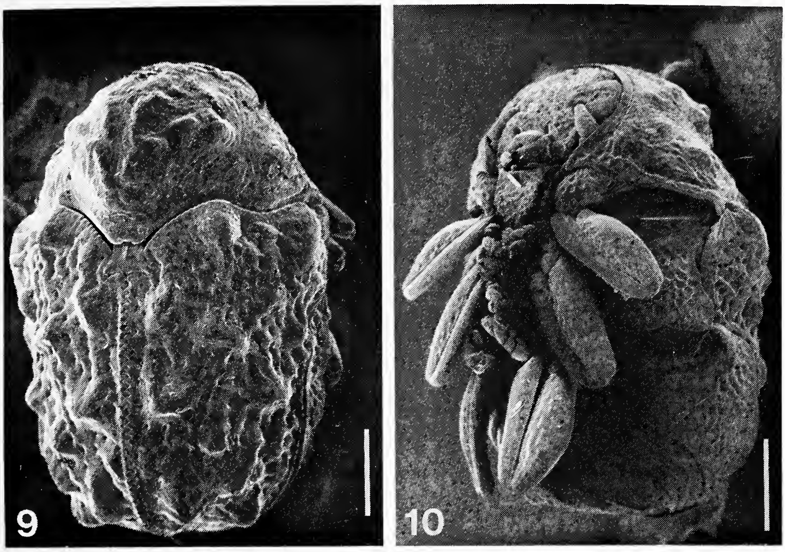
No predators were seen to attack the larvae of *E. canadensis* during the many hours that we and our associates, E. W. Evans and J. A. Gowan, have spent observing the goldenrod fauna in the field. The three species of predaceous insects used in our experiments, however, were frequently observed to kill the larvae of other chrysomelid species that are associated with *Solidago* in central New York (Evans 1982; Messina 1982). In the laboratory, exposed *E. canadensis* larvae were readily captured and eaten by these predators (Table 2). In contrast, few encased larvae were consumed even though the confined space in the petri dishes must have increased



Figs. 5–8: Case and larval morphology of *E. canadensis*. 5, Case of 3rd instar larva. 6, 3rd instar larva, lateral view. 7, Tarsal claw. 8, 2nd abdominal spiracle. Arrow indicates juncture between original egg case and larval additions. Scale bars = 500 (Figs. 5–6) or 10 (Figs. 7–8) μm.

the frequency of encounter between predator and prey far above the usual conditions in nature. The coccinellid, *H. glacialis*, never succeeded in capturing an encased larva and nine of the ten encased prey consumed by the pentatomid, *P. maculiventris*, were taken only after all of the exposed larvae in the dish had been eaten. The rate that exposed larvae were consumed by *N. subcoleptrata* and *H. glacialis* was increased by starvation (Fig. 11).

The protective function of the larval case is further illustrated by its influence on predator behavior. The predator appeared to approach in response to prey movement with the outcome that attacks were launched, without apparent discrimination, on both exposed and encased larvae. Attacks on exposed larvae were quickly and invariably successful. Upon encountering an encased larva, the predators with sucking mouthparts (*N. subcoleoptrata* and *P. maculiventris*) touched the case with their forelegs and extended their beaks. They were never able to penetrate the case



Figs. 9–10: Adult *E. canadensis*. 9, Dorsal view. 10, Ventral view. Scale bars = 500 μm.

even though they made repeated probes. In those instances when these hemipterans did consume encased prey, they fed through the case opening on the few occasions when a larva had been knocked on its side. This is an unlikely event in nature because dislodged larvae fall from the plant. The chewing predator, *H. glacialis*, attacked the encased larvae by attempting to insert the mandibles under the rim of the case; we never observed success in this endeavor.

The case is an ineffective barrier to certain adapted parasitoids. Larvae at both field sites were parasitized by a *Tetrastichus* sp. (Eulophidae); this was possibly *T. chlamytis* Ashmead, a species that is only known to attack chlamisine beetles (Burks 1979). Rates of parasitism ranged from 16 to 42% (Table 3). We obtained an average of 8.6 *Tetrastichus* adults/infested host (range, 5-14 wasps; n = 37 hosts). Parasitoids emerged from larvae that were collected in the field as both early (I-II) and late (III-IV) instars. The cuticle of a parasitized larva turns from white to black and the host dies shortly before the time it would normally pupate. The wasps usually emerged from the case opening, but a small exit hole was observed

Table 2: Consumption of exposed and encased larvae of *E. canadensis* by three arthropod predators in laboratory arenas.

	% available prey consumed			
Predator	Exposed	Encased	N[1]	P[2]
Podisus maculiventris nymphs	69	19	54	.001
Nabicula subcoleoptrata adults	70	7	30	.001
Hippodamia glacialis	87	0	30	.001

[1] Number of each prey type offered.

[2] Chi-square test, where expected values assume equal consumption of each prey type.

in the case of a larva that had cemented the opening to the substrate before it died. We could not determine if *Tetrastichus* females oviposit through the case wall or under the rim. In the field, however, we commonly observed *Tetrastichus* adults that remained perched on the side of a larval case for prolonged periods. Perhaps these wasps were waiting for the larva to move and thus expose a vulnerable spot for oviposition.

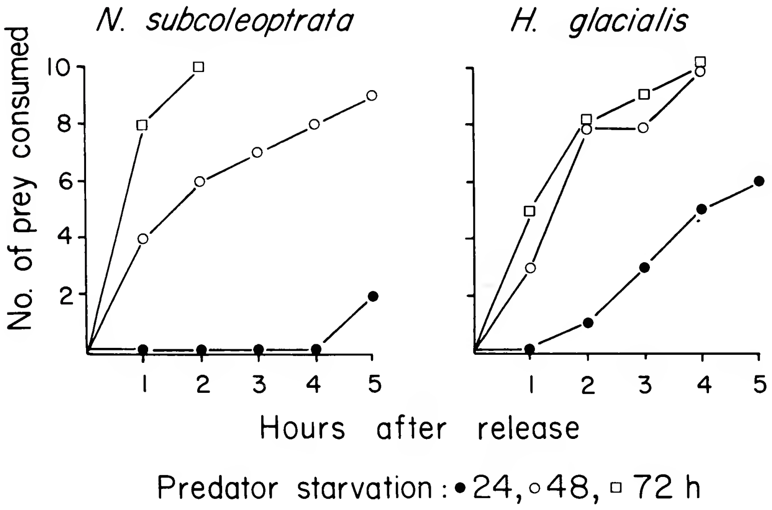


Fig. 11: Consumption of exposed *E. canadensis* larvae by *Nabicula subcoleoptrata* and *Hippodamia glacialis* in the laboratory. Predators were starved for 24–72 h before release. Ten prey were offered per trial.

Six of 22 pupae that were collected on August 21, 1979, were parasitized by *Spilochalcis albifrons* (Walsh) (Chalcidae), a species that has previously been reported from *Exema dispar* Lacordaire (Burks 1979). One chalcid emerged from each host. No *S. albifrons* were found in *E. canadensis* that were collected as larvae. If this chalcid attacks only pupae, it must be able to oviposit through the case wall because the case rim is sealed to the substrate by the prepupae. In this regard, it is interesting to note that *S. albifrons* has been taken from a broad range of unrelated case-bearing and leaf-mining insects. Moreover, at least four of the seven species in the *side* group, to which *S. albifrons* belongs, parasitize case-bearing chlamisines and coleophorids (Burks 1979). These observations suggest that the evolution of specializations in *Spilochalcis* is more closely linked to the abilities required to penetrate materials that cover the host than it is to factors that are more narrowly associated with the host's taxonomic affinity.

Larval mermithid nematodes were found in dissections of a few field collected *E. canadensis* larvae. These parasites are functionally similar to parasitoids, killing the hosts as they exit the body following development (Nickle 1974).

Larvae of an erythraeid mite, *Leptus* sp., were found attached at several locations on beetles. In a survey done in late August 1979, 67% of the 43 adult beetles sampled bore at least one mite. There was an average of 1.7 mites on the infested beetles and as many as five mites were found on a single host. Nothing is known about the influence of these mites on the beetles.

Table 3: Per cent of *E. canadensis* larvae parasitized by a *Tetrastichus* sp. in 1979 and 1980. (Sample sizes in parentheses.)

Site	Collection date			
Brooktondale 1979	3 July	29 July	21 August	21 August[1]
	17(107)	16(57)	38(21)	27(22)[2]
Whipple Farm 1980	28 June	1 July	4 July	16 July
	23(61)	42(19)	40(55)	31(13)

[1] These cases contained pupae; the larvae had cemented the case rim to the substrate prior to collection.

[2] An additional 27% of the pupae were parasitized by *Spilochalcis albifrons*.

Discussion

The defensive adaptations of the immature and adult stages of *E. canadensis* are quite different even though they occur in the same microhabitats, overlap in their seasonal occurrences, and encounter similar predators. The cases that cover the eggs and larvae appear to deter most, if not all, of the several invertebrate predators that forage on goldenrods (see Messina 1982 for a list). Wallace (1970) has found that the case of another chlamisine, *Neochlamisus gibbosus* (F.) (= *Anthrochlamys plicata* F.), protects the larvae from imported fire ants. The defenses of adult chlamisines require further investigation. Nevertheless, it seems obvious that a variety of escape mechanisms are derived from the adults' morphology. As a consequence of their hard, compact body form, adults are well-armored against the initial thrusts of predators and they are more likely to tumble into a refuge after dropping from the foliage. Furthermore, because of their resemblance to caterpillar frass, adults may be overlooked by many predators that rely on vision (Jenks 1940).

Many chrysomelids are chemically defended against predators (e.g. Meinwald et al. 1977; Howard et al. 1982). Adults in the camptosomate group, however, lack the defense glands found in most chrysomelid subfamilies (Deroe and Pasteels 1982). This suggests that chlamisine adults must rely primarily on the mechanical and behavioral defenses discussed above.

The major enemies of *E. canadensis* are the parasitoids, *S. albifrons* and *T. chlamytis*. Specialized parasitoids have been highly successful in overcoming most of the defenses (e.g. reflex bleeding, fecal shields, glandular secretions) employed by chrysomelid larvae to deter predators (Eisner et al. 1967; Wallace 1970; Matsuda and Sugawara 1980).

Several characteristics of *E. canadensis* can be grouped into an adaptive syndrome that is associated with the case-bearing habit. This coordinated set of traits includes the bowed posture, long legs, and other morphological adaptations that accommodate the larvae to life within the confinement of a case. In addition, casebearing probably influences other aspects of the natural history. For instance, the time and case-building material that the female must invest in each egg may result in a lowered reproductive rate. We observed that 30 females laid an average of only 1.2 eggs per day over a six-day period; Karren (1972) reports similar oviposition rates. This low output is reflected in the females' reproductive morphology. In dissections we found that females of *E. canadensis* have only four or five ovarioles per ovary and that each ovary never contains more than one fully mature öocyte. Camptosomate beetles, in general, have relatively few ovarioles per ovary (Robertson 1961; Suzuki 1974; Mann and Singh 1979). Beetles may compensate for gradual egg production by ovipositing over an extended period. In central New York, overwintered females begin egg-laying in early May and continue until mid-July.

The low fecundity of *E. canadensis* may be related to its normally low and relatively stable population size. Over a three-year period, the population densities of five other chrysomelid species that feed on goldenrod fluctuated by at least an order of magnitude (Messina and Root 1980). During this same period the population of *E. canadensis* varied less than twofold. Furthermore, during the course of our long-term investigations on the goldenrod fauna at several localities in central New York, we have yet to observe a host plant that was significantly depleted by *E. canadensis.* Karren (1964) has also noted the stable densities of *Exema* populations. Le Sage (1982), however, reported that during 1980–81, populations of *E. canadensis* increased greatly over a large area in southern Canada.

The evolutionary steps that produced the case-bearing habit are unclear. Since the larval case is added to the egg case, it can be argued that the defense originated with the female's habit of covering the eggs with fecal material (this may be mixed with secretions from the anal gland; Hinton 1981). This initial step is exhibited by other chrysomelids, e.g. the eumolpine, *Chrysochus auratus* (Fabricius). The extant species of camptosomate beetles differ in their manner of oviposition and egg case deposition. Some clytrine beetles lay eggs in clusters (a typical trait of non-camptosomate chrysomelids), with each egg connected to the substrate by a separate stalk (Hinton 1981). A cryptocephaline, *Pachybrachis bivittatus* (Say), apparently does not connect the egg to the substrate at all. Instead, the female covers the egg with fecal material while holding it with her hind legs, and then simply drops the egg to the ground (Lawson 1976). Further comparative data on the details of egg-case provisioning are needed to trace further the evolution of the case-bearing habit and the often enigmatic phylogeny of the camptosomate line (Mann and Crowson 1981).

ACKNOWLEDGEMENTS

We thank E. W. Evans and M. K. Hausmann for technical assistance. N. F. Johnson and B. M. O'Connor identified the parasitoids and mites respectively. The research was supported by NSF grant DEB77-25120.

SUMMARY

Morphological and behavioral defenses of *Exema canadensis* are illustrated with scanning electron micrographs. In laboratory experiments, the fecal case was shown to protect larvae from three predaceous insects (a nabid, a pentatomid, and a coccinellid) that occur in the same microhabitats with *E. canadensis*. Exposed larvae were readily consumed by predators. The case did not deter parasitoids; larvae were heavily parasitized by a eulophid, *Tetrastichus* sp., and pupae were attacked by a chalcid, *Spilochalcis albifrons*. Other enemies include mermithid nematodes and erythraeid mites. The adaptive syndrome associated with the case-bearing habit and its possible evolution are discussed.

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STUDIES ON NORTH AMERICAN CARBONIFEROUS INSECTS. 7. THE STRUCTURE AND RELATIONSHIPS OF *EUBLEPTUS DANIELSI* (PALAEODICTYOPTERA)*

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Eubleptus danielsi was described by Handlirsch in 1906 from a single, poorly preserved specimen in a concretion from the Francis Creek Shale, Illinois (Middle Pennsylvanian). The systematic position of the insect has been controversial. It was placed by Handlirsch in a new family, Eubleptidae, in the order Palaeodictyoptera. However, Martynov, in 1938, expressed doubt about its assignment to that order, and in 1952 Laurentiaux transferred it to a new order, Eubleptidodea, which Rohdendorf accepted in the Osnovy Paleontologii in 1962. Neither Laurentiaux nor Rohdendorf gave a diagnosis of the new order, although vague reference was made to the presence of large eyes and to the absence of pronotal lobes. From my study of the reverse half of the holotype (all that is now known) I came to the tentative conclusion (1965) that the insect was a member of the Palaeodictyoptera, probably related to the family Spilapteridae.

During the past decade, many additional specimens of *Eubleptus* have been found in a strip-mine pit on the Will-Kankakee County line, Illinois, mostly by private collectors. These new specimens, some of which are exceptionally well preserved, have been loaned to me for study. The purpose of this paper is to present the results of my examination of these specimens and to discuss the relationships of the insect, as it is now known.

I am grateful to Mr. Frederick J. Collier of the Department of Paleobiology, National Museum of Natural History, Washington, for the loan of the holotype of *Eubleptus danielsi*; and to Mrs. J. S. Lawless of the Peabody Museum of Natural History, Yale University, for the loan of the holotype of *Athymodictya parva*, a synonym

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of *danielsi.* I am especially grateful to the following private collectors for the opportunity of studying their specimens: Mr. Paul Harris, now of Mountain Home, Arkansas; Helen and Ted Piecko, Chicago; Mr. and Mrs. Francis Wolff, now of Port Charlotte, Florida; Mr. Daniel Damrow, Mosinee, Wisconsin; Mr. Raymond Bandringa, Willow Brook, Illinois; Mr. Joseph Pohl, Belgium, Wisconsin; and Mr. Richard Rock, Crest Hill, Illinois. As will become apparent from the account below, our present extensive knowledge of *Eubleptus* has resulted mainly from their fossil collecting and their cooperation in making the specimens available for study.

I am deeply indebted to the late Dr. Eugene S. Richardson, Jr., formerly of the Department of Geology, Field Museum of Natural History, for his unfailing cooperation and his assistance over the past fifteen years in the course of our investigations on the insects in the concretions from the Francis Creek Shale.[1]

Order Palaeodictyoptera

Family Eubleptidae Handlirsch

Eubleptidae Handlirsch, 1906a, p. 679; 1906b, p. 111.[2]
Eubleptidae Laurentiaux, 1953, p. 423.
Eubleptidae, Carpenter, 1965, p. 178.

Small species, with slender, pointed wings. Fore wing; SC extending nearly to wing apex, terminating on the costal margin; RS dichotomously forked, with 4 (rarely 5) terminal branches; M forking just basad of the origin of RS; MA with a long fork; MP with 3 terminal branches; CUA with a short fork; CUP with 3 (rarely 2) terminal branches; 3 short anal veins present; relatively few cross veins, unbranched, and forming a distinct pattern; archedictyon absent. Hind wing: similar to the fore wing in venation but slightly broader near or before mid-wing, the hind margin strongly curved. Body: moderately slender; antennae very long and thin; head apparently

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[1] Shortly before his death in January, 1983, Dr. Richardson and I completed a joint paper on the Archaeognatha (Insecta) in the concretions. This will be published in the next issue of *Psyche*.

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[2] The family, genus, and species were described and designated as new in both of Handlirsch's 1906 publications; the 1906a article obviously has priority, since many of its pages are cited by number in the 1906b work.

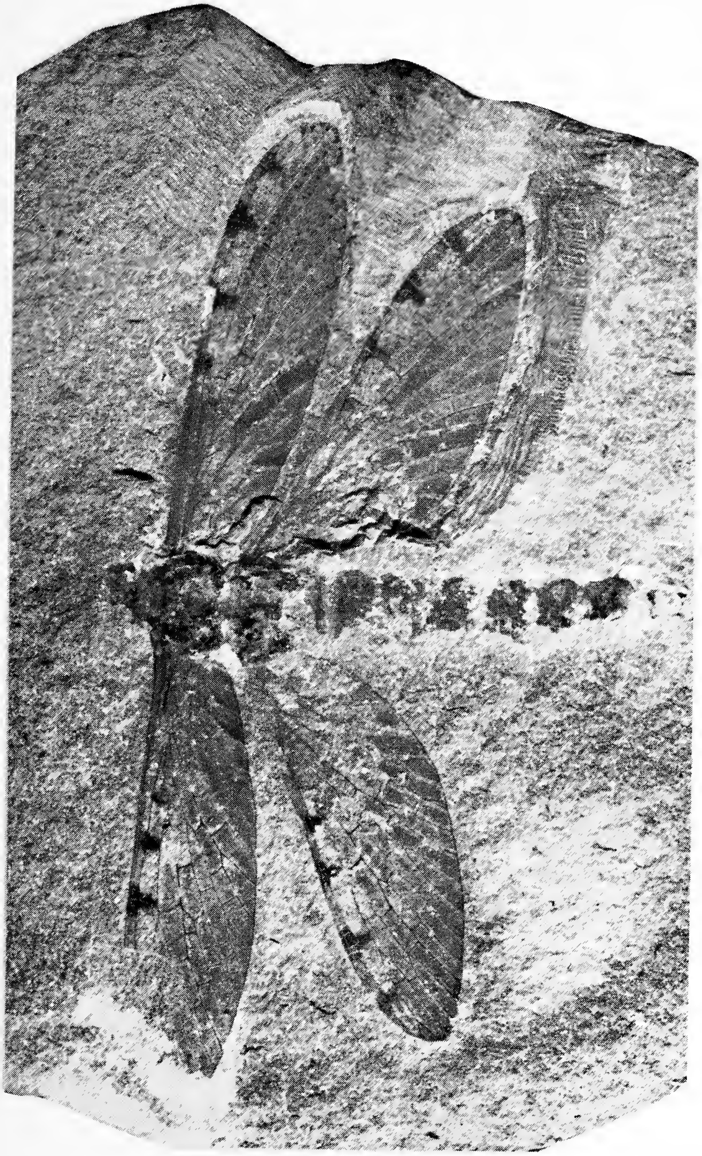

Figure 1. *Eubleptus danielsi*. Photograph of specimen PH15 (reverse) in the Paul Harris collection. Length of fore wing, 13 mm.

small in dorso-ventral view, but eyes prominent and protuding; beak well developed; prothorax short, with small and weak pronotal lobes; mesothorax and metathorax subequal; abdominal segments apparently with small lateral lobes; cerci very long; female with short, curved ovipositor.

The family is known only from the Francis Creek Shale.

Genus *Eubleptus* Handlirsch

Eubleptus Handlirsch, 1906a, p. 681; 1906b,p. 111.
Athymodictya Handlirsch, 1911, p. 298. NEW SYNONYMY.

Fork of MA at nearly the same level as the first fork of RS; first fork of MP well before mid-wing, its posterior branch forked near the wing margin.

Type-species: *Eubleptus danielsi* Handlirsch; by monotypy.

Eubleptus danielsi Handlirsch

Figures 1–8

Eubleptus danielsi Handlirsch, 1906a:681; 1906b:112; 1920:137. Rohdendorf, 1962: 54. Carpenter, 1965: 180.
Athymodictya parva Handlirsch,1911:298. NEW SYNONYMY.

Fore wing: length 13–14 mm; maximum width, 3.5–3.8 mm; hind wing: length 13–14 mm; maximum width, 4–4.3 mm; length of antennae (complete), 11 mm. The venational pattern is shown in figure 2. Only slight individual variations seem to occur: RS usually with four terminal branches, but a fifth, short branch may be present; CUP usually with three branches, though the shortest one may be absent. Head about 3 mm wide across the eyes, and about 1.5 mm long as seen from above (i.e., not including the beak, which is 3 mm long). Pronotum about 1 mm long and 2.5 to 3 mm wide, including the small pronotal lobes; meso- and metathoracic segments apparently subequal, although the compression of the body has probably altered the true proportions of both segments; the abdomen is about 13 mm long and 2 mm wide at mid-length.

Holotype: no. 38731, U.S. National Museum of Natural History, Washington (L.E. Daniels, collector). This is a poorly preserved specimen, showing the proximal three-fourths of a fore wing and very little of the hind wings and body. Handlirsch described the species from both obverse and reverse halves, but when I examined

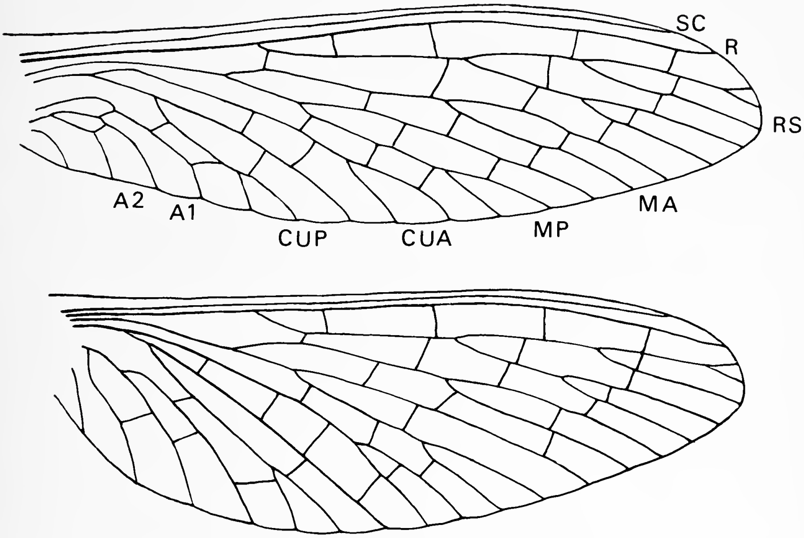

Figure 2. *Eubleptus danielsi.* Venational diagram of fore and hind wings. SC, subcosta; R, radius; RS, radial sector; MA, anterior media; MP, posterior media; CUA, anterior cubitus; CUP, posterior cubitus; A1 and A2, anals. Drawing based mainly on specimen PH15 Paul Harris collection, with some details from specimens PE32046 and PE32045.

the specimen in 1965 only the reverse half could be found.[3] Having now examined many additional specimens, I am convinced that both Handlirsch and I incorrectly interpreted several of the vaguely indicated structures in the type. Most of the cross veins that I described and figured are obviously wrinkles in the wing membrane; in the well-preserved specimens discussed below the cross veins are as strongly developed as the longitudinal veins. Also, the structures that I considered to be pronotal lobes are, in part, the large eyes to which Handlirsch referred. The pronotal lobes are indeed present but they are small.

Handlirsch's *Athymodictya parva,* described in 1911 from a single, poorly preserved specimen (YPM18ab) in the Peabody Museum

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[3] According to the records of the National Museum, counterparts of some of the Daniels specimens were kept by Mr. Daniels after Handlirsch had studied them; their present location is unknown.

at Yale University, is without question a synonym of *danielsi*. Handlirsch mentioned a fine archedictyon on the wings and he placed the insect in the family Dictyoneuridae, but I can find no suggestion of it in the fossil. The matrix of that particular concretion is unusually granular and I surmise that Handlirsch interpreted the granulation as an archedictyon. If the fossil is moistened with alcohol, the characteristic cross veins of *Eubleptus* are discernible. The venational pattern, even as shown in Handlirsch's drawing, is identical with that of *danielsi*, although his figure incorrectly depicts some of the veins with pectinate instead of dichotomous branching. The type of *parva* is about the size of that of *danielsi*, the fore wing being 13 mm. long, with a maximum width of 4 mm.

Specimens of *Eubleptus danielsi* Studied

I have been able to examine seventeen specimens of *danielsi* during this investigation. For convenience of reference, I include here an annotated list of these:[4]

1. National Museum of Natural History, Washington, No. 38731 (reverse half only). Mazon Creek. Holotype of *danielsi*. Poorly preserved, showing about three-fourths of a fore wing, but virtually nothing of the body and hind wing. Fore wing, as preserved, 13 mm. long.
2. Peabody Museum of Natural History, Yale University, No. 18. Mazon Creek. Holotype of *Athymodictya parva*. Poorly preserved, showing proximal portions of fore and hind wings, as well as pronotum, pterothorax, and parts of abdomen.
3. Paul Harris collection, no. PH15. Pit Eleven. Excellent preservation of entire insect, except end of abdomen; the best specimen known. Especially good are the wings (which include the color markings), the pronotum, and the head, which shows the antennae, and eyes, and the location of the beak.

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[4] There are apparently only two exposures of the Francis Creek Shale at which specimens of *danielsi* have been found: Mazon Creek, the bed of the stream about 4 miles west and a mile north of Coal City; and Pit Eleven, a strip mine of the Peabody Coal Co., in Will and Kankakee Counties, Illinois.

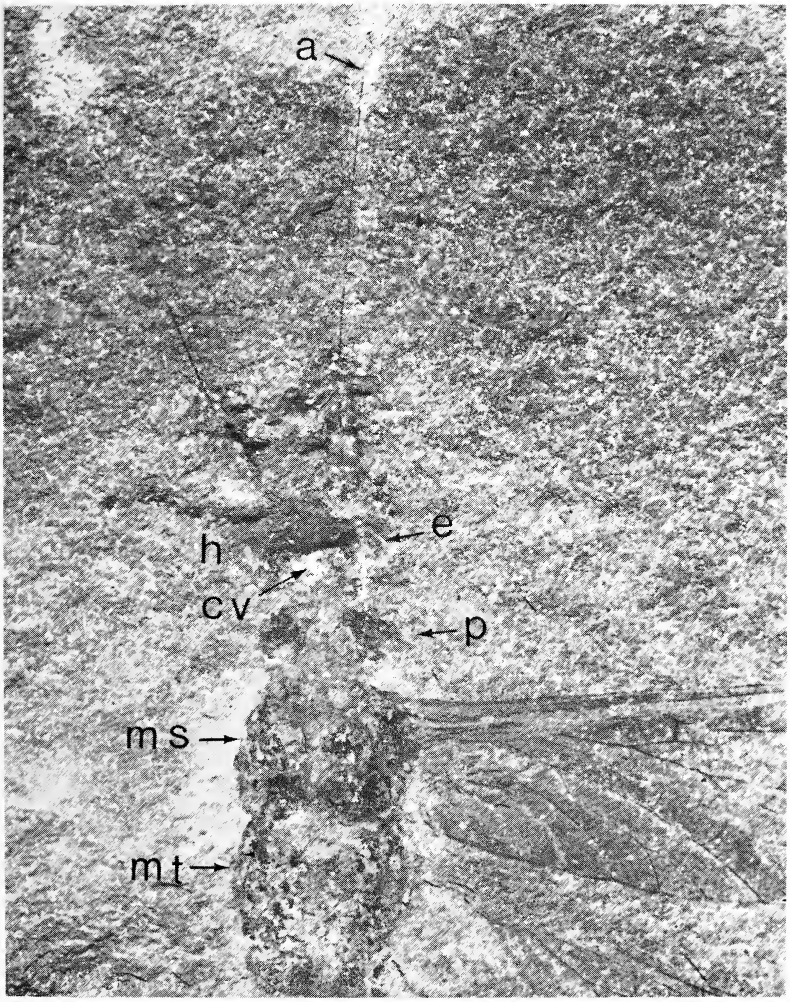

Figure 3. *Eubleptus danielsi*. Photograph of specimen PH15 (obverse), Paul Harris collection. Dorsal view of head and thorax; a, antenna; h, head; e, eye; p, pronotum; ms, mesonotum; mt, metanotum; cv, small cavity in the matrix of the concretion, several millimeters deep and partially filled with kaolinite; cavity originally occupied by the beak. Width of mesonotum, 3 mm.

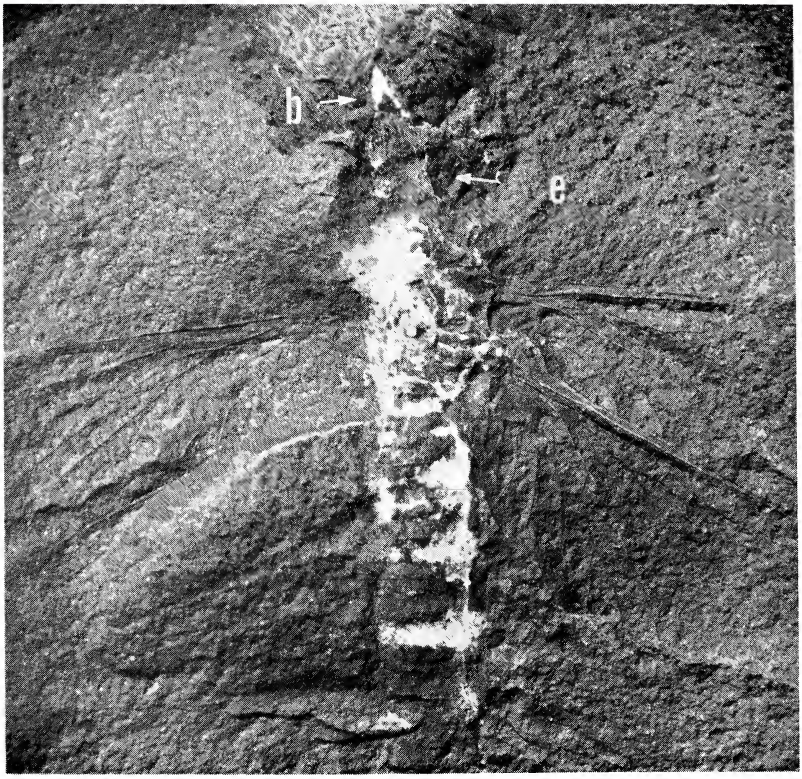

Figure 4. *Eubleptus danielsi.* Photograph of specimen 236, Daniel Damrow collection; dorsal view of thorax, but frontal view of head: b, beak; e, eye. The three thoracic segments are partially covered by kaolinite. Maximum width of fore wing in photograph, 3.5 mm.

4. Field Museum, No. PE32046 (J. Herdina collection, no. H424). Pit Eleven. Very good preservation of all wings, especially of basal parts; also, thorax and abdomen, including proximal part of cerci. Head crushed.

5. Field Museum, No. PE32045 (J. Herdina collection, no. H540). Pit Eleven. Good preservation of basal parts of all four wings; body very poorly preserved.

6. Francis and Terri Wolff collection, No. 229. Pit Eleven. Good preservation of basal portions of all wings; poor preservation of body, but good view of head from above; one fore leg present.

Figure 5. *Eubleptus danielsi.* Photograph of head of same specimen shown in figure 4, with greater magnification and different illumination. Scale line is 1 mm long.

7. Francis and Terri Wolff collection, No. 233. Pit Eleven. Good preservation of basal two-thirds of wings; most of body not preserved.

8. Raymond Bandringa collection, No. 66-PBSM-11-(3). Pit Eleven. Good preservation of basal parts of wings, part of antennae, eyes, and thorax.

9. Field Museum collection, No. PE22016 (from Dwayne Stone collection). Pit Eleven. Excellent preservation of whole insect in lateral view; wings overlapped but venation clear; shows abdomen, including cerci; head, including eyes; beak, in side view.

10. Daniel Damrow collection, No. 236. Pit Eleven. Good preservation of basal part of wings; thorax strongly compressed; entire head well preserved in front view, showing beak, with excellent preservation.

11. Joseph Pohl collection, No. MPH8. Pit Eleven. Good preservation of basal parts of all four wings, with general features of body.

12. Helen and Ted Piecko collection, No. 402. Pit Eleven. Fair preservation of basal parts of all wings, but body not clear.

13. Helen and Ted Piecko collection, No. 422. Pit Eleven. Good preservation of most of all four wings and parts of thorax and abdomen.

14. Helen and Ted Piecko collection, No. 432. Pit Eleven. Fair preservation of body and of basal portions of all wings.

15. Helen and Ted Piecko collection, No. 436. Pit Eleven. Poor preservation of wings and body.

16. Richard Rock collection, no. 729. Pit Eleven. Good preservation of body and of basal parts of fore and hind wings.

17. Richard Rock collection, No. 817. Pit Eleven. Good preservation of basal parts of wings, poorly preserved body.

A composite drawing of *Eubleptus danielsi* is given in figure 8. The general habitus of the insect, as drawn, is based on the Paul Harris specimen, PH15 (see figures 3 and 4), but details from other fossils have been added, as follows (the numbers refer to the specimens in the above lists): head, PE22016, Wolff 229, Damrow 236; beak, PE22016, Damrow 236; pronotum, YPM 18; mesothorax and metathorax, PE32046,YPM18; fore leg, Wolff 229; abdomen, PE32046, PE22016; ovipositor, PE22016; cerci, PE32046,PE22016; wings, PE32046,PE32045,Wolff 229, HTP 422. All structures shown in the composite drawing are present in one or more of the fossils studied.[5]

Discussion of the Structure of *Eubleptus danielsi.*

Head: The head of *danielsi* was obviously hypognathous. In the specimens preserved in dorsal view (i.e., PH15, figure 2) there is a distinct hole in the matrix, at about the center of the insect's head, marking the point at which the beak penetrated the matrix; and in

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[5] Handlirsch's restoration of *Eubleptus*, based on the unique type (1920), bears little resemblance to the insect in this composite drawing.

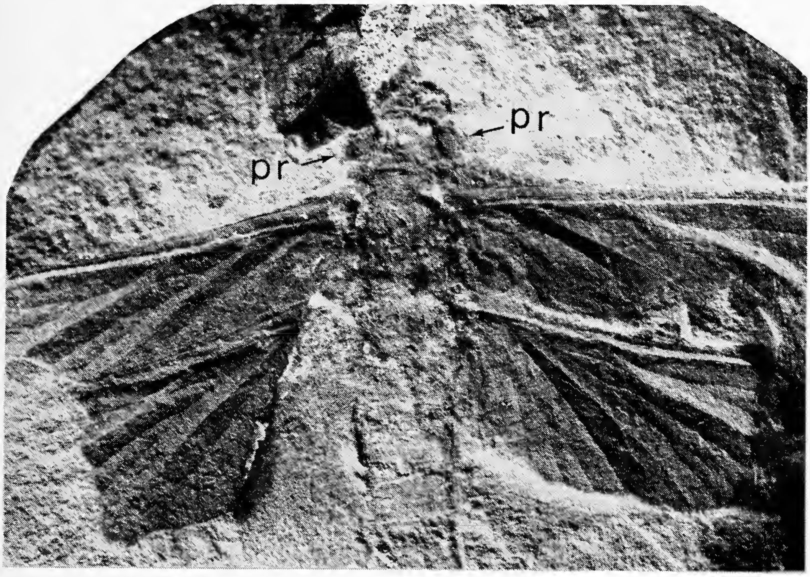

Figure 6. *Eubleptus danielsi*. Photograph of specimen YPM18 (holotype of *Athymodictya parva* Handlirsch. Dorsal view (reverse); pr, pronotal lobes. maximum width of left fore wing in photograph, 4 mm.

the one specimen preserved in lateral view (PE22016, figures 4 and 5) the head is clearly hypognathous. The antennae are extraordinarily long and thin (PH15, Wolff 229; Bandringa specimen 66–PBSM); for most of its length it is .04 mm in diameter and the segments are about .1 mm long. The antennae of PH15 include about 110 segments and are almost certainly complete. The beak, as preserved in lateral view in PE22016 is 3 mm long and slender; several stylets project from its end. In specimen Damrow 236, the beak is 2.8 mm long and as seen in front view (figure 4) is triangular in shape, relatively broad basally, and bears long striae, as has been noted in other species of Palaeodictyoptera (Kukalová, 1970). The eyes are large and bulging, as shown in PH15, Wolff 229, Bandringa specimen 66–PBSM, and especially in PE22016, in which the eye, in lateral view, is preserved in strong relief.

Thorax. The prothorax is very small and, as Handlirsch showed in his drawing of *parva*, bears small lateral lobes about 1 mm wide (YPM18); the folded and twisted condition of the lobes in some specimens suggests that they were thin and weak. The legs ae known

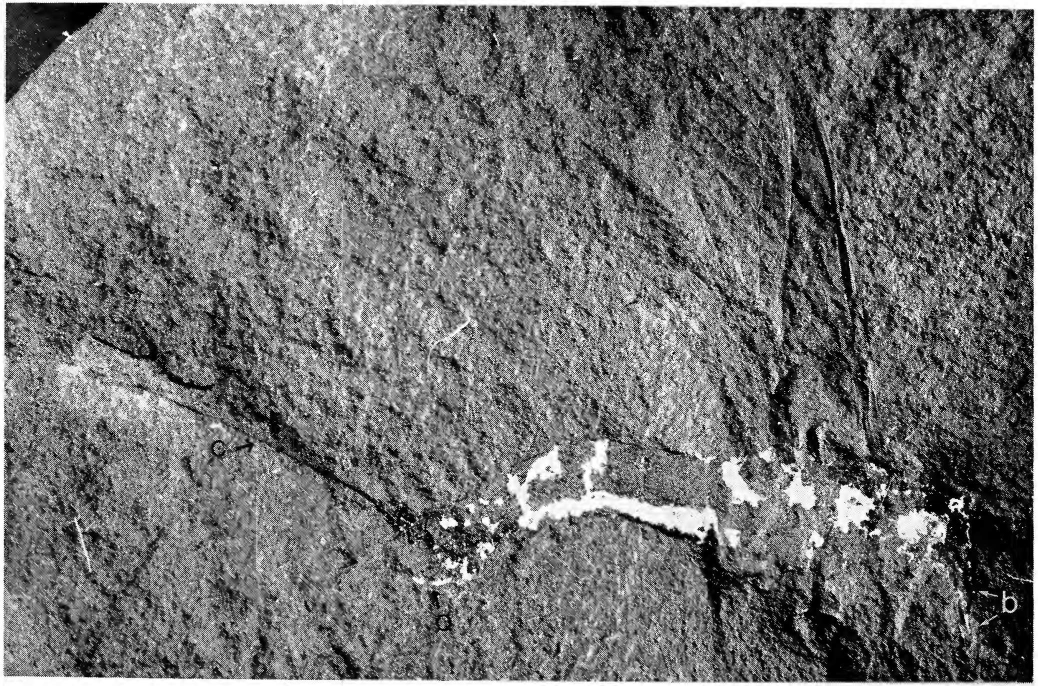

Figure 7. *Eubleptus danielsi*. Photograph of specimen PE22016. Lateral view: b, beak; c, cerci; o, ovipositor. Length of ovipositor as preserved, 10 mm.

only from a single fore leg in Wolff 229; the preserved part, apparently consisting of the femur, tibia, and tarsus, has a total length of 3.5 mm; the tarsus appears to have five subequal segments. The wing venation, as previously noted, shows only a slight amount of variation among the 17 specimens examined. The shape of the wings is more diverse, but that has undoubtedly been determined to some extent by the process of preservation and the amount of movement of the sediment in which the specimens were entombed. The degree of variation in wing shape in the specimens of *danielsi* seems to be comparable with that reported by Kukalová-Peck (1971) for the Permian *Dunbaria fasciipennis*. The wing markings, consisting of four triangular spots along the anterior margins of both wings, are similar in both specimens in which they are preserved (PH15 and PE32046).

Abdomen. The segmentation of the abdomen is nearly homonomous, except for the 9th and 10th segments, which are slightly smaller than the others. The lateral margins of the tergites are extended posteriorly only slightly (YPM18), about as in the Spilapteridae. The ovipositor, preserved only in PE22016, is strongly curved and only 2.5 mm long, not extending beyond the end of the abdomen. The cerci (PE22016, and PE32036) are preserved to a maximum length of 10 mm, but since they end at the edge of the concretion, that is almost certainly not their full length. Segmentation of the cerci is clear at intervals; the segments are .3 mm long (beyond the basal segments) and .3 mm wide, and covered with short hairs. The largest piece of a cercus includes about 34 segments.

Relationships of *Eubleptus*

Study of the new specimens of *Eubleptus danielsi* provides no evidence to justify the recognition of the order Eubleptidodea. On the contrary, all the evidence supports Handlirsch's assignment of the family Eubleptidae to the Palaeodictyoptera. Furthermore, both the wing venation and the newly acquired knowledge of the body structure of *Eubleptus* show a close relationship to the family Spilapteridae of the Palaeodictyoptera. The wings of *Eubleptus* have the same general shape as those of the spilapterids, the hind wings being slightly broader than the fore wings. The only significant difference between the venational patterns of the two families is the reduction of CUA in the family Eubleptidae: it has only a small

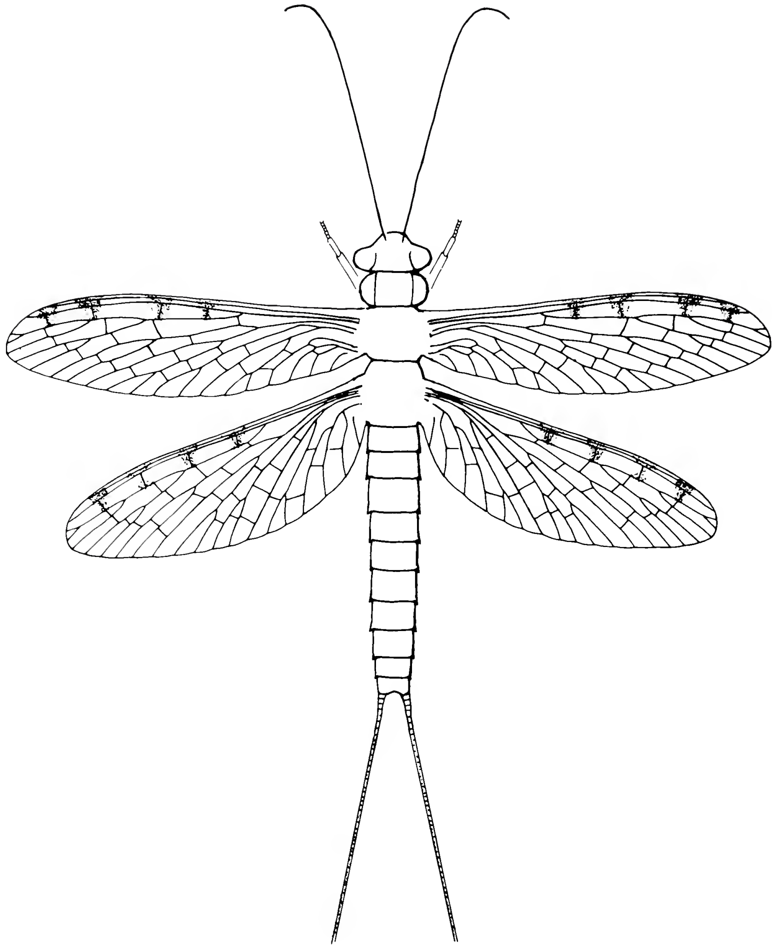

Figure 8. *Eubleptus danielsi*. Reconstruction based mainly on specimen PH15, in the Paul Harris collection, with some details from specimens PE32046,PE32245, PE22016, YPM18, USNM35576,FTWolff 229 and 233, HTP 422, and Bandringa 66-PBSM. All structures shown are preserved in at least one of these fossils. Length of fore wing, 13 mm.

terminal fork, whereas in the spilapterids CUA has several long branches. This difference serves to justify the separation of *Eubleptus* into its own family, but does not have any significance at the ordinal level. The body structure of *Eubleptus* turns out to be very similar to that of the spilapterids. The pronotal lobes are small in both, the beaks are relatively small and of similar shape in both, the legs (so far as they are known) are short in both, and the ovipositors are similarly formed. *Eubleptus danielsi* is the smallest known species in the Palaeodictyoptera, but it is not much smaller than the Permian *Dunbaria fasciipennis* of the family Spilapteridae.

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THE BIOLOGY OF *TRICHADENOTECNUM ALEXANDERAE* SOMMERMAN (PSOCOPTERA: PSOCIDAE). III. ANALYSIS OF MATING BEHAVIOR

By B. W. Betz[1]

Introduction

Several authors have described mating behavior in species of Psocoptera (Pearman 1928, Sommerman 1943a, 1943b, 1944, 1956, Badonnel 1951, Thornton and Broadhead 1954, Klier 1956, Mockford 1957, 1977, Broadhead 1961, Eertmoed 1966). Only one or at most a few matings in a species were observed. This paper presents a comprehensive analysis of pre- through post-copulatory behavior in *Trichadenotecnum alexanderae* Sommerman. Evidence is presented for a sex-attractant pheromone, produced only by females that were receptive to mating.

Trichadenotecnum alexanderae is a relatively common psocid in eastern United States (Betz 1983a). The species inhabits trees and rock outcroppings providing its principal food source, pleurococcine algae. Betz (1983a) found that *T. alexanderae* is capable of facultative thelytoky. Formerly, the species was confused morphologically with three other species, all obligatorily thelytokous, which have been identified and described as *T. castum* Betz, *T. merum* Betz, and *T. innuptum* Betz (Betz 1983a).

This paper is part of a series (cf. Betz 1983b, c, d) detailing the life history of *T. alexanderae*.

Materials and Methods

Cultures of *T. alexanderae* were obtained from three populations in Illinois: at Moraine View State Park (McLean County), along the Sangamon River at Lake of the Woods (Champaign County), and along the Salt Fork River at Champaign County Forest Preserve District—Homer Lake (Champaign County).

Specimens were collected from tree trunks with an aspirator and kept with pieces of bark in cotton-stoppered test tubes. Cultures were transported to the laboratory over ice-water in a cooler.

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Laboratory cultures were kept in cotton-stoppered test tubes. Each tube was supplied ad libitum with food in the form of pleurococcine algae on bark. Culture tubes were stored in closed, glass desiccator jars over a saturated potassium chloride (KCl) solution to maintain a relative humidity of 80 ±5%. The temperature regimen for rearing was 23.3°:18.0° C light:dark, and the photoperiod was 15 h light:9 h dark. Illumination was 4300 lumens/m², supplied by incandescent and fluorescent lamps.

Because the other species of the *T. alexanderae* complex are obligatorily thelytokous and often occur sympatrically with the biparental species, I began a laboratory culture of *T. alexanderae* from each locality with females mated in the laboratory to assure the identity of the culture as the biparental species. Several breeding pairs were used to begin a culture, an attempt to represent the genetic diversity of the original sample from the field population. I also examined the morphology of the original breeding pairs to verify that they were *T. alexanderae*. I used bark obtained only from the original field locality in cultures; bark was examined for eggs before it was placed in a culture.

Mating behavior was studied in adults from Lake Dawson, Lake of the Woods, and Salt Fork cultures. Adults were isolated as late stage nymphs and reared in shell vials (four dram size). Each vial was supplied with a flat piece of bark which lessened the interference of the substrate on mating behavior. Females were 2–3 days old and males were 2–5 days old when brought together, the times when they were the most receptive to mating (Betz 1983c). Isolated specimens were brought together by the following method. The cotton stopper on each vial was removed, the open ends of pairs of vials were apposed, and the vials were tilted carefully until the piece of bark in the vial containing a male contacted the bark in the vial containing a female. The open ends of pairs of vials were kept together and the vials were not moved during observation of the insects. The method I used to bring together isolated specimens did not appear to disturb the insects greatly, and thus probably provided accurate observations of courtship behavior.

RESULTS

Precopulatory Behavior

The behavior of male and female *T. alexanderae* was somewhat variable among the successful matings (N = 99) and the unsuccessful attempts (N = 45) I observed. Most precopulatory behavior followed the patterns outlined in Figure 1.

When bark bearing an isolated, receptive female was brought together with bark bearing a sexually active male, the male always ran onto the female's bark. A male displayed a higher level of activity under these conditions than if his piece of bark was brought together with bark bearing a nymph, a female of *T. alexanderae* in an unreceptive state, or a piece of bark without an insect (N = 7). In five of the mating encounters I observed, the male flew onto the female's bark before the two pieces of bark were touching.

This higher level of activity in males occurred even if females were placed out of the males' sight. Almost immediately after a male ran onto the bark of a female, he began a search over the substrate. Sometimes a female remained motionless during this search, even though she might have been active prior to the introduction of a male. The manner in which males elicited this reaction of females remains unknown, although the reaction may have resulted from the slight disturbance caused by the introduction of pieces of bark into the females' vials.

A male searched in the direction of a female, often stopping momentarily to flick his antennae and adjust his course.

When a male approached within about 1 cm of a receptive female he began a quick, sideways gait while moving toward her, even though she may have remained hidden from the male's view. The sideways gait lasted about 1–2 seconds. Occasionally a male approached a receptive female, or courted her, without the sideways gait (N = 12). Females always fled from these encounters. When a female fled, a male remained in the vicinity of the encounter and spun completely around one or more times flicking his antennae. Then a male usually ran off in the general direction of a female's flight. Unless unsuccessful courtship occurred many times (usually the result of a male not performing the sideways gait), a female would always acquiesce at the next courting.

After performing the sideways gait, a male ran up to a female's side, about midway along her length; a male approached a female almost perpendicularly from her side. If features on the substrate made a male's approach difficult, his contact with a female was as perpendicular to her as the substrate permitted. When a male ran up to a female, he touched her briefly (less than a second) with both his antennae. A male's antennae usually struck a female's thorax or head and the distal end of her forewing because his antennae were

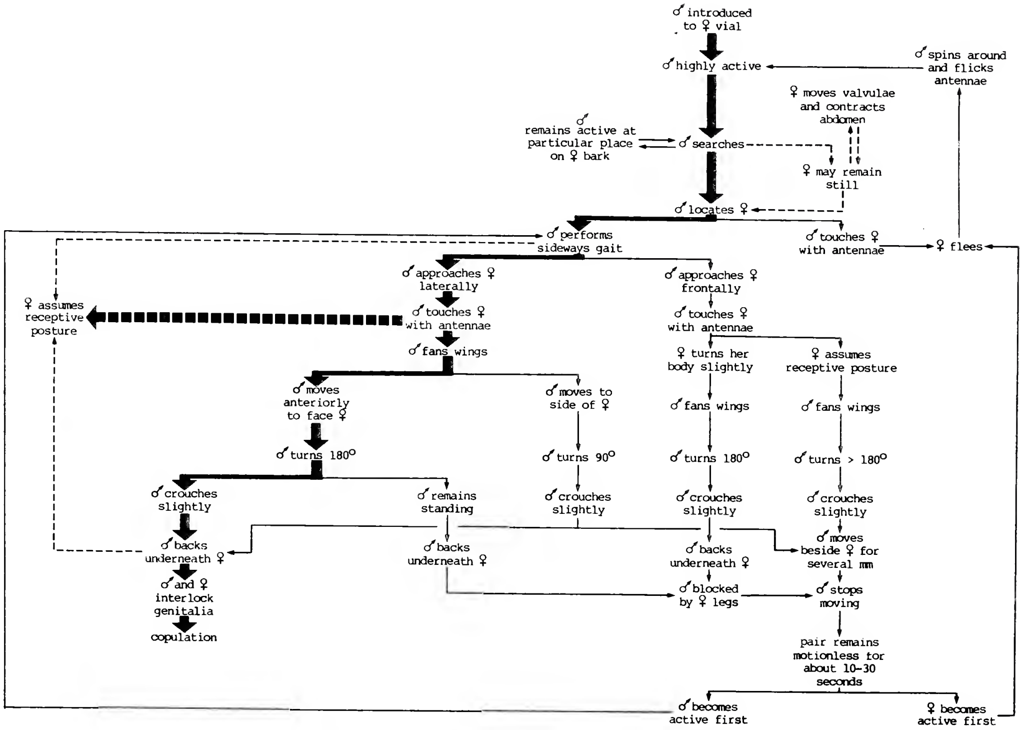

Figure 1. Schematic diagram depicting precopulatory behavior in *Trichadenotecnum alexanderae*. Typical behavior is indicated by bold face arrows. Female behavior coinciding with male behavior is indicated by dashed arrows.

usually held about 90° apart and at about 45° off the substrate at rest and also during the search for a female. Directly after contacting her, a male backed away slightly, then rapidly fanned his wings over his body. The wings were fanned at such a rapid rate and at such a small angle (never more than 90°) that they became blurred. As a male continued to fan his wings, he began to move anteriorly along a female's side, while still remaining perpendicular to her. A male continued this motion until he was almost facing a female. When this occurred, a male stopped fanning, dropped his wings slightly, turned about 180°, and backed underneath a female between her legs. The genitalia were apposed in this manner.

Occasionally a male stopped fanning when he was only laterally apposed to a female's head, then turned about 90°, and tried to back under her. Of the 14 mounting attempts I observed progressing in this way, only two of them led directly to copulation. Of the failed attempts, eight were unsuccessful because males were blocked from backing in by females' legs; in the remaining four attempts, males turned around farther than necessary and kept moving backward beside the females rather than beneath them.

When a female remained hidden from a male's view, he sometimes approached her directly from the front ($N = 3$). In two encounters, the female assumed the receptive posture (see below) as the male fanned his wings. However, both of these males were unable to locate the female after they turned around and began to move backwards. One of the males approached the female on her left, turned counterclockwise about 240°, and finally stopped after moving 8 mm away from her. He then tried to mount her end-to-end (i.e., facing away from her), but this failed. The pair remained motionless in the end-to-end position for about 30 seconds with their genitalia nearly touching, then the male courted the female from her side and was able to orient himself correctly.

The male of the third encounter courted frontally, but the female turned her body slightly instead of assuming the receptive posture, and the male was unable to move far enough backward for their genitalia to come together. The courtship did not lead to copulation.

Most (73.7%) courting attempts were successful on the first try (Table 1, A). When an attempted mounting failed, a male and female always remained motionless for about 10–30 seconds. After this period, if a male and female remained within about 1 cm after

Table 1. Precopulatory behavior in *Trichadenotecnum alexanderae*

		% of Total
A. Number of courting attempts by a male (including the one leading to copulation)	1. One	73.7
	2. Two	15.2
	3. Three	10.1
	4. Four	0.0
	5. Five	1.0
	N=99[a]	100.0
B. Length of time between the introduction of a male and the beginning of mating (i.e., genitalic contact)	$\bar{x}$	1.1 minutes
	s.d.	1.3
	range	0.1–9.0 minutes
	N	62
C. Stage in courtship when a female assumed the receptive posture		
1. During the approach of a male		15.6
2. When touched by a male's antennae		83.3
3. Just before a male backed underneath		1.1
N=96		100.0

[a] The number of mating pairs for which the states of this behavioral character were recorded.

they separated, a male courted again by approaching a female on her side, touching her with his antennae, and fanning his wings. Once either sex had fled from an unsuccessful courtship. males always began further courtship with a sideways gait.

I observed the behavior of females that had fled from a failed courtship (N = 4). Each female eventually stopped moving, and at this time I observed each female flexing her valvulae dorsoventrally in a pairwise manner, and making about ten contractions of her abdomen.

The time required by males to establish genitalic contact after they were introduced to females varied among mating encounters (Table 1, B). This period was usually less than 1 minute if the first courtship was successful. A male ran directly to a female in some encounters, and the time between introduction and the beginning of copulation was usually less than 30 seconds. Some males (N = 5) were slower to find females because each remained within a small area on a female's bark. Even though a female was not nearby, three males exhibited sideways gaiting, wing fanning, and backward movement, while two others only displayed a higher level of activity. All five males were active, and each found a female about 10 minutes after introduction to the female's bark.

A female had to raise the anterior part of her body for a male to be able to fit beneath her. Females always assumed a characteristic appearance for this purpose that I here term the receptive posture. In the receptive posture, the fore- and midlegs were moderately extended, the hindlegs were slightly extended, and the antennae were swept back along a female's body (Fig. 2b). Most (83.3%) females assumed the receptive posture when males touched them with their antennae (Table 1, C). Some (15.6%) females assumed the receptive posture when males performed the sideways gait. One female waited until a male was backing underneath her.

Females assuming the receptive posture early in courtship (i.e., before antennal contact was made by a male) elicited less wing fanning from males. Males exhibited all of the actions involved in courtship, but performed them more rapidly. On the other hand, the female not assuming the receptive posture until a male began to move beneath her did not appear to inhibit the male from courting normally.

After a courtship failed, a male often fanned his wings around a female for a longer period of time during the next one, regardless of whether a female assumed the receptive posture when a male was approaching or courting ($N = 10$). These prolonged courtships always led to copulation.

A male had to crouch slightly just prior to moving beneath a female, even though she had assumed the receptive posture. This position is shown in Figure 2a. Males remaining in a standing position were blocked from moving past the coxae of the females' legs ($N = 2$). Furthermore, at this time a male's abdomen became slightly arched along its length, raising the posterior end.

A male's wings were kept extended over his body as he backed underneath a female, and she rested her fore- and midlegs on him. When the genitalia of a pair were apposed, the head of a female was positioned between and slightly caudad of a male's raised hindwings.

As a male moved under a female, the shelf of his epiproct, which normally rested in a posterodorsal position, struck a female's sterna

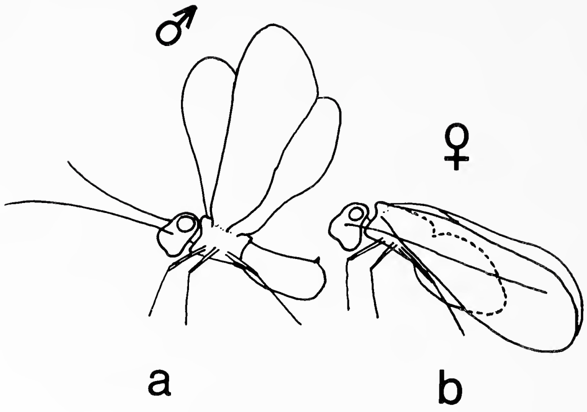

Figure 2. Typical precopulatory behavior in *Trichadenotecnum alexanderae*. a. A male in position to move beneath a female. b. The receptive posture of a female.

and was brought anteriorly. This flattened the shelf against the male's abdominal terga, and caused his paraprocts to extend slightly posteriorly. When fully beneath a female, a male's epiproctal shelf was brought into apposition with the basal arms of a female's subgenital plate and the sterna of her posterior abdomen.

I studied how males orient themselves with females to produce a successful mounting. Individual females (N = 18) that had been freshly killed (by pressure from a forceps) from a Lake of the Woods culture were placed in a standing position on the substrate. Males always courted and mounted the females without losing orientation (N = 5). When I reoriented a female while a male was turning around after touching her with his antennae, he did not reorient to mount successfully (N = 3). If a female was moved as a male approached (that is, prior to antennal contact), a male was always able to orient and mount in the proper direction (N = 10). Hence, antennal contact by males appeared to be important for a successful mounting.

When I placed a teneral male with a receptive female (N = 1), he ran to her, paused briefly at her side, but then did not exhibit any other courting behavior (e.g., antennal contact, wing fanning, etc.). Instead, he repeatedly climbed over her for about 10 seconds until she fled. The male made no attempt to mount, and the female did not assume the receptive posture.

Copulatory Behavior

When a male was fully beneath a female, the posterior end of his abdomen probed for hers. The valvulae of a female dropped ventrally somewhat, and moved until contact was made with a male. The genitalia of male and female *T. alexanderae* interlocked strongly together during copulation.

When their genitalia became locked, a male lifted a female off the substrate by extending his legs, which were still crouched from backing beneath her.

A normal copulatory position for a pair of *T. alexanderae* is shown in Figure 3. The hind legs of most (67.8%) males were extended slightly more than the other pairs of legs, causing a male's head to be lowered, and raising and slightly arching his abdomen (Table 2, A). Males greatly extending their hindlegs usually also had greatly arched abdomens; males extending all pairs of legs about

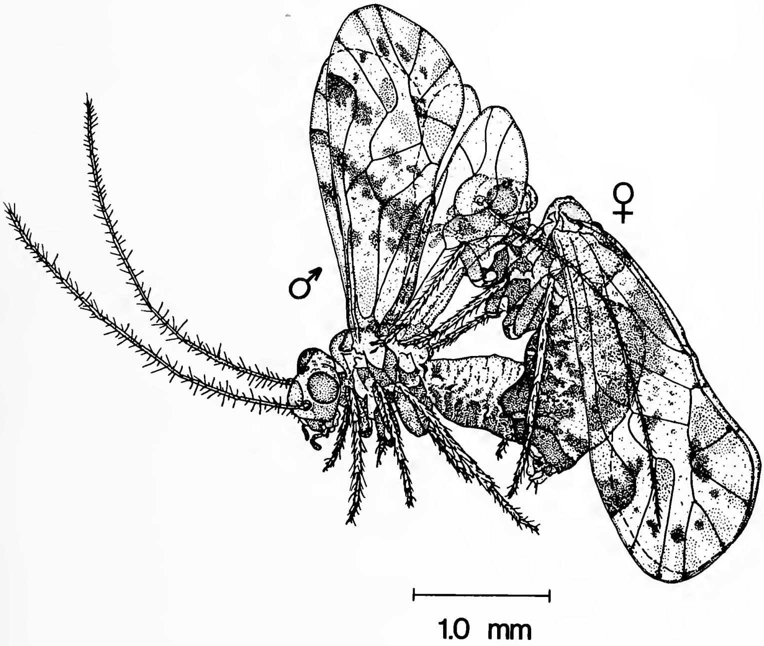

Figure 3. *Trichadenotecnum alexanderae* in copulation.

equally had no abdominal arch. Because the degree of abdominal arching and the extension of the legs compensated for each other, the overall position of a male, and thus the relative positions of a male and female, generally differed little among the matings I observed. A male's abdomen became slightly more arched and his head dropped lower as copulation progressed. Some males lowered their heads so much during copulation that their maxillary palps touched the substrate.

After a female was raised off the substrate, a male's abdomen contracted more or less rhythmically. A female contracted her abdomen in synchrony with a male. Her paraprocts were periodically flexed medially during copulation.

At the beginning of copulation, the wing pairs of a male were usually extended high over his body, forming a small angle between them (Table 2, B). As copulation progressed, the angle formed by the wing pairs increased; the angle of the wings at the end of copulation was about 60° greater (Table 2, C). I found 45.7% of all males had both wing pairs locked at the nodus (Table 2, D). Wing pairs remaining free were in a position as though they were locked, and thus did not interfere with copulation.

Table 2 (E and F) shows that a male's antennae generally remained in a normal resting position during copulation.

A female was lifted off the substrate until the angle formed by her body and the substrate was about 31°–60° (Table 2, G). Females whose bodies inclined more than 60° (7.4%) had been pushed up into this position when males mounted beneath them.

A female placed her fore- and midlegs on a male when he moved beneath her. Table 2 (H and I) shows the distribution of the placement of a female's fore- and midlegs, respectively. Most (41.3%) forelegs were placed on males' hindwings and most (50.0%) midlegs were placed on males' anterior abdominal pleura. However, as reflected in Table 2, the first two pairs of legs were positioned in many other ways.

Table 2 (J) shows the distribution of the placement of a female's hindlegs. Most (93.3%) females kept their hindlegs on the substrate. The rigidity of the hindlegs indicated that they were supporting some of a female's weight.

The forewing tips rested lightly on the substrate in 84.8% of the females (Table 2, K). This contact did not appear to support much of a female's weight.

Table 2. Copulatory behavior in *Trichadenotecnum alexanderae*

Position of a male		% of Total
A. Extent of the arch of the abdomen	1. Not arched	21.9
	2. Slightly arched	67.8
	3. Greatly arched	10.3
	N=87	100.0
B. Angle formed by the forewings at the beginning of mating	1. 0°–30°	52.3
	2. 31°–60°	38.5
	3. 61°–90°	6.1
	4. 91°–120°	3.1
	N=65	100.0
C. Angle formed by the forewings at the end of mating	1. 0°–30°	5.6
	2. 31°–60°	11.1
	3. 61°–90°	37.0
	4. 91°–120°	40.7
	5. 121°–150°	0.0
	6. 151°–180°	3.7
	7. 181°–210°	1.9
	N=54	100.0
D. Number of wing pairs locked at the nodus	1. None	35.7
	2. One	18.6
	3. Both	45.7
	N=70	100.0
E. Angle formed by the antennae	1. 0°–30°	5.2
	2. 31°–60°	32.8
	3. 61°–90°	56.9
	4. 91°–120°	3.4
	5. 121°–150°	0.0
	6. 151°–180°	1.7
	N=58	100.0
F. Angle formed by the antennae and the bark substrate	1. 0°–30°	40.5
	2. 31°–60°	59.5
	N=74	100.0

Table 2. (continued)

Position of a female		% of Total
G. Angle formed by the body of a female and the bark substrate	1. 0°-30°	1.90
	2. 31°-60°	90.7
	3. 61°-90°	7.4
	N=54	100.0
H. Placement of a foreleg on a male	1. Forewing	5.6
	2. Base of forewing	29.1
	3. Hindwing	41.3
	4. Base of hindwing	3.1
	5. Metanotum	8.7
	6. Anterior abdominal terga	6.6
	7. Anterior abdominal pleura	4.6
	8. Hind tibia	1.0
	N=196[a]	100.0
I. Placement of a midleg on a male	1. Hindwing	3.7
	2. Hindwing base	3.1
	3. Metanotum	17.7
	4. Anterior abdominal terga	6.3
	5. Anterior abdominal pleura	50.0
	6. Anterior abdominal sterna	0.5
	7. Hind tibia	13.5
	8. Hind femur	0.5
	9. Bark substrate	4.7
	N=192[a]	100.0
J. Placement of a hindleg on a male	1. Anterior abdominal pleura	1.0
	2. Anterior abdominal sterna	0.5
	3. Hind tibia	5.2
	4. Bark substrate	93.3
	N=194[a]	100.0

Table 2. (continued)

		% of Total
Position of a female		
K. Position of the forewing tips	1. On the bark substrate	84.8
	2. In the air	15.2
	N=92	100.0
L. Angle formed by the antennae	1. 0°–30°	25.0
	2. 31°–60°	51.7
	3. 61°–90°	18.3
	4. 91°–120°	5.0
	N=60	100.0
M. Angle formed by the antennae and the bark substrate	1. 0°–30°	88.3
	2. 31°–60°	11.7
	N=60	100.0
General Features		
N. Relative positions of a male and female	1. Both in-line	55.3
	2. Female skewed right or left	44.7
	N=47	100.0
O. Duration of copulation	$\bar{x}$	14.3 minutes
	s.d.	2.2
	range	8.3–19.9 minutes
	N	99

[a] Recorded for both legs.

In contrast to the position of a male's antennae, a female's antennae were swept back along her body when she assumed the receptive posture. Usually the antennae were held close to her sides, and the angle formed by the antennae was between 31°–60° (Table 2, L). Most (88.3%) antennal pairs were slightly raised from the substrate (Table 2, M).

Copulation did not always proceed uneventfully. The number of positions among the pairs reflects the incidence of minor problems that were encountered during mating. The conformations occurring with lower frequency were usually the result of some difficulty during copulation. The relative positioning of a male and female (Table 2, N) generally indicates whether a problem occurred during copulation. If the bodies of a male and female were in-line, copulation usually had proceeded normally. A female was skewed left or right in 44.7% of the matings. Some of the complications that occurred during mating are discussed below.

Sometimes a male lifted a female far off the substrate, so her head was almost over his. Other males pushed females backward during mounting, then locked genitalia, causing females to be inclined almost vertically and males to have greatly arched abdomens. When events such as these occurred, the positioning of a pair, especially a female's legs, changed to maintain her balance. For example, the hindlegs of a female typically rested on the substrate. However, when a male lifted a female relatively far off the substrate, copulation proceeded with more stability when her hindlegs were placed on a male's abdomen. When a male's abdominal contractions increased to an amplitude that caused his hindwings to strike a female on the head, she placed one (N = 8) or both (N = 3) forelegs about midway up on a male's fore- or hindwings. This response lessened the force of a male's contractions. Sometimes a mating pair fell on their sides (N = 3), but their genitalia remained locked. These pairs never regained a normal copulatory position, yet they did not break off copulation because of this problem.

Except for the abdominal contractions and adjustments for stability, other movements by a mating pair were uncommon. Occasionally the maxillary palps of a male or a female moved or pulsed rapidly.

I observed courtship and mating on a vertical bark substrate in the laboratory (N = 3). When a male courted a female, she oriented herself so her head faced downward, then she assumed the receptive posture. A male lifted a female off a vertical substrate during copulation. A female was positioned dorsally and posteriorly on a male, similar to mating on a horizontal surface, but in a vertical orientation a female balanced directly above a male. On a vertical substrate the fore- and midlegs appeared to have supported more of a female's weight.

The duration of copulation varied considerably (Table 2, O), although it was never less than eight or more than 20 minutes.

Postcopulatory Behavior

The final stage of copulation was indicated by a slowing of the rate of abdominal contractions and by contractions of a slightly more spasmodic nature. Males suddenly became active and broke off copulation (Table 3, A) by quickly running forward, dragging along the females for about 1 second until their genitalia unlocked. Of the 60 pairs I observed for this behavioral character, only two females (3.3%) appeared to break off copulation. In each of these matings, the female became active during copulation and tried to dismount laterally, but her genitalia were locked with the male's and this caused her to fall on her side. One female successfully dismounted, thus terminating copulation. The other female failed to dismount, and instead tried to assume a normal mating position three times, but because the genitalia were locked she was kept off-balance. Copulation continued with the female supported tenuously off a side of the male.

A spermatophore was passed in all copulations, including the one broken off by a female.

Table 3 (B) shows the reactions of males after copulation was broken off. Most (53.5%) males ran forward about 1 cm, then remained motionless for at least 5 minutes. Some of these males had their wings parted slightly and held laterally along their bodies, but most males brought the wings back to a normal resting position. Some (28.2%) males were highly active after copulation, and ran over the substrate without stopping for over 5 minutes. Other (12.7%) males broke off copulation and remained almost at the place where copulation occurred. A few (5.6%) males courted the females they had just mated, but this always caused the females to flee.

The reactions of females after copulation (Table 3, C) were somewhat different than those of males. Most (60.0%) females remained in the area where copulation occurred; almost all of these females spun around about 90°, some females spun around about 180°. If a female ran off, she usually ran in the direction of a male because both faced in the same direction during mating. Females that ran, even for 1 cm, never spun around more than 90°.

Unless disturbed by another insect, once females stopped walking after mating they rarely moved until the contents of the spermatophore that they held had been transferred. Even the antennae did

Table 3. Postcopulatory behavior in *Trichadenotecnum alexanderae*

		% of Total
A. Identity of the sex breaking off copulation	1. Male	96.7
	2. Female	3.3
	N=60	100.0
B. Reaction of a male after copulation was broken off	1. Ran off (> 1 cm)	28.2
	2. Ran about 1 cm, then remained still	53.5
	3. Stayed in the area where mating occurred	12.7
	4. Tried to court the female again	5.6
	N=71	100.0
C. Reaction of a female after copulation was broken off	1. Ran off (> 1 cm)	8.6
	2. Ran about 1 cm, then remained still	31.4
	3. Stayed in the area where mating occurred	60.0
	N=70	100.0

not change position during this time. Only one of three postcopulatory females I observed at length changed her location once, about 2 minutes after copulation, but did not move after this.

Initially, a spermatophore had an appearance of a whitish, semi-opaque, hemispherical droplet, protruding between the terminalia of a female. A female manipulated her terminalia so its contents passed her genital opening. When it was first visible on a female, a spermatophore seemed adhesive and somewhat fluid in shape, allowing it to be manipulated on a female's terminalia. During the transfer of its contents, a spermatophore covering seemed to lose adhesiveness and harden, allowing a female to dispose of it easily.

A female manipulated a spermatophore between her paraprocts and valvulae. These movements were accomplished by a rhythmical, medial flexion of the terminalia. Contractions were spaced about 1–2 seconds apart, and each contraction lasted about 1–2 seconds. The epiproct was less active in this respect; it was flexed once about every 30 seconds. Epiproctal flexion probably forced the contents of a spermatophore into a female's genital area. The abdominal contractions were pronounced for about the first 4–5 minutes after copulation, then slowly decreased in rate and intensity.

The females I observed (N = 3) required about 10–25 minutes to transfer the contents of a spermatophore and discard it. A spermatophore either fell from a female's genital area when she ran (N = 2), or a female dragged the posterior end of her abdomen along the substrate for about 1 mm to discard it (N = 1). A female sometimes intermittently flexed her terminalia after a spermatophore had been discarded.

Evidence for a Sex-attractant Pheromone

The following observations present evidence indicating that the attraction of males to females of *T. alexanderae* was mediated by a pheromone. All females discussed here were unmated, receptive females from cultures of all three field localities unless noted otherwise.

Males introduced to bark bearing receptive females often became more active than when they were introduced to pieces of bark which had no exposure to receptive females. Some males became so active they flew across the gap between the pieces of bark before I could join these together. A male was usually able to find a receptive female, even though she may have remained hidden from his view. Additionally, males would court females of *T. castum* and *T. merum,* two obligatorily thelytokous species of the *T. alexanderae* species complex, if vials containing these females had previously contained receptive females of *T. alexanderae* (Betz 1983a).

Females of *T. alexanderae* which had just mated ceased rapidly to be a source of attraction to males, although males occasionally tried to court females engaged in mating. Teneral females, or females in the stage of oviposition, failed to attract males (Betz 1983c).

In one mating encounter involving a male and female from a Lake of the Woods culture, when the male was introduced into a vial containing the female, she deposited a clear droplet from her genital area on the bark. The droplet was absorbed rapidly. The male was highly active and quickly found the female, who was still in the area where she deposited the droplet, and mated with her. In another encounter, the female deposited a droplet about 3 minutes after a failed courtship attempt. This pair mated eventually. Another female intermittently dragged the tip of her abdomen over the substrate after the male was introduced into her vial. In two encounters, each involving a male and female from a Lake of the Woods culture, two from a Lake Dawson culture, and one from a Salt Fork culture, the male persistently courted a particular place on the female's substrate, even though she was not nearby. Eventually, after about 10 minutes, males stopped courting these areas.

I have not observed females of *T. castum* or *T. merum* depositing any type of droplet in the above manner, or observed males courting places on a substrate bearing females of *T. castum* or *T. merum.*

In the orientation experiment, it was important to use freshly killed females because after about 5 minutes they lost attractiveness to males. Anesthetizing females with ether ($N = 3$) or carbon dioxide (from dry ice) ($N = 3$) caused an immediate loss of interest by males.

From the evidence cited above it appears the females of *T. alexanderae* produce a pheromone that attracts males. It appeared to be highly volatile; a loss of mating receptivity in a female was almost immediately evident, as indicated by the lack of attractiveness to males.

The area around a female in which the pheromone was effective in attracting males was rather small, having a radius of about 1 cm. I determined this by placing individual receptive females ($N = 10$) in uncovered petri dishes (standard size), then introducing sexually active males.

DISCUSSION

Mating behavior in *T. alexanderae* followed a pattern outlined by Pearman (1928) for "winged Psocids." This courtship pattern, which has since been categorized (Badonnel 1951) and further documented (Klier 1956), is the one found in most species of Psocoptera that have been studied. This pattern differs from those in other species in two details: males do not run over the dorsum of females prior to mounting, and the duration of copulation is relatively long.

A receptive posturing by females has been noted in several other species of Psocoptera (Pearman 1928, Sommerman 1943a, 1956, Schneider 1955, Broadhead 1961). Apparently only females of *T. alexanderae* have been observed assuming the receptive posture before males began backing underneath them.

The receptive posture appeared necessary only to permit males to fit beneath females during mating. Lifting the anterior end of a female's body did not communicate a female's orientation to a male. Males courting one of the freshly-killed females always moved anteriorly along her body, even though she was not in the receptive posture. However, the contact made by a male's antennae after the sideways gait probably was important in discovering how a female was oriented because a male was unable to adjust his course to find a reoriented female after antennal contact was made. Also, males that had difficulty moving beneath females began the next courtship with wing fanning, but males not contacting females recourted with a sideways gait and antennal contact. A differential concentration of pheromone along a female's body may have informed a male of her orientation. A perpendicular approach to a female allowed maximum extension of a male's antennae along her body, thus perhaps facilitating a determination of her relative position.

I found that the receptive posture was assumed by some females of *T. alexanderae* when males approaching to court began a sideways gait. Largely auditory cues, rather than visual ones, were probably given by a male to signal his approach, thereby eliciting the receptive posture in a female. The sideways gait may cause stridulation of a male's Pearman's organs because a male approaching a female in this way never caused her to flee, even though he may have remained hidden from her view during the sideways gait.

The purpose of the females' genital movements and abdominal contractions after failed courtship is unknown. These motions were only observed in females involved in some phase of the mating process. Perhaps this action released more pheromone to attract males again.

The role of the droplets (apparently containing pheromone) which were deposited by females is also uncertain. This behavior would assist a male in locating a female only if she remained in the area where a droplet was deposited. Because the pheromone appears to be highly volatile, to have any effect on males a female probably must deposit many of these droplets during her receptive period.

The epiproctal shelf of a male played an important role during mating in *T. alexanderae:* the shelf and a female's hindlegs on the substrate supported almost all of a female's weight. A male's epiproctal shelf and the basal arms of the subgenital plate of a female are structures apparently functioning to distribute her weight because both structures are well-sclerotized and have large surface areas.

The support given by the epiproctal shelf and the interlocking genitalia apparently increased the lateral stability of a mating pair. This can be adduced in the following observations. A mating pair had greater stability during copulation than when a male had backed fully beneath a female but before their genitalia had interlocked. Also, it was difficult for a mating pair to fall over to one side when problems in stability occurred during copulation, although once they fell regaining a normal mating position was impossible. The stability supplied by the contact between the epiproctal shelf-subgenital plate and posterior abdominal sterna, the positioning of a female's legs, and the interlocking genitalia probably also expedited the lifting of a female by a male, although the reason for the necessity of lifting a female is unknown.

ACKNOWLEDGEMENTS

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SUMMARY

Pre- through postcopulatory behavior in *Trichadenotecnum alexanderae* Sommerman is here quantified and discussed. Mating behavior follows a pattern described for many other species of Psocoptera, in which a male approaches a female, fans his wings over his head, and backs underneath her without running over her dorsum. Additional behavioral actions, including possible stridulation and antennal contact of a female by a male and a female assuming a receptive posture prior to mounting by a male, are believed to promote copulation. Evidence is presented for a sex-attractant pheromone produced by receptive females.

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PREDATORY CAPTURE OF BOMBARDIER BEETLES BY A TABANID FLY LARVA*

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While collecting bombardier beetles (*Brachinus* spp.) on the evening of August 27, 1982, by a pond near Portal, Cochise County, Arizona, a group of us, including Rodger Jackman of the British Broadcasting Corporation and Maria Eisner, came upon an unusual phenomenon. Thousands of young adults of the spadefoot toad, *Scaphiopus multiplicatus*, were active beside the pond on that night, having just emerged from the water after metamorphosis. On close observation we noted a number of these toads that were dead or dying and in various stages of partial submergence in the mud. Each had been grasped from beneath by a larva of the horsefly *Tabanus punctifer*, a mud-dwelling predator, which had seized it with its hooked mouthparts, had pulled it partly into the substrate, and was embibing its body fluids. Details of this first known occurrence of predation by a fly larva on an adult amphibian will be published elsewhere. Our purpose here is to call attention to another extraordinary ability of this larva: the capture of bombardier beetles.

We transported several of the larvae to our Cornell laboratories and established them individually in mud-filled enclosures, where they quickly buried themselves, leaving only their mouthparts exposed at the surface (Fig. 1A). We maintained the larvae on young spadefoot toads, which they captured as they had in the field, and also on insects, which judging from published accounts on tabanid larvae (Webb and Wells, 1924; Oldroyd, 1964; Burger, 1977), must be a principal staple of their diet. They proved capable even of capturing large crickets (*Teleogryllus oceanicus*), which they hooked by a leg, drew partly into the mud, and then held for hours while sucking out their body contents.

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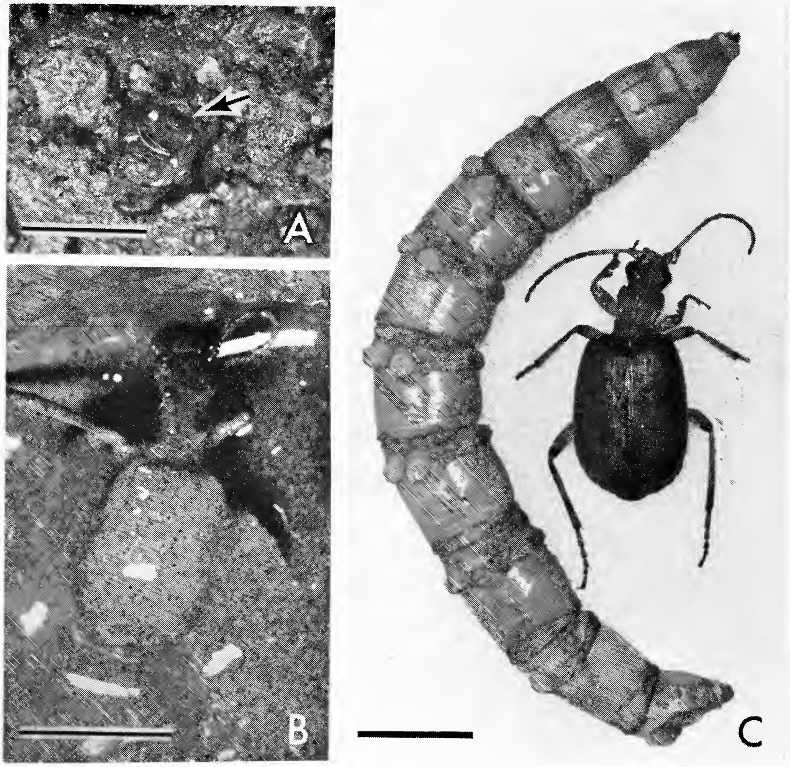

Figure 1. (A) Mouthparts (arrow) of a buried *T. punctifer* larva, projecting just above the surface of the mud, as the animal lies in wait of prey. (B) Bombardier beetle, caught by a submerged larva and partly drawn into the mud, in the process of being eaten (the larvae can also pull beetles into drier mud than here shown). (C) Full grown *T. punctifer* larva beside an average-sized bombardier beetle. Reference bars = 5 mm.

Bombardier beetles are doubtless among the most invulnerable of insects. The quinone-containing spray that they eject from their abdominal defensive glands when attacked is hot (100° C) and is aimed accurately toward the predator by rotation of the abdominal tip (Eisner, 1958; Aneshansley *et al.*, 1969). A number of broadly insectivorous predators have been shown to be repelled by the spray, including ants, spiders, preying mantids, and toads (Eisner, 1958; Eisner and Dean, 1976; Dean, 1980).

We staged encounters between bombardier beetles and *T. punctifer* larvae by releasing the beetles singly onto the mud in the larval enclosures. The beetles all stemmed from the larval collecting site, where they were taken at the very places on the edge of the pond where the larvae were also abundant. In three encounters we were fortunate to witness the beginnings of the attack. The events proceeded quickly and were the same in each case. No sooner had a beetle brought one of its tarsi to rest upon the mouthparts of the larva, than it was grasped by that tarsus and caused to spray. There were sometimes several discharges, audible at times and visible as misty puffs, but the larva, which had withdrawn below the surface the moment it hooked on to the beetle's leg, was already out of reach. The beetle struggled as it was gradually pulled into the mud, but the larva never released its hold. Partly submerged, the beetle eventually died (Fig. 1B), and when retrieved next day was found to be largely eaten out. Five additional encounters that were not witnessed from the outset were equally fatal to the beetles. We assume that the death of the beetles was hastened by the salivary toxins that tabanid larvae are said to inject into their insect prey (Schmidt, 1982).

Given the ecological co-occurrence of *T. punctifer* larvae and bombardier beetles, we feel that encounters between the two must inevitably occur also in nature, with the same outcome as in the laboratory. Moreover, the larvae must have access also to diverse other insects that discharge noxious secretions, includings ants, tiger beetles, and additional Carabidae. Species of *Chlaenius*, for example, whose odor was unmistakably suggestive of the phenolic output that characterizes other beetles of the genus (Eisner *et al.*, 1963), scurried about together with *Brachinus* at our collecting site at night. Against such chemically protected insects, the predatory tactic of lurking just beneath the surface, and of withdrawing into the mud for total cover the moment a victim is seized and caused to activate its defenses, doubtless serves the larvae well. Other mud-dwelling tabanid larvae of similar opportunistic feeding habits might equally profit from the tactic.

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PREY SELECTION BY THE NEOTROPICAL SPIDER *ALPAIDA TUONABO* WITH NOTES ON WEB-SITE TENACITY[1]

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Introduction

Prey selection by web-building spiders includes 2 principle components. First, webs may catch a nonrandom sample of the available prey (passive selection). Among items caught in the web, the spider may then feed on preferred prey but reject unsuitable prey (active selection). As evident from a recent review (Riechert and Luczak 1982), quantitative field measurements of either component are relatively rare and particularly so for tropical species.

Here I compare the web contents of *Alpaida tuonabo* (Chamberlin and Ivie) with sticky trap samples of available prey. Field work was conducted at one site over a relatively short period of time thus reducing potential complications arising from habitat and seasonal differences in prey availability. As Olive (1980) and Uetz et al. (1978) found, however, prey availability may vary over short vertical distances, and to examine this possibility potential prey were sampled at several different heights.

In addition, a second comparison was made between captured items being eaten and those left unattacked and uneaten. Since prey ignored during the day may have been consumed at night with the web, uneaten prey did not necessarily represent rejected prey. This comparison, however, does quantify the probability of immediate attack upon different types and sizes of captured prey.

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[1] While *Araneus* is the accepted generic designation, this species is not closely related to other members of this genus and should perhaps be placed in the genus *Aplaida* (H. Levi pers. comm.).

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MATERIALS AND METHODS

The study was conducted between July 23 and August 25, 1980, on Barro Colorado Island (BCI), Panama. This time period falls near the middle of a rainy season which annually extends from late April to mid-December (Croat 1978). The island is covered by a lowland tropical moist forest (Holdridge et al. 1971). *Alpaida tuonabo* was most abundant on the island's central plateau, and all work was conducted there.

Very little is known about the biology of *A. tuonabo.* A description of the female has been published (Chamberlin and Ivie 1936), but males have not yet been described (H. Levi, pers. comm.). Females are relatively small; the mean wet weight and body length of 8 adult females were 0.023 g (SD 0.005) and 5.6 mm (SD 0.94), respectively. Females appeared to construct and tend webs during the day and consume them at night. In 4 nights of searching, I never saw a female or an intact web. On BCI *A. tuonabo* is abundant only in the mid to late wet season (July to December) and is rarely found during the rest of the year (Lubin 1978).

Flying insects were sampled at 10 different sites. At each site I implanted a 2.7 m PVC pole (diameter 25 mm) by driving 0.30 m — 0.45 m of its length into the ground. Wooden rods (length 30 mm; diameter 5 mm) were then fastened to the pole at 0.3 m intervals (from 0.3 m to 2.1 m above ground). Fastened at one end, each rod projected perpendicularly from the vertical pole and hence was parallel to the ground's surface. Insects were collected on tanglefoot covered traps suspended from the wooden rods. Each trap was a 15 cm by 23 cm rectangle of 3 mm thick transparent plastic coated on both sides with tanglefoot. Insects were sampled during the day only on August 7–9. Each day the traps were set between 0800 hrs–0900 hrs, taken down between 1600 hrs–1700 hrs, and stored overnight in closed boxes. Aside from Diptera and Hymenoptera, all trapped insects were identified to order. Flies were categorized as either nematocerous or non-nematocerous, and hymenopterans were subdivided into bees and wasps, parasitoids, and winged ants. All trapped insects were measured to the nearest 0.1 mm using a dissecting microscope equipped with a disc micrometer.

Each day of the study I walked through different areas of the forest (between 0900–1630 hrs) and examined every web encountered. All caught items were collected and labelled as either eaten or

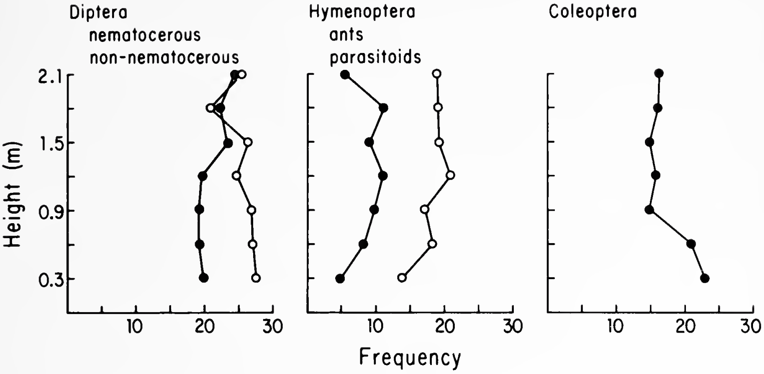

Figure 1. Vertical distributions of the major prey categories. Each value represents the total number of individuals captured on 10 sticky traps suspended at a particular height. See text for details of sampling method.

uneaten. Uneaten prey were also examined for evidence of wrapping. For each web thus sampled, the height of the spider was also recorded. Collected prey were later assigned to the appropriate prey category and measured to the nearest 0.1 mm.

Prey selectivity was quantified using Ivlev's (1961) index of electivity. Electivity (E) is calculated as follows: $E = (r_i - p_i)/(r_i + p_i)$ where r_i is the proportion of the predator's diet represented by prey type (or size class) i, and p_i is the proportion of the available prey represented by prey type (or size class) i. Values of E range from −1.0 (complete avoidance) to +1.0 (complete preference). In this study electivity values with absolute values less than 0.40 were not considered to differ significantly from zero. In addition, two sets of electivity values were calculated. For web selectivity (E_W) r_i is the proportion of the web contents (both eaten and uneaten items) represented by prey type i, and p_i is the proportion of available prey (as measured by the sticky traps) represented by prey type i. For spider selectivity (E_S) r_i is the proportion of the spider's observed diet (the eaten prey) represented by prey type i, and p_i is the proportion of the web contents (both eaten and uneaten items) represented by prey type i.

RESULTS

Alpaida tuonabo females generally constructed webs in relatively open sections of the forest or at the edges of tree-fall gaps. Most web sites were shaded, and only rarely was a web placed in an area that received direct sunlight. Various web support structures were utilized, including leaf tips, herbaceous stems, woody vines and branches, and palm fronds. The circular webs averaged 21.6 cm in diameter and 350 cm^2 in catching area (n = 8).

Individuals do not appear to remain at a particular web-site for more than 1–2 days. On August 3 I marked the location of 20 occupied webs. These sites were then revisited daily for 7 days, and the presence or absence of the spider and the web was recorded. In terms of the number of spiders remaining at their initial site, the results obtained were as follows: Day 1—12; Day 2—3; Days 3 and 4—2; Days 5 and 6—1; Day 7—0. In no instance was a spider absent but the web present; spider and web were always both present or both absent. In addition, in examining a 2 m–3 m radius about each vacated web-site, I never observed the presence of a newly constructed web.

Five prey categories comprised 89.0% of the total sample, and vertical abundance patterns were examined for these groups only. Beetles, parasitoid Hymenoptera, nematocerous and non-nematocerous Diptera all exhibited a similar trend in vertical abundance (Figure 1). That is, the greatest numbers of individuals were collected at the two lowest sampling heights (0.3 m and 0.6 m). While similar numbers of parasitoid Hymenoptera were captured at the two lowest sampling heights, nearly twice as many beetles, nematocerous and non-nematocerous Diptera were captured at 0.3 m than 0.6 m. Ants were captured in relatively constant numbers over all sampling heights.

Although the numbers of trapped individuals varied greatly with height for 4 prey categories, each major category comprised a relatively constant proportion of the total sample at each height (Figure 2). Similarly, within each category size frequency distributions did not vary with height in any obvious manner (Figure 3). Thus, while the abundance of flying insects varied with height, the taxonomic and size composition of this fauna did not.

The vertical distribution of *A. tuonabo* did not closely match that observed for available prey (Figure 4). *Alpaida tuonabo* preferred web-sites between 0.6 m–1.2 m, and approximately 60% of the spiders measured were within this range. Thus, while traps nearest the ground caught the greatest numbers of flying insects, only 18% of *A. tuonabo* were found below 0.6 m.

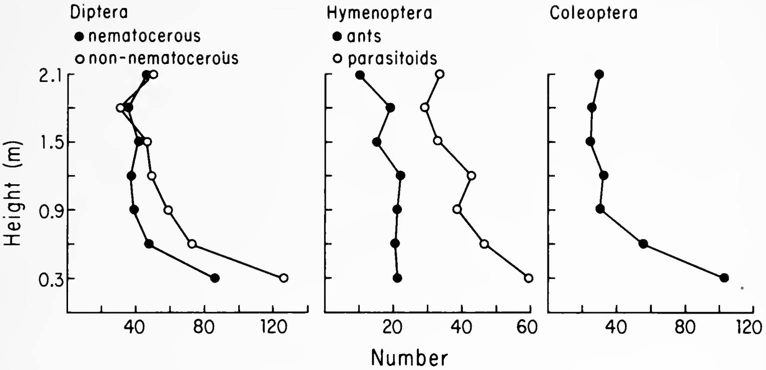

Figure 2. Relative abundances of major prey categories over all heights sampled. Each value represents a proportion of the total number of individuals captured on 10 sticky traps suspended at a particular height. See text for details of sampling method.

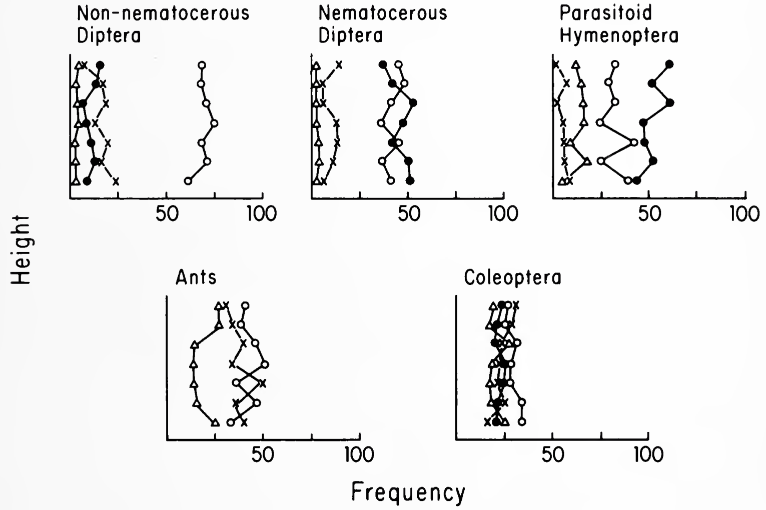

Figure 3. Size frequency distributions for the major prey categories over the 7 heights sampled. Within a category each value represents the proportion of individuals captured at a particular height that fell within a particular 1 mm interval. The symbols used for the various size classes are: 0 — 1 mm (●), 1 — 2 mm (○), 2 — 3 mm (×), and >3 mm (Δ).

A total of 446 insects representing 6 orders were taken from 320 webs of *A. tuonabo*. Approximately 95% of these insects belonged to those 5 prey categories which were most abundant in the sticky trap samples. Consequently, analysis of both web and spider selectivities will focus only upon these groups. In addition, since the composition of the flying insect fauna did not much vary with height, both the data regarding prey availability and diet were combined over all heights.

Web selectivity values did not differ greatly from zero for beetles, nematocerous Diptera, or parasitoid Hymenoptera (Table 1). Non-nematocerous Diptera, however, comprised a small proportion of the web contents relative to their proportion on the traps. Conversely, ants represented a large proportion of the web contents relative to their proportion on the traps.

Aside from nematocerous Diptera, *A. tuonabo* were observed to consume prey types in proportions roughly equal to their proportion in the web (Table 2). Spider selectivity values for beetles, ants, non-nematocerous Diptera, and parasitoid Hymenoptera were all less than 0.20 (absolute value). In contrast, the E_S value for nematocerous Diptera was large and negative.

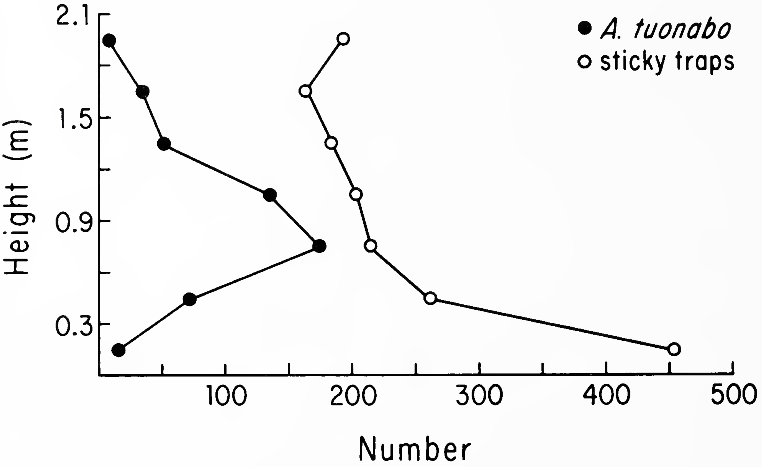

Figure 4. Vertical distribution of *A. tuonabo* and available prey. Heights of hub-resting spiders were measured to the nearest cm and then placed into 0.3 m intervals. Values for prey represent the total number of insects captured on 10 sticky traps suspended at a particular height. See text for details of sampling method.

Table 1. Web selectivity (E_W) values for prey types collected from webs of *A. tuonabo*.

Prey type	Collected from webs (eaten and uneaten)		Captured on traps		
	no.	r_i	no.	p_i	E_W
Beetles	56	12.5	320	19.2	−0.21
Nematocerous Diptera	164	36.8	337	20.2	+0.29
Non-nematocerous Diptera	34	7.6	453	27.1	−0.56
Ants	128	28.7	119	7.1	+0.60
Parasitoid Hymenoptera	42	9.4	264	15.8	−0.25
Others	22*	4.8	175**	10.4	-----

*Others include: butterflies (6), bees and wasps (10), leafhoppers (4), thrips (2)
**Others include: butterflies (2), bees and wasps (2), leafhoppers (80), thrips (27), Hemiptera (8), Orthoptera (5), Collembola (3), Zoraptera (4), Plecoptera (3), Isoptera (21), Psocoptera (20)

As the E_S values imply, the majority (87%) of uneaten prey were nematocerous Diptera. Most of these, in turn, did not appear to have been wrapped. Many, in fact, were observed struggling in web while stuck by a single wing. Similarly, most uneaten non-nematocerous Diptera and parasitoid Hymenoptera were apparently unwrapped. In contrast, 9 of the 12 uneaten ants had clearly been attacked and wrapped.

Only 2 groups, nematocerous Diptera and ants, were found in webs in sufficient numbers to allow meaningful calculation of web selectivity values for different size classes. Nematocerans less than 1 mm were relatively more abundant in webs than on the traps, while the opposite was true for those between 1 mm–2 mm (Table 3a). Web selectivity values, however, did not differ greatly from zero for either size class. Ants in webs were rather uniformly distributed among 8 size classes (Table 3b). The majority (76.0%) of ants on the sticky traps, however, were less than 3 mm long. Consequently, web selectivity values for the 1 mm–2 mm and 2 mm–3 mm size classes were large and negative, while those for larger classes were all large and positive.

Only ants were eaten in sufficient numbers to allow meaningful calculation of spider selectivity values for different size classes. Yet, since nearly all (90.6%) of the ants taken from webs were being eaten, these selectivity values provide little new information. Among the remaining groups, only nematocerous Diptera had large enough

Table 2. Spider selectivity (E_s) values for prey types collected from webs of *A. tuonabo*.

Prey type	Collected from webs (eaten only) no.	r_i	Collected from webs (eaten and uneaten) no.	p_i	E_s
Beetles	52	18.8	56	12.5	+0.20
Nematocerous Diptera	32	11.6	164	36.8	−0.52
Non-nematocerous Diptera	28	10.1	34	7.6	+0.14
Ants	116	42.0	128	28.7	+0.19
Parasitoid Hymenoptera	32	11.6	42	9.4	+0.10
Others	16*	5.8	22**	4.8	-----

*Others include: butterflies (6), bees and wasps (10)

**Others include: butterflies (6), bees and wasps (10, leafhoppers (4), thrips (2)

numbers of eaten (32) and uneaten (132) individuals to permit comparison. Mean body lengths for eaten (x = 1.6 mm; SD = 1.8) and uneaten (x = 0.8 mm; SD = 0.29) nematocerans were significantly different (t = 4.86; p <.001).

Discussion

The present findings highlight 2 features of the predatory behavior of *A. tuonabo.* First, the webs captured and the spiders consumed nonrandom samples of the available prey. Nonrandom web captures have been recorded for other spiders (e.g. Uetz and Biere 1980; Brown 1981; Turnbull 1960) and most likely reflect differing abilities for web avoidance or escape among different prey. While no avoidance was observed, I did see several large flies (Asilidae and Tabanidae) strike webs but then successfully escape. Among insects successfully restrained by the web, the spider may attack, ignore, or reject different types and/or sizes of prey. Numerous studies (e.g. Robinson and Robinson 1970, 1973; Riechert and Tracy 1975; Turnbull 1960) note rejected prey, but few studies (Uetz and Biere 1980) quantify attack vs. ignore probabilities for different prey. Here, the tendency of *A. tuonabo* to ignore nematocerans probably does not reflect avoidance but rather the inability of these small, weak-flying insects to escape or damage the web. Thus, *A. tuonabo* may have ignored these weak prey only to consume them with their web in the evening. Interestingly, the mean body length of nematocerans being consumed was nearly twice that of nematocerans

Table 3. Web selectivity (E_w values for size classes of nematocerous Diptera and ants collected from webs of *A. tuonabo*.

a. Nematocerous Diptera

Size (mm)	Collected from webs (eaten and uneaten)		Captured on traps		
	no.	r_i	no.	p_i	E_w
0–1	118	71.9	138	40.7	+0.28
1–2	40	24.4	163	48.1	−0.33
2–3	4	2.4	31	9.1	−0.58
>3	2	1.2	7	2.1	−0.27

b. Ants

Size (mm)	Collected from webs (eaten and uneaten)		Captured on traps		
	no.	r_i	no.	p_i	E_w
0–1	0	0.0	0	0.0	-----
1–2	17	13.3	43	36.7	−0.47
2–3	11	8.6	46	39.3	−0.64
3–4	21	16.4	7	6.0	+0.46
4–5	16	12.5	3	2.6	+0.65
5–6	10	7.8	3	2.6	+0.50
6–7	24	18.7	7	6.0	+0.51
7–8	13	10.2	2	1.7	+0.71
>8	16	12.5	6	5.1	+0.42

caught in the web but ignored. Spider selectivity for larger prey has also recently been demonstrated for *Micrathena gracilis* (Uetz and Biere 1980).

Second, *A. tuonabo* did not construct their webs at heights where total prey abundance was greatest. Since the taxonomic and size composition of the flying insect fauna varied only slightly with height, *A. tuonabo* was apparently not responding to the vertical distribution of a particular type or size of prey. Several factors potentially affect web height in *A. tuonabo*. First, although females use various support structures, the number of suitable "web spaces" may be limited (Lubin pers. comm.). Also, other species of similar size (e.g. *Pronous tuberculifer, Edricus crassicaudus,* and *Leucauge* sp.) construct webs closer to the ground (Lubin 1978; Shelly pers. obs.). Thus, the higher webs of *A. tuonabo* may reflect a behavioral means to lessen interspecific competition for food. In addition, increased web height may reduce risks of predation from ground- or litter-dwelling predators.

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REPRODUCTIVE BEHAVIOR OF *CLAEODERES BIVITTATA* (COLEOPTERA: BRENTIDAE)*

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Promiscuous aggregations of adult brentid weevils often occur on host trees, where females gather to oviposit (Meads 1976; Johnson 1982). In such a circumstance, in which a male can potentially inseminate many females, intense competition by males for females typically occurs (cf. Thornhill 1976; Alexander and Borgia 1979; Fincke 1982). In addition, members of the family Brentidae show considerable intraspecific variation in adult size (Sharp 1895; Soares 1970; Damoiseau 1967). From the numerous studies that show that larger body size enhances competitive aggressive success (e.g. Johnson and Hubbell 1974; Hamilton et al. 1976; Heinrich and Bartholomew 1979), it might be predicted that larger male brentids would enjoy greater mating success in breeding aggregations, and—provided that male size is an important competitive characteristic—that variation in male mating success would be commensurate with variation in male body size. I tested these predictions on an aggregation of *Claeoderes bivittata* Kirsch. (Coleoptera: Brentidae) in which the adults varied more than ten-fold in body weight.

The results of the present study support the idea that body size is an important trait. Males of nearly equal size engaged in a ritualized contest which appeared to permit sensitive assessment of relative size, and larger males enjoyed greater success in fights over females. However, small (11–22 mm) as well as large males (31–39 mm long) were disproportionately represented in mating. Small males had greater than expected success partly because they at times took shelter under, rather than guarded, their females, emerging for copulation when a larger rival was not present.

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MATERIALS AND METHODS

Claeoderes bivittata adults were studied on a dying tree of *Quararibea asterolepis* (Bombacaceae) on Barro Colorado Island (9°09′ N, 79°51′ W) in the wet season of 1980.

On June 9 all weevils from ground level to 2 m on the standing tree were collected, placed in a bag, sexed, measured in length to the nearest mm, and replaced. On June 13 all weevils up to a height of 2 m were collected and brought to the laboratory, where they were sexed, measured, cleaned of most mites with masking tape, and weighed to the nearest tenth mg on a Mettler H35AR balance. On June 14 these weevils were replaced on the trunk. On six dates between June 28 and July 14 the behavior of individually marked weevils of different sizes was described into a portable tape recorder, for a total of 13 hours. Rectangular and trapezoidal arenas about $1/3$ m^2 were drawn on the sides of the trunk between buttresses. On a given date the trunk was circled clockwise. The reproductive and competitive behavior that was centered around all male-female pairs in an arena was recorded, until none of the pairs originally in the arena remained. Durations of acts were timed with a stopwatch. Weevil density on the trunk slowly dwindled from 27–36/m^2 on June 28 to 15 or fewer/m^2 on July 14. A few weevils were collected in alcohol for identification and dissection.

DESCRIPTION OF WEEVIL ACTIVITIES

Oviposition

Before drilling, a female walks slowly over the smooth trunk, touching the substrate with her antennae. When a favorable site is found the female chews for 30–60 min until her rostrum is buried to the depth of the antennal insertion. Periodically she withdraws her snout, lifts her head, and expels sawdust from her jaws.

To oviposit, a female turns around and locates the drilled hole by tapping with rear end and hind legs. She then everts her telescoped sclerites, bringing the ovipositor to the hole, and remains still for 70 sec to 3 min. The hole drilled is the right size for one egg.

After oviposition the female rocks by bending and straightening her forelegs 12 times per min for 3.5–12 min, repeatedly moving the tip of her abdomen between the hole and positions further back. As the female rocks out, a bristled tergite is everted, to which bits of sawdust and other debris adhere. As she rocks in, the material appears to be added to the hole.

A female may drill and oviposit three times in succession (Fig. 1).

Female Aggression

Aggression is instigated by females before they drill and by females that have just completed oviposition. The aggression is usually directed against drilling females. The encounter may involve only an intention movement, or the instigator may push, poke, or swat a drilling female with her snout, or pry her out of her hole by sticking the snout under her abdomen and lifting. A fleeing female may be pursued several cm. Reciprocated aggression may result in a fight lasting 6 min or more in which the combatants kick, face one another and swivel their heads and forebodies, or thrust the snout under the other and lift suddenly; females of the same length may also stack themselves head-to-tail and sweep their snouts over the tip of their opponent's abdomen. Fights end when a female leaves or is flipped from the tree.

Guarding

A guarding male stays with a female as she antennates the trunk, drills, or oviposits, keeping his rostrum or his body over her (Fig. 2). He responds aggressively if a rival male draws near, and he may also threaten a female if she approaches his female too closely, by facing her, advancing on her, or chasing her with a yawing movement of the head.

Mating

A male mates with the female he is guarding one to several times during drilling, and is especially likely to do so just before the female pulls her beak out of the wood to oviposit (the onset of oviposition occurs less than a minute after the termination of copulation in about 80% of the cases (see Fig. 1)). A few seconds before mating a male accelerates his movements, antennates the female, and then mounts, sometimes trying the female's head. Copulation lasts about a minute.

Rejection

A female not ready to drill or oviposit will walk away from males that approach. A drilling female can thwart mating attempts by walking her hind end in a circle around the pivot point of her snout in wood, or by withdrawing her snout entirely and walking away.

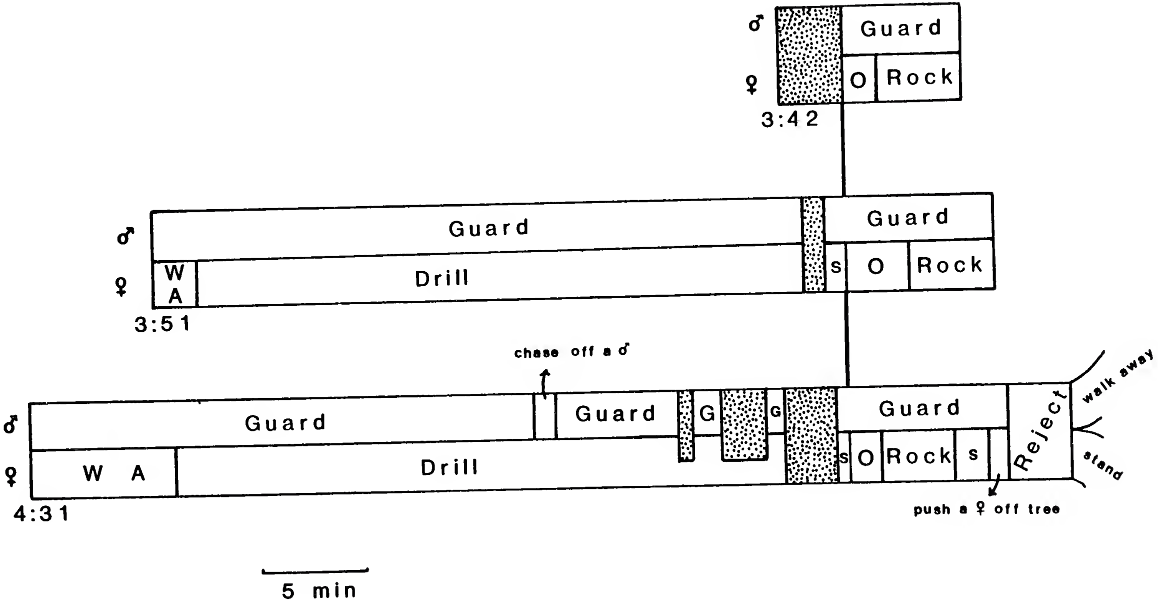

Fig. 1. Behavior of 33 mm male and 25 mm female in period spanning three successive ovipositions, from 3:42, when first seen together, until 5:22, when they parted company. Duration of activity is indicated to nearest half-minute. Above midline, male activity. Below midline, female activity. Stippled blocks = copulation. G = guard, O = oviposit, WA = walk and antennate trunk, S = stand. The onsets of oviposition are aligned over one another; notice that oviposition is immediately preceded by copulation.

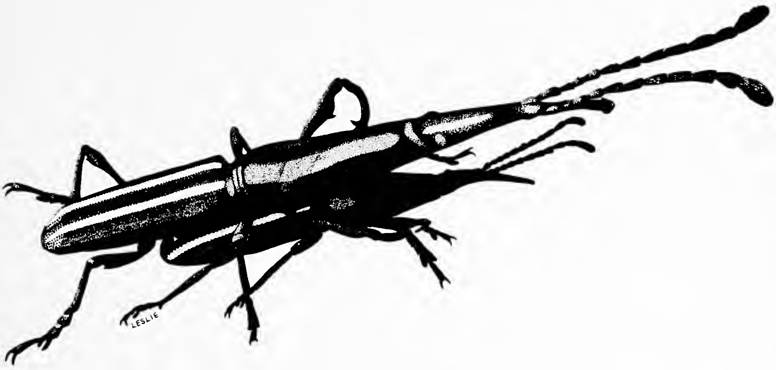

Fig. 2. A male, with enlarged jaws for nipping rivals, guards a female *Claeoderes bivittata* as she prepares to drill an oviposition hole. A guarding male typically places all or part of his body (particularly the rostrum) over the female. A small male in the presence of a large male, however, may insert himself partly under the drilling female.

Male Aggression

Males fight for access to females. Initially they may intermingle, jerk, or lash their antennae. Attacks involve nipping, kicking, poking with the snout, or putting the snout under the rival's body and jerking upwards 3 times/sec. A male may also interfere with copulation by thrusting his snout between a mating pair and pushing. An attacked male may flee, or reciprocate in kind.

Two males of approximately the same length may engage in a more stylized contest in which they align themselves, side by side, 1–10 mm apart, facing opposite directions. On the side of the rival a male taps his antenna and hind leg 4–5 times/sec, and when the opponent does likewise, the males fence leg against antenna at either end. The "appendage-fencing" contests observed in this study lasted 3 sec to 9 min.

RESULTS

Size Variation

Male weevils in the June 13 sample (n = 67) ranged from 12–38 mm in length and from 19–334 mg wet weight, i.e., the biggest male was 3 times as long and 17 times as heavy as the smallest. Males 11 and 39 mm long were found subsequently. The females (n = 81) ranged from 12–29 mm and 19–247 mg with the biggest female 2½ times as long and 13 times as heavy as the smallest. At all lengths females were heavier than males, and they increased in weight faster with length than did the males (Fig. 3).

A frequency histogram of the lengths of males (n = 101) and females (n = 128) measured June 9 is shown in Fig. 4. Mean male length ±S.D. was 25.91 ±7.21; mean female length ±S.D. was 20.97 ±4.35.

Five females were dissected. Each had two ovarioles and 3 or 4 large, yolked eggs. The length of the largest yolked egg increased monotonically with female length, from a 1.3 mm egg in a 13 mm female to a 2.1 mm egg in a 29 mm female.

Size and Aggressive Success

In aggressive encounters between females the female that fled was deemed the loser. The winners by this criterion were larger in 14 of 14 contests involving weevils of unequal length ($p = .0001$, sign test). Even if four additional encounters involving females of equal length were conservatively counted as victories for the smaller weevil, the winners were still significantly more likely to be the larger ($p = .0154$).

In male encounters the winner was considered to be the male that remained by the female. Here again the larger weevil was significantly more likely to win ($p < .005$, sign test). Defending males (the ones originally with the female) were not significantly more likely to win encounters than intruding males ($p \approx .18$).

The relative size of the rivals was also a factor in the occurrence of the appendage-fencing contest. An analysis of the differences in length between the rivals in five encounters in which the contest occurred and sixteen encounters in which it did not, showed that rivals using the contest were significantly more similar in length ($p = .002$, Mann-Whitney U test). The mean ±S.D. difference in length for rivals using the contest was 1.8 ±2.0 mm; for rivals not using it, 8.1 ±7.4 mm.

One effect an intruding male may have, whether or not he wins the female, is to shorten the duration of the defending male's copulation. Uninterrupted copulations lasted a mean ±S.D. of 82.4 ±48.7 sec, with 2/3 of the copulations lasting between 40 and 90 sec. Copulations interrupted by rivals, however, lasted 31.0 ±15.1 sec ($p = .026$, Mann-Whitney U test).

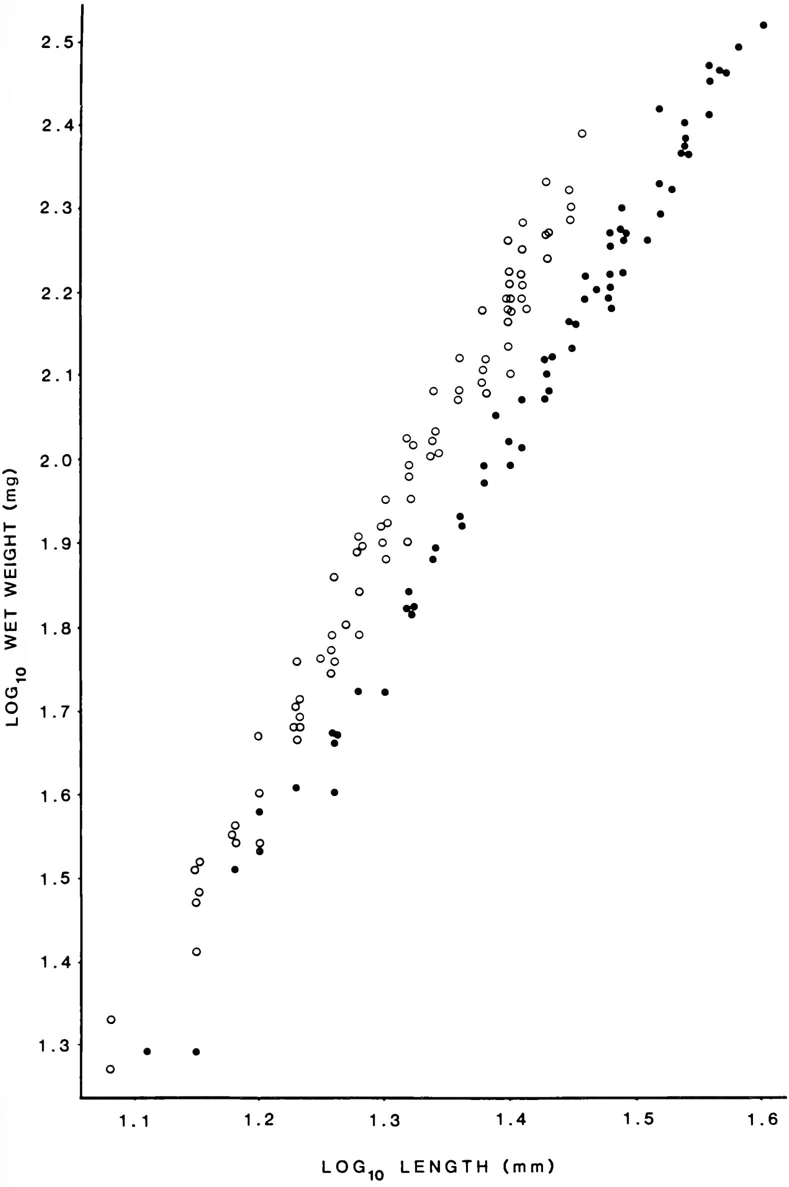

Fig. 3. Log_{10} length (mm) vs. $\log_{10}$ wet weight (mg) of male (●) and female (○) *Claeoderes bivittata*. For males, $\log_{10}$(weight, mg) = −1.53 + 2.54 $\log_{10}$ (length, mm). For females, $\log_{10}$ (weight, mg) = −1.78 + 2.83 $\log_{10}$ (length, mm).

Size and Mating

Individual weevils were compatible with mating partners of many sizes. In 52 different pairings, females mated with males as much as 10 mm shorter than themselves, and males with females as much as 16 mm shorter. Despite this, mating was size-assortative overall. The Pearson product moment correlation for male and female length was $r = .323$ ($p = .021$) for the 52 different pairings, and $r = .398$ ($p = .002$) if multiple matings of a pair were included.

Females, however, tended to reject males smaller than themselves when such males attempted to mate. In 57% of the cases of rejection (4 out of 7) the female was larger, whereas in only 37% of the cases of mating (22 out of 60), was the female larger. When lengths of males rejected and accepted for mating were examined, it was found that rejected males were shorter ($p < .05$, 1-tailed, Mann-Whitney U test).

Given the more frequent rejection of small males, and the greater success of larger males in aggressive encounters over females, it was expected that males found mating would tend to be larger than males simply present in the aggregation. Whereas females that mated were larger than unattended drilling females ($p < .02$, 2-tailed, Mann-Whitney U test), males that mated were not significantly larger than guarding males, males in a random sample, or males that were alone (Table 1). Instead, a frequency histogram of mating males showed a bimodality in the size of males that mated compared to an unimodal distribution of males in the breeding aggregation (Fig. 4). There appeared to be a dearth of medium-sized mating males. Indeed, a chi-square test on the 52 different pairings found that mating males were significantly more likely to be large ($\geqslant$ 31 mm) or small ($\leqslant$ 22 mm) than would be expected if they mated in proportion to their abundance in the random sample ($\chi^2 = 4.87$, 1 df, $p = .027$).

Extra opportunities for small males to mate could arise if guarding males drove away small rivals less frequently than they did rivals more their size. With this in mind, I compared the 7 cases in which two males co-occurred at a drilling female for 3 min or more with the 19 cases in which one male drove off the other within the first minute. In 6 of the 7 cases of co-occurrence, one male was small ($\leqslant$ 22 mm) and the other large ($\geqslant$ 31 mm). In the remaining case both males were medium-sized. In the 7 cases of co-occurrence the

Table 1. Lengths (mm) of *Claeoderes bivittata* individuals in different categories. The two means marked with an asterisk are the only two compared within a sex that are significantly different.

Females				Males			
	n	x̄	S.D.		n	x̄	S.D.
♀♀ drilling alone	11	19.73*	2.45	♂♂ without partners	14	25.21	7.30
Guarded, drilling ♀♀	49	20.08	3.67	Guarding ♂♂	49	24.55	6.76
Random sample of ♀♀	128	20.97	4.35	Random sample of ♂♂	101	25.91	7.21
♀♀ that mated	52	22.21*	4.20	♂♂ that mated	52	24.77	8.09

mean ±S.D. size difference between the males was 13.6 ±8.5mm. In the 19 cases of intolerance, the mean S.D. size difference was only 5.8 ±5.7 mm. The males in the cases of co-occurrence were, in fact, significantly more disparate in size ($p < .02$, 2-tailed, Mann-Whitney U test).

The joint attendance of a drilling female by the two medium-sized males was short-lived (4 min). The small and large male combinations, on the other hand, were more persistent ($\bar{x} = 19.8 \pm 10.5$ min). Stability was achieved in part because the small male kept a "low profile." The small males were unaggressive, even if poked, and 5/6 of them spent most of their time partway under the drilling female. Usually it was the rostrum that was tucked under the female, but two individuals crawled under the female at right angles to her long axis and centered themselves beneath her. Postures in which a male placed part of himself under the female were exhibited only by small males in the presence of a large male guard.

Opportunities to mate did arise for 5 of the 6 small males, despite the existence of the larger guards. Three of the small males mated while the large male was fighting off a large intruder. One small male mated while the large male stood with his snout resting on the female's head. Another small male waited until the onset of oviposition, when the large male left. He then interrupted the post-oviposition rocking behavior of the female in order to copulate. The small male that did not mate was driven off by the large male guard, who was aroused from quiescence by a 38 mm intruder who nipped him and mated with his female.

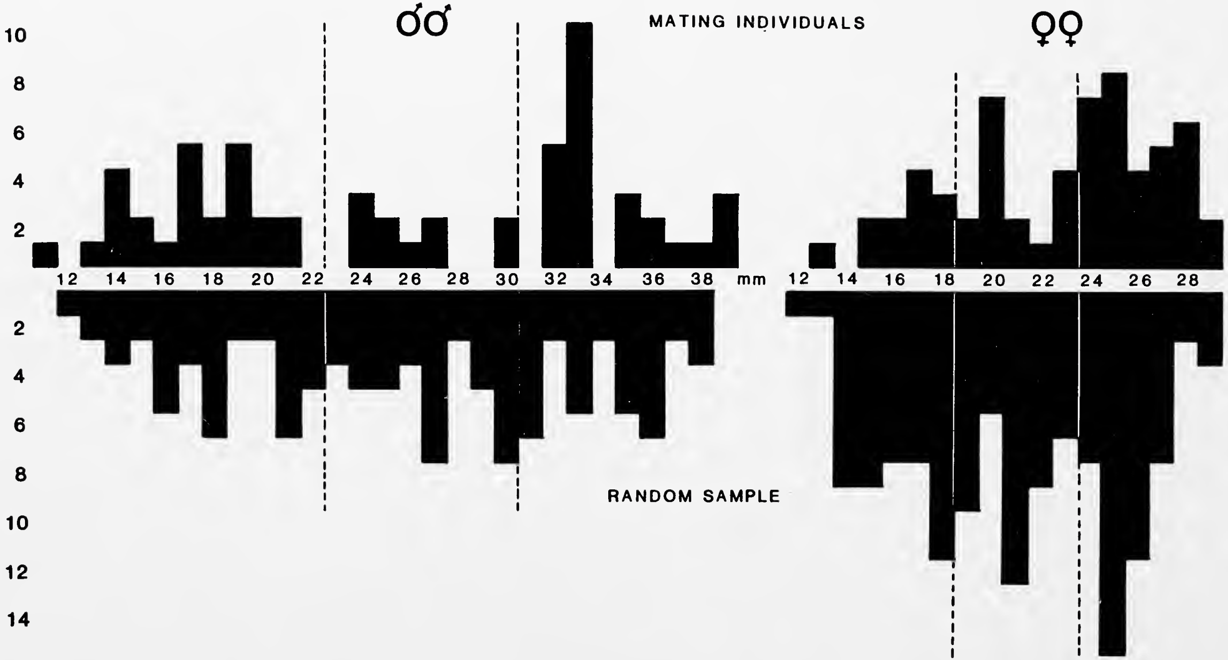

Fig. 4. Frequency of males (left) and females (right) in different length classes. Above the line: frequency distribution of mating individuals. Below the line: frequency distribution of individuals in the June 9 sample of the population. The dashed lines divide the June 9 sample into "small", "medium", and "large" weevil classes. Boundaries of these categories were arbitrarily established so that 31–36% (i.e., 1/3) of the weevils of one sex fell into each class.

Despite their mating successes, the small males were not the equal of the large ones. The copulations of the small males appeared to require the absence or inattention of the larger attendant. In contrast, the large males mated when they chose. All 6 large males, for instance, were the last to mate before the female oviposited, after which they left.

DISCUSSION

In *Claeoderes bivittata,* there is a great deal of variation in adult size, presumably due in part to variable growth conditions experienced by the larvae (Kleine 1933; Haedo Rossi 1961; Galford 1974; Peters and Barbosa 1977). As with another brentid, *Brentus anchorago* (Johnson 1982), the larger individuals have several reproductive advantages. In both species, larger females can clear from the region in which they just oviposited, more of their drilling rivals (thus possibly reducing later crowding of their larvae), and are less likely to be ousted from their chosen drilling site. Larger females also lay larger eggs, an initial advantage which in other beetles has been shown to significantly affect final adult size (Palmer 1983). Larger males do more mating than average, and assortatively mate with larger females who have the reproductive advantage of larger eggs and greater competitive success at oviposition sites.

There is, however, a principal difference between *B. anchorago* and *C. bivittata.* In *B. anchorago,* the bigger the male, the more he mates (Johnson 1982). In *C. bivittata,* the middle-sized males mate the least. In *B. anchorago,* males are highly intolerant of other males at a drilling female. In *C. bivittata,* a female can sometimes have two attendants if one is large and one is small.

The circumstances that permit the co-occurrence of a large and small male at one female need further investigation. In a proximal sense, small males may be less easily perceived than larger ones. Certainly, the small males appeared to assist this process by making themselves less conspicuous. They frequently tucked their snout under the female, along with the antennae which in other encounters permit male-male recognition. The small males were not seen to advertise their presence by initiating acts of aggression. Similar unprovocative tactics were noted in the smallest males of the wood-boring weevil, *Rhinostomus barbirostris,* at females guarded by large males (Eberhard 1980). Then too in the ultimate sense, it may not be worth the energy expenditure for a large male to keep small, persistent males from the vicinity of the female. Despite matings by small males, large males may enjoy most of the paternity.

A true answer to the question of the relative reproductive success of large and small males awaits determination of the mode of sperm competition in *C. bivittata.* Whatever the mode, the relative reproductive success of a small male is probably less than the relative number of matings he achieves. If there is sperm mixing, the small males (which in the six cases observed here averaged 200 mg lighter than the males with which they co-occurred), probably transfer less sperm per copulation than the large ones. In two species of heliconiine butterflies, for example, smaller males transfer smaller spermatophores (Boggs 1981). If there is sperm precedence, we would expect large males, with the advantage of weight and strength in aggressive encounters, to copulate at will when the probability of fertilizing the egg is the highest. Small males, mating when they could, might or might not transfer sperm at the opportune time.

The mode of sperm competition is unknown in *C. bivittata;* however, sperm displacement has been found thus far to be the rule in Coleoptera (Walker 1980). If sperm displacement does occur in *C. bivittata,* the last male to mate before oviposition would have the advantage in paternity. That last male advantage occurs in *C. bivittata* is suggested by the fact that copulation immediately precedes oviposition, and that when the female ceases to explore the trunk and drill, the male ceases to guard her.

I would argue, then, that small males of *C. bivittata* do not enjoy nearly as much reproductive success as their proportion of the copulations would suggest, and that there has not been intense selection for large males to assiduously expend energy excluding them from drilling females they are guarding. For small males, however, there must at times be an advantage to lingering near a female guarded by a larger rival, for otherwise one would predict that small males would avoid such females. If there is complete or partial sperm mixing in *C. bivittata,* there exists a possibility, however small, that a given copulation by any male at any time will result in fertilization. Even if sperm displacement is complete, there remains the possibility that the larger rival, distracted by competitors or a more attractive female, will not return before oviposition begins, leaving the way open for the small male to copulate last. Similarly, a small male that mates just after oviposition might still fertilize the next egg to ripen if by chance the female went unmated during her next drilling.

The above arguments do not provide an ultimate explanation for why small males of *C. bivittata* enjoy greater mating success than small males of *B. anchorago.* Comparative studies are planned for these two species, which have similar breeding ecologies. Sperm competition and methods of detecting rivals will be explored, and the behavior and reproductive input of small, medium, and large males of both species will be compared. Possibly the system in *C. bivittata* represents an early stage of the development of dual male strategies, and may be a step on the evolutionary road to male dimorphism (Eberhard 1980). If so, elucidation of the differences between *C. bivittata* and *B. achorago* could help our understanding of the selective environments favoring dimorphic male behavior and structure.

SUMMARY

Adults of *Claeoderes bivittata* aggregated on a *Quararibea* tree in Panama. Males ranging in length from 11–39 mm guarded and mated with females 12–29 mm long as they bored holes in the wood for their eggs. Fights often ensued as females tried to pry other females from their drilling sites; larger females more often won. Males fought males for access to females; larger males won significantly more often. Disputes involving males of similar size could be settled by a contest in which the two males stood closely parallel head-to-tail, while an antenna lashed a hind leg at either end. Such an appendage-lashing contest may permit rivals to assess one another's relative size.

Although individuals differing by at least 16 mm in length could couple, significant size-assortative mating was observed (r = .4). Due to the greater aggressive success of larger males and the fact that males rejected by females were smaller than males they accepted for mating, it was expected that mating males would be above average in size. Instead, mating males were significantly more likely to be large (≥ 31 mm) or small (≤ 22 mm). The disproportionate mating of small males may be explained in part by the tendency of smaller males to wait partly sheltered under a drilling female, emerging for copulation when larger males are not guarding the female.

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POLYDOMY IN THE SLAVE-MAKING ANT, *HARPAGOXENUS AMERICANUS* (EMERY) (HYMENOPTERA: FORMICIDAE)[1]

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Introduction

Slavery in ants is a form of social parasitism in which parasitic "slave-making" species exploit the labor of workers derived from host-species colonies. The slave makers raid host-species nests, where they capture all or part of the brood. Subsequently, workers maturing from the captured brood form a social attachment to the slave makers and perform all the usual worker-ant functions in the parasites' colony (see review in Buschinger *et al.* 1980).

Harpagoxenus americanus (Emery) is an obligatory slave maker living in eastern North America, where it forms mixed colonies with members of certain *Leptothorax* species (see Alloway 1979). Two kinds of *H. americanus* nests are found: "primary nests" containing a single slave-maker queen and slaves with or without slave-maker workers, and "secondary nests" consisting of slave-maker workers and slaves without a slave-maker queen (Creighton 1927; Sturtevant 1927; Buschinger & Alloway 1977). Primary nests are apparently established when a parasite queen successfully invades a host-species nest (Wesson 1939), but the origin of secondary nests is questionable. The problem is compounded by the fact that secondary nests are usually more numerous than primary nests and frequently produce slave-maker females (workers and/or queens) from

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their broods (Wesson 1939; Buschinger & Alloway, 1977). In the related European slave maker, *H. sublaevis,* "ergatoid queens" (individuals with fully functional ovaries and a spermatheca, but with a more or less worker-like external morphology) are common and function as the usual female reproductives (Buschinger, 1978). However, Buschinger and Alloway (1977) found that, while many *H. americanus* workers have functional ovaries and lay eggs that can mature to produce males, they rarely, if ever, possess a spermateca. Thus, "ergatoid queens" are absent or very rare in *H. americanus.* Moreover, these authors thought that thelytoky was unlikely in this species.

Wesson (1939) observed the formation of secondary nests in the laboratory. Slave-maker colonies which had conducted several ordinary slave raids sometimes concluded the final raid of the season by splitting into two components. In these cases, a few slave-maker workers and slaves remained indefinitely in the raided nest with part of the captured brood. Wesson suggested that this might be a sufficiently common late-season activity to account for the frequent occurrence of secondary nests. However, even if secondary nests are formed in this manner, there are still two possibilities for the relationship between secondary and primary nests and for the origin of the female slave-maker brood in secondary nests. Following their formation, secondary nests might become autonomous entities functionally separate from their parental primary nests. In this case, if we exclude thelytoky, the female slave-maker brood in secondary nests would have to be derived exclusively from brood carried over from the primary nest when the secondary nest was initially occupied (Buschinger & Alloway 1977). Alternatively, the primary nest and one or more secondary nests might comprise a single multiple-nest (polydomus) colony (Sturtevant 1927). Interactions between the nests of such polydomous colonies would be protracted, and the slave-maker queen would continue to supply female brood for all nests in her colony. The latter possibility is supported by the fact that polydomy of this type has recently been demonstrated in two of the host species of *H. americanus, Leptothorax ambiguus* Emery and *L. longispinosus* Roger (Alloway *et al.* 1982). The objective of the present study was to examine these two possibilities by collecting and mapping *H. americanus* and host-species nests in nature, reconstructing their spatial relationships in the laboratory, and observing the interactions among them.

MATERIAL AND METHODS

The ants were collected on the Erindale Campus of the University of Toronto in Mississauga, Ontario, during the spring and summer of 1980 and 1981. Since our purpose was to determine whether colonies of *H. americanus* sometimes occupy more than one nest, we looked for areas where two *H. americanus* nests occurred within 2 m of each other. Whenever such a place was located, we layed out a 2 m by 2 m quadrant centering on the two nests and then collected, numbered and mapped the location of every *H. americanus* nest and every nest of its host species *(L. ambiguus* and *L. longispinosus)* in the quadrant. In some cases, adjacent quadrants were combined to permit the collection of a larger group of slave-maker nests.

In the laboratory, we removed the ants and their brood from their natural nests and established them in artificial nests of the type described by Alloway (1979). For censusing, the artificial nests were placed in petri dishes (diameter = 14.5 cm; height = 1.5 cm) containing a water bottle and food (Bhatkar & Whitcomb 1970). Then the ants were transported to an unairconditioned, naturally lighted room. On the floor of this room, quadrants were layed out with masking tape; and the field maps were used to locate the position occupied by each nest. A thick layer of petroleum jelly on the masking tape formed a barrier which confined the ants to their respective quadrants. A water bottle and food were placed near each nest. In this way, it was possible to set up the artificial nests so that we duplicated the spatial arrangement of the natural nests.

In addition to the quadrants collected from the field, we set up one control quadrant to study behavioral interactions between two *H. americanus* nests which had not been collected near one another in nature. The sides of this control quadrant were 100 cm long, and the two nests were placed 80 cm apart.

During the course of our observations, some of the ants were marked so that they could be individually identified. Each mark consisted of a very small dot of colored nail polish applied to the dorsal surface of the gaster with the tip of a minuten pin embedded in the end of a wooden stick. Ants remained marked for periods of 1 day to 1 month.

Observations were made 8 h a day, 5 days a week between 10 June and 27 August 1980 and between 7 May and 30 August 1981. Five quadrants were collected and observed during 1980; and 14 quadrants were collected and observed during 1981.

RESULTS

There was a total of 19 quadrants. However, quadrant 1 was merged with quadrant 2 and quadrant 9 with quadrant 10 when an additional *H. americanus* nest was found in close proximity to a group of other *H. americanus* nests, but outside the original quadrant boundary. Altogether, the quadrants contained 49 *H. americanus* nests, 57 *L. ambiguus* nests, and 59 *L. longispinosus* nests (see Table 1).

Our most common observation was "fusion" of all the *H. americanus* nests in a quadrant. By "fusion", we mean that eventually all the ants from two or more *H. americanus* nests peacefully moved into a single nest after exchanging adult nest-mates and brood among the different nests for varying lengths of time (Figure 1). This exchange was carried out exclusively by slaves. The ability of nests to fuse shows that there is no behavioral barrier to interactions and exchange of nestmates among nests and thus indicates either that all the ants are members of the same polydomous colony or that *H. americanus* is a unicolonial species with no behavioral barriers between its nests. Fusion of all the slave-maker nests was observed in quadrants (1 + 2), 5, 6, (9 + 10), 11, 12, 13, 16, 17, and 18, in which there was never more than one slave-maker queen.

However, we did not always observe fusion among *H. americanus* nests:

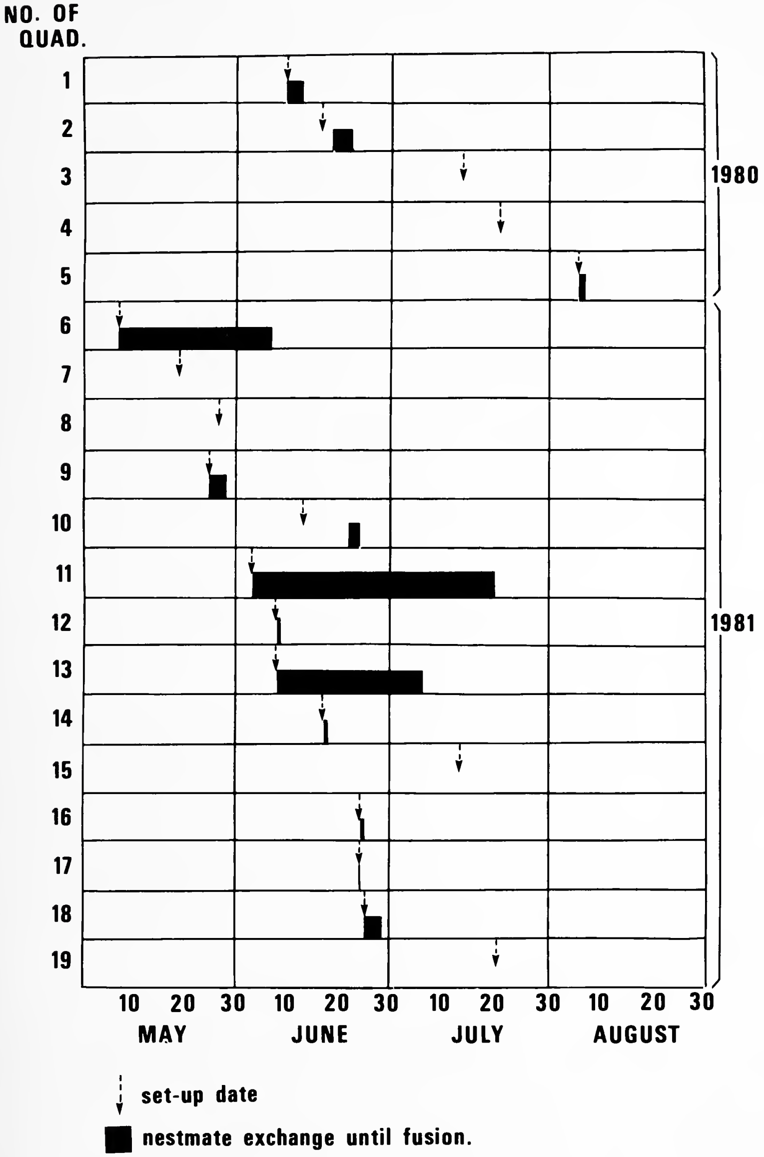
a. In the control quadrant where two *H. americanus* nests from different collection sites were arbitrarily set up near each other, the ants showed no tendency to fuse; and the slave makers from one nest successfully raided the other slave-maker nest.

b. Quadrants 3 and 8 each contained two *H. americanus* queens living in different nests with slaves and a brood. In quadrant 3, there was little behavioral interaction between the ants in the two nests. However, in quadrant 8, after the brood matured, the *H. americanus* workers in one nest raided the other slave-maker nest.

c. In quadrant 4, there was little contact between the ants in the two *H. americanus* nests, but the small amount of contact observed was hostile.

d. In quadrant 14, slaves and slave makers in two nests fused and then fought with the slaves and slave makers in a third nest.

Figure 1 - Set-up date, duration of nestmate exchange until date of fusion.



e. In quadrant 19, both the slaves and the slave makers from different nests fought whenever they met; and the slave makers in one nest mounted an incomplete raid against the other slave-maker nest.

These observations indicate that *H. americanus* is not a unicolonial species. Aggressive behavioral barriers preventing the exchange of nestmates and nest fusion exist between some *H. americanus* nests. This fact strengthens the conclusion that exchange of nestmates and brood and nest fusion, when they do occur, are indicative of the existence of a polydomous colony.

Somewhat peculiar partial fusions were observed in quadrants 7 and 15. In both quadrants, the slaves peacefully moved into a single nest. In quadrant 7, the slave makers from the two nests fought. In quadrant 15 where there were 5 *H. americanus* nests, some of the slaves attacked slave makers which had been living in other nests prior to the fusion. These partial fusions may represent situations in which lack of contact between nests had begun to produce autonomy between nests.

Once the raiding season was over, we observed the formation of secondary nests in quadrants 1 and 6. In both quadrants, some of the ants which had been occupying a single nest moved into a second nest. In both cases, exchange of nestmates and brood continued for two weeks, when observations ended.

In 7 quadrants, we were unable to find an *H. americanus* queen, despite our efforts to collect each nest completely and to search beyond quadrant boundaries for additional slave-maker nests belonging to these nest groups (see Table 1). However, in each of these cases, all the maturing *H. americanus* adults were males, a fact which indicates that these particular nests had not been receiving female brood from a primary nest and is consistent with the supposition (Buschinger & Alloway 1977) that thelytoky does not occur in *H. americanus*.

The total number of adults of various species in all nests studied is summarized in Table 1. The total number of *H. americanus* workers was 115, with the average slave-maker nest containing about 2 *H. americanus* workers. The largest number of slave makers in a single nest at the time of the original census was 13; and the largest number of nests in a single apparently polydomus *H. americanus* colony was 6 in quadrant (9 + 10). Altogether, this colony contained 19 *H.*

americanus workers, 54 *L. longispinosus* slaves and 53 *L. ambiguus* slaves. The average distance between *H. americanus* nests in nest groups apparently comprising a single colony was 43.5 cm, with a range of 11 to 159 cm. The average distance between *H. americanus* nests among which there were aggressive interactions was 61.36 cm, with a range of 19 to 180 cm.

In the *H. americanus* nests, *L. longispinosus* slaves outnumbered *L. ambiguus* slaves by a ratio of almost 4:1, the total number of slaves being 803 (79.5%) for *L. longispinosus* and 207 (20.5%) for *L. ambiguus.* All the *H. americanus* colonies contained *L. longispinosus* slaves, and 9 colonies contained slaves of both species. However, none of the *H. americanus* colonies used in this study had only *L. ambiguus* slaves, although such colonies are occasionally found in the Toronto region (Alloway unpublished data). Nevertheless, 7 of the quadrants studied contained no nests of free-living *L. longispinosus,* and one of the quadrants in which there were *L. ambiguus* slaves contained no nests of free-living *L. ambiguus* (see Table 1). Unenslaved nests of *L. longispinosus* were on average somewhat more populous than the unenslaved nests of *L. ambiguus,* the mean number of workers per nest being 25.6 for *L. longispinosus* and 16.8 for *L. ambiguus.*

Discussion

Our observations indicate that many *Harpagoxenus americanus* colonies are polydomus. This conclusion is based primarily on observations of peaceful interactions and of nest fusion among nests collected close together in nature, contrasted with observations that ants from different *H. americanus* nests do not always interact peacefully. The fighting and raiding observed indicate that *H. americanus* does not possess a unicolonial population structure. Thus, peaceful exchange of nestmates and nest fusions, when they occur, signify the existence of polydomous colonies. However, polydomy in *H. americanus* is not obligatory. New colonies are monodomous, becoming polydomous as they grow. Finally, our observations of partial fusions suggest that nests in polydomus colonies may gradually become autonomous, perhaps due to cessation of regular contact between nests. Under these circumstances, new queenless "secondary colonies," similar to those envisaged by Wesson (1939), could be formed.

Table 1. Total number of nests and individuals by species in each quadrant.

Quad No	H a		slaves				H a nests	free living						total of all nests
	♀	☿	l 1		l a			L 1		L 1 nests	L a		L ȧ nests	
			♀	☿	♀	☿		♀	☿		♀	☿		
1	1	5	0	44	0	13	2	0	0	0	2	70	4	6
2	1	8	0	44	0	23	3	1	53	1	3	112	7	11
3	2	0	0	24	0	0	2	2	63	3	0	0	0	5
4	1	6	0	22	0	0	2	4	112	5	0	0	0	7
5	0	6	0	21	0	0	2	2	116	3	0	0	0	5
6	1	11	0	131	0	0	3	2	166	5	2	99	3	10
7	0	8	0	67	0	0	2	7	291	13	0	0	0	15
8	2	2	0	39	0	0	2	4	125	6	0	0	0	8
9	0	7	0	37	0	10	6	0	4	2	9	107	7	15
10	0	19	0	54	0	53	2	1	82	3	19	261	14	19

11	0	11	0	64	0	3	3	1	76	4	8	136	7	14
12	0	3	0	21	0	0	2	5	204	7	4	29	2	11
13	0	6	0	37	0	63	3	0	0	0	2	18	3	6
14	0	4	0	15	0	5	3	0	0	0	4	100	7	10
15	0	4	0	22	1	42	5	0	0	0	8	57	5	10
16	1	5	0	52	0	0	3	0	0	0	0	0	0	3
17	1	14	0	84	0	18	3	0	0	0	0	0	0	3
18	1	7	0	36	0	0	2	0	0	0	0	0	0	2
19	1	1	0	70	0	0	2	1	222	8	0	0	0	10
TOT	11	115	0	803	1	207	49	30	1509	59	59	958	57	164

H a = *Harpagoxenus americanus.* L 1 = *Leptothorax longispinosus.*
L a = *Leptothorax ambiguus.* ♀ = queen. ☿ = worker.

Nevertheless, the fact that ants which had been living in several different nests in nature so frequently moved into a single artificial nest in the laboratory is somewhat problematic. Under our laboratory conditions, polydomy seldom persisted, possibly because our artificial nests were somewhat more spacious than the acorn nests which these ants inhabit in nature. If the ants live in more than one acorn because no single acorn is large enough for the whole colony, then giving the colony a larger artificial nest might produce nest fusion. However, many factors other than space may be involved in producing and maintaining polydomy in these ants (see discussion in Del Rio Pesado, 1983).

Our observations of nest divisions in two quadrants further supports the polydomy hypothesis. However, the nest fusions which we saw did not closely resemble those described by Wesson (1939). In only one of our colonies did raiding parties tend to remain in target nests; and even these raiders returned home after 1 to 3 days. What we observed was that ants which had been occupying one nest came to occupy two nests after the "raiding season" was over.

Several previous investigators have noted that many *H. americanus* nests are queenless (Buschinger & Alloway 1977; Creighton 1927; Sturtevant 1927; Wesson 1939). The usual conjecture has been that most of these queenless nests are "branches" located near queenright nests. Our data confirm this supposition by showing that many queenless nests are parts of queenright polydomus colonies. However, there were 7 quadrants in which we could not find a nest containing an *H. americanus* queen. Since these queenless nests produced only male slave-maker brood, it is unlikely that they represent components of a queen-right polydomous colony; and the males produced in these nests are probably the offspring of *H. americanus* workers (Buschinger and Alloway 1977). Some of these isolated nests may be remnants of colonies whose queen has died, while others may be products of long-distance raids from which the raiders failed to return. The presence in some *H. americanus* nests of slaves belonging to a species for which there were no free-living nests in the same quadrant suggests that *H. americanus* raids may occur over distances of several meters; and far-ranging raiders may sometimes fail to return to their base (Creighton 1927).

In our study area, *L. longispinosus* slaves outnumbered *L. ambiguus* slaves by a ratio of almost 4:1. This finding is typical throughout southern Ontario and the adjacent parts of New York state, despite the fact that *L. ambiguus* colonies are generally more abundant than *L. longispinosus* colonies (Alloway *et al.* 1982). Two factors probably account for the prevalence of *L. longispinosus* slaves in *H. americanus* nests. First, *H. americanus* seems to manifest an ecological preference for rather cool, shady places, a habitat preference which closely matches that of *L. longispinosus.* Second, at our study site, we found that *L. longispinosus* nests were on average ore populous than *L. ambiguus* nests. Thus, a raid against a nest of *L. longispinosus* might net more worker pupae than a raid against a nest of *L. ambiguus.*

SUMMARY

Field maps were made while collecting nests of the slave-making ant, *Harpagoxenus americanus,* and two of its host species, *Leptothorax ambiguus* and *L. longispinosus.* The ants were then transferred to artificial nests arranged to reconstruct the natural spatial relationships among nests. Ants from adjacent slave-maker nests often exchanged nestmates and brood for a period of time before moving into a single nest; and ants which had been living in a single nest in the laboratory sometimes moved into two nests. However, in other instances, ants from adjacent nests fought. These observations were interpreted as indicating that colonies of *H. americanus* sometimes occupy more than one nest (facultative polydomy). Nest population data were also presented and discussed.

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SITUATION AND LOCATION-SPECIFIC FACTORS IN THE COMPATIBILITY RESPONSE IN *RHYTIDOPONERA METALLICA* (HYMENOPTERA: FORMICIDAE: PONERINAE)*

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Introduction

Hangartner, Reichson, and Wilson (1970) reported some years ago that individual communities of harvester ants of the genus *Pogonomyrmex* are able to distinguish the scent of their own nesting material from that of other conspecific colonies. Holldobler and Wilson (1977) were able to show that the African weaver ants, *Oecophylla longinoda*, mark and advertise individual community territories by means of colony-specific pheromones deposited in the rectal fluids. And Traniello (1980) has recently demonstrated that, in the typically densely packed aggregations of colonies of *Lasius neoniger,* persistent trunk trails are maintained which arise from recruitment trails marked, again, with hindgut material. Here we describe what we believe to be nest-area marking with hindgut material in the primitive Ponerine ant *Rhytidoponera metallica.*

Experiments and results

The tests reported here were a continuation of a series carried on for some years, and earlier reported in part (Haskins and Haskins, 1979). Material and methods were essentially as described there, and need only be briefly reviewed. The specific population used in this work was collected as a single, rather small colony taken at Montville, in the Blackall Range of northern Queensland, Australia, on December 23, 1963. It was maintained as a closed inbreeding unit in the laboratory until the fall of 1979, at which time it had greatly increased in numbers, was active and vigorous, and contained

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numerous "worker", female and male brood.[1] Other things being equal, it might have been expected to have attained considerable genetic homogeneity, since new generations of "workers" and young queens were fathered exclusively by males reared within the colony.

On November 4, 1979 this population was divided into two roughly equal halves and placed in separate arenas standing side by side on the same laboratory bench. All conditions were kept constant for the two moieties, designated *A* and *B*, except that they were maintained on differing diets, comprising crickets and dilute honey water for *A* and mealworm larvae and dilute sugar water for *B*. Two years later, on November 7, 1981, a series of compatibility tests were run between pairs of individuals taken one each from the two halves and allowed to encounter one another in fingerbowls, as described earlier. These demonstrated only very limited incompatibility, as reported earlier (Haskins and Haskins, 1979), and suggested that diet, though possibly a measurable influence, was almost certainly not a critical factor in mediating compatibility as characterized in this test procedure.

Individual pair-tests after isolation on the same diets

On November 11, 1981 a further separation of the population was made by dividing Moiety *B* into two, designated *B′* and *B″*, and continuing to maintain both on the identical diets of mealworms and sugar water, and continuing with no worker interchange or communication between them. They were held in this manner for a further year. Then, on November 15, 1982, fifty pair-tests were run between Moieties *B′* and *B″*. In all but two of these pairs, full compatibility was exhibited in the fingerbowl trials. The same tests run the next day, November 16, between members of one of the pair of moieties maintained on the same diets (*B′* and *B″*), and the first moiety, *A*, still maintained on crickets and sugar water, showed

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[1] In *R. metallica* reproduction occurs exclusively through fertilized ergatogynes which may make up from 5% to as much as 15% of the colony population and are morphologically indistinguishable from unfertilized sister workers. Thus reproduction is continuous and self-sustaining. Colonies are thus characteristically highly polygynous, and may persist nearly indefinitely under laboratory conditions. "True" females, fully winged and otherwise morphologically typical, can also be produced (and frequently were in the present population) but they seem to be without reproductive function, soon dealating themselves, functioning briefly as workers, and dying in a short time.

results generally confirmatory of those reported earlier, though with somewhat higher levels of aggression than the year before. Thus, of fifty-one pairs tested, 37 showed full compatibility, 8 exhibited "startle" reactions, in 2 cases there was momentary seizure with immediate release, and in 4 cases there was violent attack. Thus noncompatibility between the members of Moieties *B′* and *B″* maintained for a year separately on the same diets, was virtually negligible, while that of moiety *A* and the other pair, maintained on different diets, was generally confirmatory of earlier findings: significantly higher but still, after two years of separation, not nearly comparable with reactions toward the members of another, widely separated population taken near Sutherland, N.S.W., as earlier reported. From all these tests it might have been concluded that, as indicated by pair compatibility encounters, genetic factors were significant but were overlain by a measureable diet factor. In fact, the situation now appears more complex.

Tests with whole nests

On June 27, 1982, a single nest, housing 70–100 workers of the second moiety (*B′*) (nests consisted of earth-filled Lubbock-type glass "sandwiches" stacked) was transferred to the arena of the first moiety (*A*). The introduced nest was placed as far away as possible from the stacked *A* nests in the arena. Arenas used throughout were fabricated from 5/8 cm. thick transparent polyster sheets glued together to form lidless boxes of dimensions 59.5 cm. × 44.5 cm. × 18.5 cm. covered with screening set in wooden frames, and lined with white paper.

The reaction was immediate, violent, and virtually universal. Massed workers from *A* entered the introduced *B′* nest in force, showing unequivocal hostility, seized and dragged out almost the entire *B* population, ultimately killing a large fraction of them. The struggle went on for two days, and resulted in the apparent total occupation of the *B′* nest by *A* workers. Subsequently, this nest was fully incorporated into the *A* colony. Thus the reaction in this experiment was in dramatic contrast to the very limited aggression shown in the pair-tests.

It remained to determine whether similar behavior would occur between moieties *B′* and *B″*, which had been maintained on the same diets and, as described, had exhibited nearly complete compatibility in the pair-tests.

At 2:03 p.m. on November 15, 1982 a nest of moiety *B′* was transferred to the arena of moiety *B″* immediately following the *B′*-*B″* pair-tests described above (workers of *B′* and *B″* which had been used in the pair-tests were not returned to their respective arenas until after the nest-transfer experiment was complete). Again, in the most conspicuous contrast to the experience in *B′*-*B″* pair-tests, but in the same pattern as the reaction when the nest of *B′* was introduced to *A*, immediate mass hostility was exhibited between the two fragments. Eight minutes after introduction it had become general, with many interlocked pairs. By 6:55 p.m. pairs "clinched" and stinging were still present within the introduced *B′* nest, and disturbed young males present in that nest were emerging prematurely. This condition persisted until the following day, by which time it appeared that occupation of the *B′* colony by members of the *B″* moiety had been completed, and things settled down, leaving many dead workers in the arena.

It therefore became clear that previous dietary history was not a dominant factor in mediating the mass hostility so conspicuous between *A* and *B* on the one hand and *B′* and *B″* on the other. It remained to test whether it was in fact the presence of the "foreign" nest with its soil that triggered the mass incompatibility or simply the introduction of many alien workers at one time near the home "site"—a "mass" effect of numbers on the one hand or the possible influence of a familiar site for the test, rather than fingerbowls, on the other. To check this, at 8:00 a.m. on November 18, 1982 ten workers of *B′* were introduced together into the *B″* arena, being placed close to the entrances of the *B″* stack of nests. Reactions were completely compatible until 8:25, when two of the introduced workers were seen being dragged about. This continued for the next five minutes, when one was released, the other being freed by 8:30. There was then entire quiet and apparent compatibility until 3:15 p.m., with no further aggression except that a single worker (living and uninjured) was being dragged about the arena at 12:00 noon of the following day. The remaining nine were apparently "adopted".

Simultaneously with this experiment, the reciprocal transfer was carried out. (10 workers of *B″* introduced into the *B′* arena, near the entrances to the *B′* nests). The experiment was begun at 8:10 a.m. Here also there was complete compatibility, except for two workers seen dragged out of a nest entrance at 3:15 p.m., as observations

TABLE I

A. 10 WORKERS OF GROUP B′ INTRODUCED CLOSE TO THE NEST ENTRANCE OF GROUP B″

Introduced at 8:00 a.m.
Totally amicable reception

8:05	″ ″ ″
8:10	″ ″ ″
8:20	″ ″ ″
8:25	2 ☿ ☿ dragged (after introduction of *A*)
8:30	2 ☿ ☿ being dragged
8:35	1 ☿ ″ ″
8:40	All quiet. No dragging seen.
8:55	All quiet. No dragging seen.
12:00M	1 ☿ seen still being dragged
2:00 pm	All quiet.
3:15 pm	All quiet.

B. 10 WORKERS OF GROUP B″ INTRODUCED CLOSE TO NEST ENTRANCE OF GROUP B′

Introduced at 8:05 a.m.
Totally amicable reception

8:10	″ ″ ″
8:20	″ ″ ″
8:25	″ ″ ″
8:30	All quiet. Most ☿ ☿ inside nest
8:35	″ ″ ″ ″
8:40	″ ″ ″ ″
8:55	″ ″ ″ ″
12:00M	″ ″ ″ ″
2:00 pm	″ ″ ″ ″
3:15 pm	2 ☿ ☿ seen dragged out of nest entrance by 2 ☿ ☿ each, released unharmed.

C. 10 WORKERS OF GROUP A INTRODUCED CLOSE TO NEST ENTRANCE OF GROUP B″

Introduced at 8:15 a.m.

8:20	No attacks whatever. Slight suspicion once or twice. Two or three ☿ ☿ bit briefly at nesting material.
8:23	1 ☿ being dragged about
8:25	2 ☿ ☿ ″ ″ ″
8:35	1 ☿ ″ ″ ″
8:40	All quiet. No further dragging seen.
8:55	″ ″ ″ ″ ″ ″
3:15 pm	″ ″ ″ ″ ″ ″

were closed. They were shortly released unharmed. The contrast with the *B′*-*B″* and *B″*-*B′* nest introductions could hardly have been more vivid.

The same experiment was also carried out between the *A* and *B″* moieties. At 8:15 a.m. on November 18, 10 workers of *A* were introduced into the *B″* arena, again close to the nest entraces of *B″*. Five minutes later there seemed complete compatibility. At 8:23 one worker was seen being dragged about, and at 8:25 two were being so treated. By 8:35 only one such pair was seen, and nothing further developed through the cessation of observations at 9:15 p.m. The results of all three of these experiments are summarized in Table I.

One further confirmation of these results was required. Only three days had elapsed between the confrontation of nest *B ′* with that of *B″* in the *B″* arena, (when the *B′* colony was apparently occupied by the *B″* moiety) and the test introduction of ten *B′* workers into the *B″* arena. If (as seemed likely) the introduced *B′* nest had been occupied by *B″* workers, could not the passive reception of the new *B′* workers be attributed either to the presence of other *B′* workers in the arena or, alternatively (or in addition) might not *B″* workers have become somewhat adapted to *B′* odors, modifying their reaction? Though the introduced *B′* nest in the *B″* arena was removed after the "nest experiment" and before the new experiment with the ten *B′* workers, since but three days had elapsed between experiments, both factors might well have been involved.

To check this, a longer time interval was allowed to intervene before the 10-worker test was repeated. On February 15, 1983, 92 days after the preceding tests (all colonies having been left undisturbed in the meantime) 10 workers of *B″* were again introduced to the *B′* arena, close to the stacked nests of *B′*. Introduction was made at 3:45 p.m. At 4:10 two workers were "clinched" and mutually stinging near a nest entrance. Five minutes later activity at the nest entrance was much diminished, and the stinging pair was not seen. At 4:12, and again at 4:30 p.m., general activity was much diminished but two workers presumed "alien" were being dragged about the arena. At 4:35 p.m. no further hostility had developed, but one or two males had emerged from a *B′* nest. At 5:00 p.m. the arena was entirely quiet, with only two workers outside the nests. An hour later the situation was similarly quiet, but one "alien" worker was being dragged about the arena and two freshly killed workers were in a corner. Except for these three, no further attacks were witnessed. The other seven workers appeared to have been "adopted". It is possible that the attacked workers were in fact egglaying individuals, which may have stimulated the hostile attacks, as found by Holldobler (in litt.) for *Novomessor* in similar situations.

Simultaneously the reciprocal introduction was performed. Ten workers of *B′* were introduced into the *B″* arena in similar fashion, at 3:45 p.m. Here the reaction was even more passive. Observations made at five minute intervals until 5:00 p.m. revealed no conflict whatever. At 6:00 p.m. the same observation was repeated and at 8:00 a.m. the following day the situation remained the same. (Table 2.)

Thus these later tests seemed entirely to confirm the earlier ones: the introduction of a "mass" of ten workers simultaneously provoked reactions not essentially different from those observed in the pair-tests on the one hand, and, on the other, in conspicuous contrast to the situation when whole nests were introduced. This was true with moieties which had been maintained since isolation both on the same and on differing diets.

Discussion

Experiments testing compatibilities between workers from three moieties of an originally single nest population of *Rhytidoponera metallica* after mutual isolation for a period of two years under conditions identical except for diet on the one hand, and for another year between halves of one of these moieties isolated and maintained under entirely identical conditions (including diet) led to some interesting conclusions. Pair-tests in fingerbowls indicated that some incompatibility, with accompanying suspicion or aggression, could occur between individuals from isolated moieties maintained on identical diets for a year, but it was infrequent. Both the frequency and vigor of aggression were somewhat greater when the tests were made between workers drawn from moieties isolated on differing diets but under otherwise identical environmental conditions. Thus it seemed possible that previous dietary history could have a minor role in mediating compatibility, but not an important—much less a decisive—one. Similar tests using ten-worker samples introduced between the moieties in all combinations yielded results essentially the same as the pair-tests, indicating that "mass

TABLE 2

FINAL RECIPROCAL TESTS OF TEN WORKERS BETWEEN COLONY FRAGMENTS B′ AND B″

February 15-16, 1983: 92-93 days after first reciprocal tests 11/15/82

February 15:

Workers *B*□ into *B*#

3:45 p.m. 10 workers introduced from B□

Many workers clustered inside nest entrance, but no hostility, *until*

4:10 p.m. Two workers "clinched" and stinging near nest entrance.

4:15 p.m. Activity much diminished at nest entrance. The "clinched" pair not seen.

4:25 p.m. Generally quiet but two "alien" workers seen being dragged in arena.

4:30 p.m. Generally very quiet, but the two "alien" workers still being dragged in arena.

4:35 p.m. *Some activity around nest entrance, and one or two males emerging.* No hostility observed.

5:00 p.m. Entirely quiet in arena with only two workers out. Some activity about nest entrance. No conflict.

6:00 p.m. One "alien" worker seen being dragged by two others. Otherwise all normal and quiet.

February 16:

8:00 a.m. Arena quiet with one or two males emerging from nest.
However, 1 dead worker (presumably alien) being dragged about arena, and two freshly killed workers in corner. These three presumably *B*□ aliens.

Thus the general picture was one of *no general arousal* (as before) but ultimate individual hostility to three out of ten workers, with eventual killing. Entirely confirmatory of earlier results.

February 15:

Workers *B*# into *B*□:

3:45 p.m. *10 workers introduced from B.*
All introduced workers immediately disappeared into *B*□ nests, without causing any sign of disturbance.

4:20 p.m. Only 5 workers seen outside nests. No conflict and no signs of disturbance.

4:25 p.m. All very quiet in arena. Only 2 workers out. No conflict.

4:30 p.m. All entirely quiet. 1 worker only seen in arena. No conflict.

4:35 p.m. Completely quiet. One worker seen in arena. No conflict.

5:00 p.m. Completely quiet. One worker seen in arena. No conflict.

6:00 p.m. All completely quiet. 1 worker seen in arena. No conflict.

TABLE 2 (CONTINUED)

FINAL RECIPROCAL TESTS OF TEN WORKERS BETWEEN COLONY FRAGMENTS B′ AND B″

February 16:

8:00 a.m. Arena entirely quiet. Only 2 workers seen in arena. No hostility, and no "alien" bodies found.

> Thus, throughout this run, there was no hostility of any kind between host and introduced individual workers. It should be noted that *B*☐ was markedly less numerous and strong than *B#*, and while *B#* contained considerable regenerating brood, none was found in *B*☐.

These test, therefore, were confirmatory of the earlier ones run on November 15, 1982. Like them, they emphasize the important role played by site nest marking, as opposed to individual odor characteristics—an interesting convergence to the Traniello findings (Naturwissenschaften 67, S. 361 (1980).

effects" were not demonstrable and almost certainly not significantly involved.

In sharp contrast, the introduction of long-occupied earth-containing Lubbock nests of one moiety into the arena of another, whether the moieties had been maintained on identical or non-identical diets, was very different, resulting in vigorous mass attacks and the invasion and occupation of the introduced nest.

This dramatic contrast suggests that, as in the cases of *Pogonomyrmex, Oecophylla,* and *Lasius*, colony-specific nest-site marking with gut contents (perhaps containing colony-specific pheromones) is important and regularly employed even in so primitive an ant, and one with so diffuse and vagile a colony structure, as *Rhytidoponera metallica.* This conclusion is reinforced by the extensive (though apparently random) marking of the substrate with fecal droplets that we have found general in arenas containing long-occupied *metallica* nests, a typical example of which is illustrated in Figure I. It strongly supports the recent findings of Holldobler (unpublished ms.) that in the Ponerine ants *Paltothyreus tarsatus*, a species of *Leptogenys* and in two species of *Hypoponera* fecal droplets deposited at the nest entrances can serve as orientation cues in homing, while in the last genus colony-specific preferences for these markings could be demonstrated.

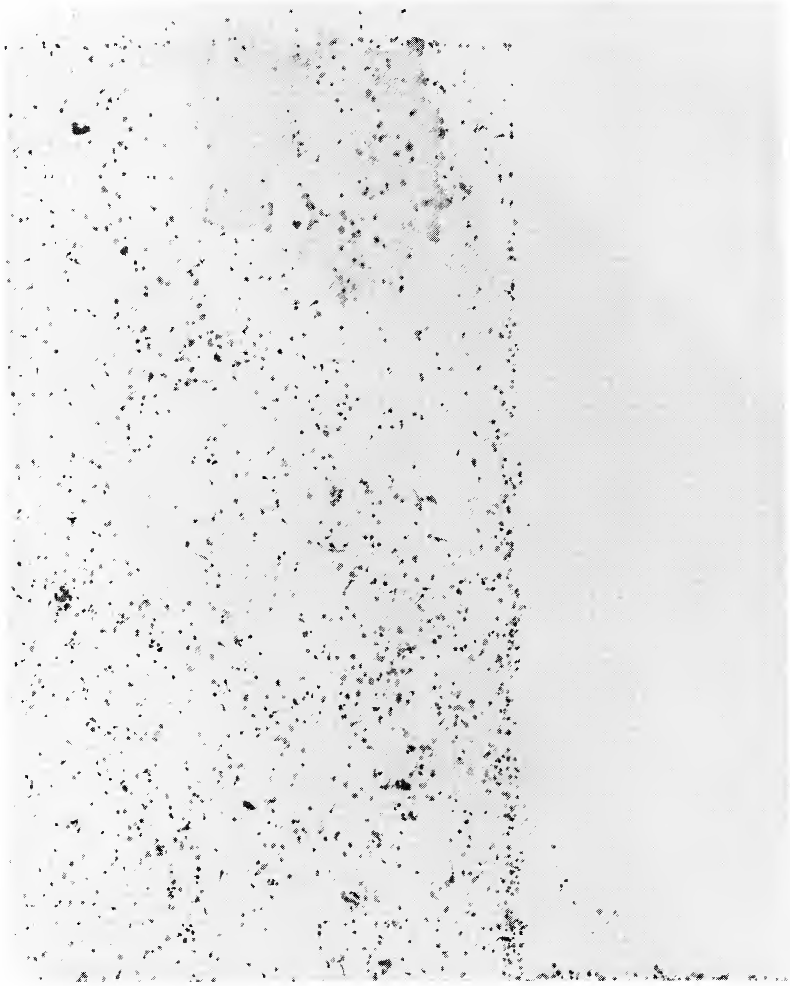

Figure 1. Random marking with fecal droplets of territory surrounding nest in *Rhytidoponera metallica* (Straight edge corresponds to margin of Lubbock nest.)

SUMMARY AND CONCLUSIONS

The following conclusions seem probable from the present work: (1) As suggested in a previous paper (Haskins and Haskins, 1979) "recognition" between the members of fragments of a single population separated for a year or more appears to remain on the whole stable through several "generations" of workers which have not been in direct contact during their ontogeny, when those workers are pair-tested in fingerbowls on an individual basis. This compatibility is not universal, however. Incompatibility was observed in a few cases even between workers of two halves of a population separated for a year or more but maintained under identical environmental conditions, including diet, whether tested in pairs or in groups of ten. When the diet had consistently differed markedly throughout the period of separation, the numbers of workers exhibiting incompatibility appeared somewhat increased, but was still a minor proportion. It is possible that such individuals eliciting attack were in fact laying workers, as found by Holldobler in *Novomessor.* (2) When earth-containing Lubbock nests occupied by one fraction of the divided population throughout the periods of separation were introduced into the arena of another, the situation was dramatically altered. Mass hositility and mass raiding of the introduced nest by the recipient moiety regularly followed, regardless of whether the preceding dietary history was the same or different. We conclude that, as reported by other investigators in a number of higher ant genera (*Pogonomyrmex, Oecophylla, Lasius*) and in the Ponerine genus *Hypoponera*) colony-specific nest site marking is important also in *Rhytidoponera metallica*, despite its relative primitiveness and the typical diffuseness and vagility of its colonies. Typical random markings of the floors of arenas about earth-containing Lubbock nests long occupied by colonies of *metallica*, as illustrated, indicate that, as with at least some higher ants, and in several Ponerine genera including *Paltothyreus, Leptogenys* and *Hypoponera*, fecal contents are the characteristic marking "vehicle", perhaps including, as in the higher ants, colony-specific pheromones. If this is true of *R. metallica,* as suggested in the experiments reported, it becomes interesting to consider the factors involved in mediating this specific reaction between two halves of a single population separated for less than two years and maintained on identical diets and in identical arenas placed side by side on the same laboratory bench during that period. No evidence has been found of trail marking, or indeed of trail laying, in *R. metallica.*

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CAPTURE OF BOMBARDIER BEETLES BY ANT LION LARVAE[1]

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Ant lions (larvae of Myrmeleontidae) are well-known for their unique method of prey capture (Wheeler, 1930). They construct a conical pit in the sand and lie buried at the bottom with only their sickle-shaped mandibles, or head and mandibles, exposed. When an ambulatory arthropod falls into the pit it is seized and pierced by the mandibles and sucked dry. Bombardier beetles, like other Carabidae, are ground foragers and thus may be expected to fall into ant lion pits. However, due to their singularly effective chemical defense, some question remained whether they might be vulnerable to capture by ant lions. Bombardier beetles respond to attack by ejecting an aimed spray of hot (100° C) repellent quinones from the tip of the abdomen (Eisner, 1958; Aneshansley *et al.,* 1969). The spray is an effective deterrent to a number of insectivores (Eisner, 1958; Eisner and Dean, 1976). Several authors (Turner, 1915; Wheeler, 1930; Lucas and Brockmann, 1981) have observed that ant lions may pull their prey under the sand after grasping it. Lucas and Brockman (1981) suggest that this behavior may protect ant lions from aggressive prey. We here report that ant lions can capture bombardier beetles providing the ant lions have pulled their head beneath the sand by the time the beetles eject their spray.

Our observations were made at the Archbold Biological Station, Lake Placid, Highlands County, Florida, where the ant lions (*Myrmeleon crudelis* larvae) and bombardier beetles (*Brachinus* spp.) were taken. Fifteen ant lions were placed in each of three metal boxes (30 × 44 × 18 cm high) filled with sand to a depth of 8 cm. After the ant lions had constructed pits, bombardier beetles were released individually into the boxes and observed until they slid or walked into a pit and were seized by an ant lion. Two things were noted each time a beetle "fired" after being grasped: (1) whether the

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ant lion's head was above the sand or had already been withdrawn below the surface, and (2) whether the beetle was retained in the ant lion's hold or released. Detection of firings posed no problem since the discharges are accompanied by audible detonations (Eisner, 1958).

A total of 37 captures were witnessed. Five of these involved beetles that were held only momentarily by the larvae and released without being induced to discharge. Another three involved beetles that also failed to discharge, although they were held persistently and were eventually killed and eaten. The remaining 29 encounters resulted in bombardier firings (Table 1). Eighteen of these ended with the beetle escaping: single firings were involved in each case, and the ant lion's head was in all instances exposed when the firing occurred. The beetles were released unharmed promptly after the discharge. In the other 11 encounters in which firings occurred, the ant lions had withdrawn the head beneath the sand by the time the beetles fired, and although there were sometimes repeated discharges, only one beetle secured its freedom. The other 10 were killed and eaten. It is clear that with their heads submerged, the ant lions are much less likely to be repelled by the spray.

One wonders why the larvae did not consistently withdraw into the sand the moment they seized a beetle. We had noted that ant lions commonly pull their victims into the sand, but usually only when the prey is smaller than the predator itself. The beetles that we tested were roughly of the size of the ant lions or even larger, suggesting that the larvae may simply have lacked the strength to pull themselves under while holding such prey. That large insects are indeed commonly "feasted upon on the surface" had previously been noted (MacLachlan, 1865).

In three instances when beetles fired at submerged ant lions, the latter pulled away from the site of discharge by tunneling backward just beneath the sand surface while keeping the beetle in tow. The option of burrowing without loss of prey, in a substrate where burrowing can potentially be quicker than the rate of diffusion of a repellent chemical, could prove helpful to ant lions also in their capture of chemically protected animals other than bombardier beetles. Indeed, a substantial fraction of prey items ordinarily available to ant lion larvae, including ants, carabid and staphylinid beetles, and millipeds, possess dischargeable defensive glands. Interestingly,

Table 1. Summary of the outcomes of all observed encounters between ant lions and bombardier beetles in which the beetle "fired" defensive secretion. Beetles were more likely to be killed if the ant lion had pulled itself under the sand by the time the beetle fired [$p < 0.001$, $\chi^2 = 24.8$, 1 d.f., with a continuity correction used (Snedecor and Cochran, 1967)].

No. Encounters	Position of Ant Lion	No. Firings/Encounter	Fate of Beetle
18	head exposed	1	all escaped
11	head beneath sand	2.7 ±1.7 (range: 1–5)	1 escaped 10 eaten

one of the few other predators known to be able to capture bombardier beetles is a tabanid larva that lies in wait while semisubmerged in mud and feeds on the beetles by catching them by a leg and dragging them into the substrate (Nowicki and Eisner, 1983).

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REPRODUCTIVE PLASTICITY IN YELLOWJACKET WASPS: A POLYGYNOUS, PERENNIAL COLONY OF *VESPULA MACULIFRONS*

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Introduction

Social wasps in the family Vespidae are thought to have originated in the southeast Asian tropics (Richards, 1971; Spradbery, 1973a; but see Carpenter, 1982). Members of the subfamily Vespinae presumably evolved monogyny and an annual colony cycle as adaptations to cold winters in north temperate regions. Exceptions to this characteristic social organization and colony ontogeny in vespines have become increasingly apparent (Ross & Matthews, 1982). In climatically favorable areas of their natural range (Tissot & Robinson, 1954; Duncan, 1939; Vuillaume et al., 1969; Akre et al., 1980), and in areas newly colonized (Spradbery, 1973b; Perrott, 1975; Thomas, 1960) several species of *Vespula* (subgenus *Paravespula)* facultatively form polygynous, perennial colonies. This capacity demonstrates great plasticity in the behavioral ecology of *Paravespula* species, and is intriguing in light of its implications for theories concerning the evolution of eusociality in the Vespidae.

We here report the discovery of a polygynous, perennial nest of *Vespula maculifrons* (Buysson) from the southeastern U.S. With this discovery, all non-parasitic Nearctic representatives of the subgenus *Paravespula* have been shown to exhibit this atypical colony ontogeny.

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METHODS

Nest site and excavation

A large *Vespula maculifrons* colony was discovered on 25 November 1981, nesting in sandy soil in sand pine scrub habitat at the Archbold Biological Station in Highlands County, Florida (27° 11′ N, 81° 21′ W). Flight from the colony was observed on 1 February 1982 and 11 March 1982 and we excavated the colony on 20 March 1982.

We placed traps (similar to Fig. 193 in Edwards, 1980) on each of the two entrances of the nest in the early morning and aroused the nest by pounding the ground. Workers (and some males) flying from the nest were caught in the traps. We discharged a carbon dioxide fire extinguisher into one of the entrances, which chilled and partially narcotized wasps remaining inside; we then excavated the nest.

Because of inadequate narcosis of the wasps and because the nest was intersected by several large roots, we were unable to remove the nest intact. Many combs were broken into several pieces. The pieces were placed in large polyethylene bags and kept frozen until examined.

Analysis of nest contents

We traced each comb fragment onto a sheet of paper of uniform weight, and recorded a visual estimate of the proportions of cells containing capped brood, eggs, and uncapped brood. Of those cells which contained eggs, we estimated the proportion which contained more than one egg. Any large (queen-size) cells present were counted individually in each of the above categories.

To determine the comb area of each fragment we cut out and weighed each tracing (weight × cm^2/g for the paper = area). We counted the number of small (worker-size) cells on 12 representative comb fragments totaling 3964 cells. We used the mean number of $cells/cm^2$ to estimate the number of cells in each of the above cell content categories for each fragment. These per-fragment estimates were then summed for the entire nest (205 comb fragments).

Sex ratio of colony

We estimated the sex ratio of the capped brood in small cells by removing 33 pupae or pharate adults from each of 16 comb frag-

Table 1 — Brood composition of cells in perennial *V. maculifrons* colony (percentages in parentheses). Values for small cells are estimates, those for large cells are counts.

		Number of cells containing:				
	empty	single eggs	supernumerary eggs	larvae	capped brood	total
Small cells	40,593 (40.8)	9,629 (9.7)	6,945 (7.0)	22,813 (23.0)	19,396 (19.5)	99,376 (100)
Large cells	257 (34.5)	308 (41.4)	61 (8.2)	48 (6.5)	70 (9.4)	744 (100)
Total	40,850	9,937	7,006	22,861	19,466	100,120

ments and determining their sex (n = 528). We counted and sexed all pupae and pharate adults in large cells.

To estimate the sex ratio of the adult population of the nest we weighed the two sub-populations of workers and males retrieved from the nest interior and the entrance traps. We then weighed, counted, and sexed 4 and 5 samples, respectively, of these populations. The mean number of wasps/g and the mean sex ratios of these samples were extrapolated to the population and sex ratio of the colony adults as a whole.

Reproductive status of queens and workers

We dissected all queens in the nest and classified their reproductive status as follows: "Developed" ovaries had oocytes greater than 2 mm in length, "undeveloped" ovaries had oocytes less than 1 mm in length. "Inseminated" queens had spermatozoa visible microscopically in a squash mount of their spermathecae, while "not inseminated" queens had none.

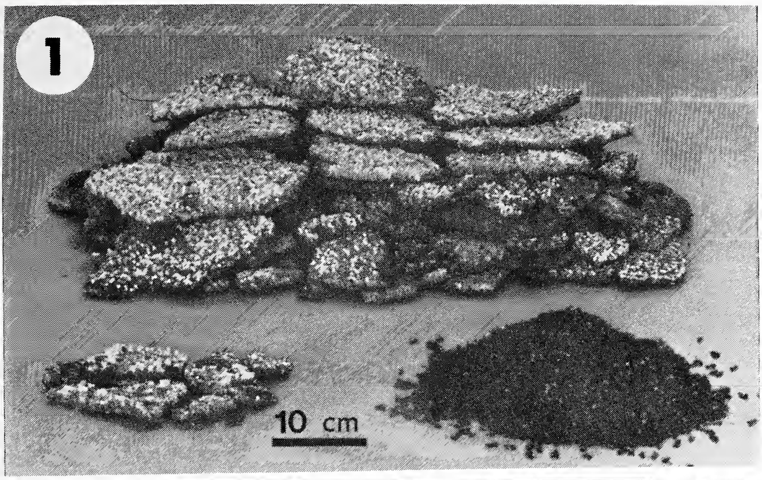
To estimate the reproductive status of workers in the colony, we dissected a random sample of 100 workers and examined their ovaries. We classified them as "undeveloped" [ovarian index less than 1 (Cumber, 1949), oocytes not developed], "moderately developed" (ovarian index 1–2, maximum oocyte length 0.9 mm), or "well developed" (ovarian index 3–12, oocyte length greater than 1.0 mm).

RESULTS

Nest structure and brood composition

Estimated cell number and brood composition of the nest are given in Table 1 (see also Fig. 1). From comb measurements the volume of the nest cavity was estimated to be ca. 80 liters. The nest structure was roughly ellipsoid, 71 cm by 45 cm. Two nest entrances were in use at the time of discovery; flight activity from each was 95 ± 14 and 15 ± 6 wasps/min returning at midday on 11 March (here and throughout this paper numbers in this form denote mean ± 1 SD, except as noted). The combs were present in at least 15 layers. Total comb area was 15,652 cm^2; the combs contained an estimated 100,120 cells.

Small (worker-size) cells comprised 99.3% of all cells in the nest (4.0 ± 0.20 mm in diameter between parallel sides, range 3.7–4.7 mm, n = 44). Of the small cells, 16.7% contained eggs; 41.9% of



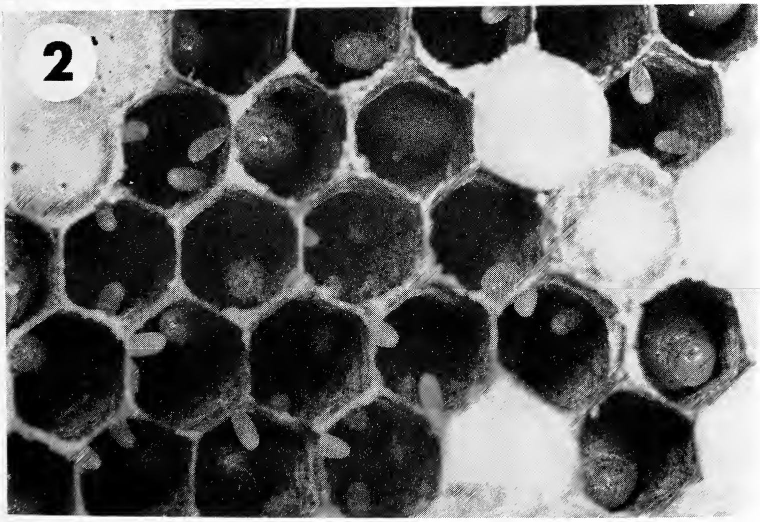


Figure 1. Comb fragments and adult inhabitants of perennial *V. maculifrons* colony. Combs positioned in left foreground contain large cells.

Figure 2. Supernumerary eggs and immatures in small cells of perennial *V. maculifrons* colony. Note positions of eggs high on the cell walls.

these contained supernumerary eggs (Fig. 2). In a sample of 119 small cells containing eggs, up to 5 eggs/cell were present (1.9 ± 0.89 eggs/cell). Most of these eggs were positioned high on the cell walls. Forty-one percent of the small cells contained no brood or eggs. Most of these empty cells had reduced cell walls or were papered over indicating disuse at the time of collection (Duncan, 1939).

The sex ratio of pupae and pharate adults in capped small cells is presented in Table 2. Note that more than half of the capped brood sampled were males.

We counted 744 large cells (5.8 ± 0.20 mm in diameter between parallel sides, range 5.4–6.1 mm, n = 22) in the nest (Table 1); these were located on 8 comb fragments, 2 of which contained exclusively large cells. Over one-third (34.5%) of the large cells were empty; some had been papered over and the cell walls reduced. Of the 49.6% of large cells with eggs, 16.5% contained supernumerary eggs. One small comb of 29 cells appeared newly constructed. The paper was light and fragile, no meconia were present, cells on the perimeter were shallow, and each cell contained a single egg.

The capped large cells contained predominantly queen pupae and pharate adults (Table 2), but a large percentage (30.4%) were males.

Adult inhabitants

An estimated total of 11,817 ± 210 (95% confidence interval) adult wasps were collected (Table 2). Of these adults, 25.8 ± 2.9% (95% CI) were males. Of the remaining female adults, only 23 were queens. An undetermined number of flying workers and males were not captured as the nest was collected.

We dissected all 23 queens found within the colony. Fifteen of these queens had undeveloped ovaries; only one of these was inseminated. Six queens were inseminated and possessed well developed ovaries. Two queens were classified as senescent. One of these had well developed ovaries but had no spermatozoa in her spermatheca; the oviducts appeared degenerated, pigmented, and clogged. Very little fat body was present. The other queen, found in the bottom third of the nest cavity, had apparently been dead for some time. Some abdominal sclerites had been punctured and the viscera were desiccated. One wing was missing while the other was very frayed. Both senescent queens and the six inseminated queens with developed ovaries had frayed wings and abdominal cuticular markings characteristic of physogastric, aged queens (Spradbery, 1973a).

Table 2 — Number of capped brood and captured adults of each caste in perennial *V. maculifrons* colony (percentages in parentheses). Values for adults and capped brood in small cells are estimates, those for capped brood in large cells are counts.

	Queens	Males	Workers	Total
Capped brood				
large cells	49 (69.6)	21 (30.4)	——	70 (100)
small cells	——	10,454 (53.9)	8,941 (46.1)	19,395 (100)
Adults	23 (0.2)	3,044 (25.8)	8,749 (74.0)	11,816 (100)

We dissected 100 workers chosen at random. While 74% of the workers exhibited no ovarian development, 12% had moderately developed ovaries, and 14% had well developed ovaries.

Discussion

Although this is the first record of such a nest for *V. maculifrons,* the nest size and number of inhabitants are typical for polygynous, perennial colonies of other *Paravespula* species (Ross & Matthews, 1982; Spradbery, 1973a; Edwards, 1980). In contrast, annual colonies of *V. maculifrons* from northern Georgia and western North Carolina average 6,104 small cells and 2,551 large cells at their greatest development (MacDonald & Matthews, 1981). The perennial *V. maculifrons* colony, while containing fewer large cells, had more than 16 times as many small cells as average conspecific annual nests. Perennial nests of *V. germanica* (F.) from Tasmania and New Zealand are reported to contain up to 180 combs and four million cells (Thomas, 1960; Spradbery, 1973b). The study colony also contained almost twice as many adult workers as the most populous conspecific annual colony studied by MacDonald & Matthews (1981).

The prodigious size of perennial, polygynous *Vespula* colonies does not result simply from the cumulative effects of two seasons of growth. The pre-existing nest structure and worker force presumably support a rate of production by each of the colony's queens early in the season attained only much later by annual colonies. In addition, newly recruited queens in such a colony avoid the inherent risks of haplometrotic colony founding, such as predation while foraging and early colony failure (Archer, 1980).

Several to 50 queens are typically present in perennial *Vespula* colonies, although Spradbery (1973b) found up to 1000 in perennial nests of *V. germanica* in Tasmania. On the other hand, Thomas (1960) reported only a single queen in each of the perennial *V. germanica* nests he studied from New Zealand. Six of the 23 queens we found in the study colony were inseminated and possessed well developed ovaries; these were probably functional queens. The large number of worker brood we found corroborates the evidence for several egg laying queens. An additional two queens were probably former reproductives. The remaining queens could have emerged recently, as queens at all stages of development were present in the colony. Newly emerged queens in perennial colonies may mate in the nest with sibs (Ross, 1983; R. E. Wagner, personal communication) or embark on mating flights and return to the parental nest as newly recruited reproductives (Spradbery, 1973a, b). Thus, functional queens in polygynous *Vespula* colonies are typically regarded as being daughters of the original foundress (Spradbery, 1973b; Edwards, 1980; but see Ross & Matthews, 1982).

The study colony contained fewer large cells than do average annual *V. maculifrons* colonies, indicating that fewer than normal queens had been reared during the first developmental season. The presence of large numbers of male and queen brood and adults indicates that the colony had been rearing reproductives throughout the winter [as is typical for other perennial *Vespula* (Edwards, 1980)], and a newly initiated queen comb with eggs suggests that queens would have continued to have been reared into the spring. Presumably the number of queens produced over two seasons would far exceed the productivity of an annual colony.

Over one-half of the capped brood sampled in small cells were males. The occurrence of so many male brood in the spring, the great number of supernumerary eggs, and the positions of eggs high on the cell walls suggest the likelihood of laying workers (R. W. Matthews, personal communication; Akre et al., 1982). Dissections confirmed that at least 14% of the workers possessed well developed ovaries and were probably ovipositing.

Greater than 30% of the brood being reared in large cells at the time of colony collection were males. This represents a considerably larger figure than has been previously reported for annual *Paravespula* colonies, in which large cells contain almost exclusively queen brood (MacDonald & Matthews, 1981; Spradbery, 1971; MacDonald et al., 1974). Perhaps pressure to find empty cells resulted in workers ovipositing in large cells.

The presence of many laying workers in large, diffuse nest structures is not unexpected if queens exert reproductive control via the dissemination of volatile or trophic pheromones (Ikan et al., 1969; Landolt et al., 1977). The percentages of laying workers and supernumerary eggs we found were in close agreement to those reported for a queenless nest of *Vespa simillima* Smith (Yamane, 1974). Laying workers in annual vespine colonies may be common during the phase of colony decline, also suggesting diminished queen control (R. W. Matthews, personal communication; Montagner, 1966; Akre et al., 1982). These workers appear to occupy regions of the nest not frequented by the queen (Edwards, 1980).

Vespine workers may indeed represent "hopeful reproductives" (West Eberhard, 1978; Lin & Michener, 1972): while many workers never lay eggs, a significant proportion of them do and all can be regarded as having some probability of directly contributing genes to subsequent generations. This factor has not been adequately considered by theories attempting to explain the origin of eusociality by reference to a polarized view of reproductive castes (Hamilton, 1964a, b; Alexander, 1974; Spradbery, 1973a).

Our discovery of an overwintered, polygynous colony of *V. maculifrons* completes the series of free-living North American species in the subgenus *Paravespula* with this life history. No members of the subgenus *Vespula* or the aerial-nesting genus *Dolichovespula* have been reported to exhibit this atypical colony cycle (Akre & Reed, 1981). Perennial, polygynous colonies have been reported for *V. squamosa* (Tissot & Robinson, 1954; Ross & Matthews, 1982), whose affinities with other *Vespula* species are unclear (Akre et al., 1980; see also Archer, 1981).

The ability to retain colony social cohesion through two developmental seasons and to tolerate the existence of multiple functional queens points to great ecological and behavioral plasticity in the subgenus *Paravespula.* Members of this group differ from other temperate vespines in additional biological attributes including: (1) delay of reproductive production until fall or early winter and consequent increased duration of colony life span, (2) development of populous colonies and large nests, (3) ability to successfully colonize new areas of the world when introduced by man, and (4) tendency for workers to become scavengers on carrion or human food and refuse in the late summer. The common possession of these derived features supports a monophyletic origin of this group within the Vespinae. The interaction of these same features accounts for the greater public health importance of these species relative to other vespines.

The vespid subfamilies Polistinae and Vespinae, comprised exclusively of eusocial species, are thought to have evolved from a common social ancestor (Carpenter, 1982). The Polistinae are diverse in their methods of colony founding and number of functional reproductives (Iwata, 1976; Jeanne, 1980); their social behavior appears loosely associated with a tropical or temperate existence. In contrast, all vespines are characteristically haplometrotic and monogynous, and form annual colonies (thought to be temperate adaptations), regardless of their distribution (Iwata, 1976; van der Vecht, 1957; Akre et al., 1980). Thus, the characteristic social organization of the Vespinae appears to be the expression of a common ancestral trait, rather than an immediate response to ecological conditions. This interpretation suggests that the Vespinae may have originated in temperate regions rather than in the tropics (Carpenter, 1982), as has been previously assumed.

The evolution of eusociality in vespids is thought to have occurred by one of two general routes: (1) the subsocial or matrifilial monogynous route in which prolonged maternal care provides opportunities for social interaction between a foundress and her offspring (Evans & West Eberhard, 1970; Spradbery, 1973a), or (2) the polygynous or parasocial route in which nesting associations of foundresses of the same generation lead to increasingly complex levels of social organization (Lin & Michener, 1972; West Eberhard, 1978). Insofar as the occurrence of occasional polygyny in the Vespinae bears on the social origins of this group, the recurrent ability of colonies to tolerate multiple functional reproductives strengthens an argument for the evolution of eusociality via the parasocial route in the Polistinae + Vespinae. The occurrence of perennial, polygynous colonies of *Vespula* may be viewed as a reversion to a more primitive behavioral and physiological mode. Further investigations of this phenomenon should aid in elucidating the environmental and social contexts under which it occurs.

SUMMARY

We describe a polygynous, overwintering colony of *Vespula maculifrons* from central Florida. The nest contained about 100,000 cells; many brood of all castes, at all developmental stages; over 8000 adult workers and 3000 adult males; and 23 adult queens, at least six of which were functional egg-layers. Supernumerary eggs were found in 7000 of the small cells, often placed high on the cell walls. Of 100 workers dissected, 14 exhibited substantially developed ovaries and had probably been laying eggs.

With this report, all non-parasitic neartic species of the subgenus *Paravespula* are known to occasionally exhibit this unusual life history, in contrast to the uniformly monogynous, annual species in the subgenus *Vespula*. *Paravespula* also exhibit more plasticity in their nesting and foraging habits. We discuss the ability of perennial colonies to tolerate multiple queens and relate this ability to the question of the evolution of eusociality in the Polistinae+Vespinae.

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NEST BUILDING BEHAVIOR AND DEVELOPMENT OF THE SUNFLOWER LEAFCUTTER BEE: *EUMEGACHILE (SAYAPIS) PUGNATA* (SAY) *(HYMENOPTERA: MEGACHILIDAE)*

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Introduction

Eumegachile (Sayapis) pugnata (Say), formerly *Megachile (Sayapis) pugnata* Say (Mitchell 1981), is a large (13–18 mm) leafcutter bee that is widely distributed throughout the United States and southern Canada (Hurd 1979). *Eumegachile pugnata* nests in a wide variety of situations including man-made borings in wood and is easily trapped in the wild (Medler 1964, Krombein 1967, Parker & Frohlich in prep.).

Since *E. pugnata* is oligolectic to flowers of the Compositae (Tepedino & Frohlich 1982), attention has recently been directed toward developing the bee as a pollinator of commercial sunflower. Parker and Frohlich (1983) described its use in hybrid sunflower pollination; Tepedino and Frohlich (1982) discussed mortality factors, pollen utilization and sex ratio; and Frohlich (1982) described various aspects of its ecology. The purpose of this study was to

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elucidate the within-nest biology of *E. pugnata*, including development, nesting and provisioning behaviors, and nest architecture.

METHODS AND MATERIALS

Within-nest behaviors were observed from a wooden box (1×1×3m) located in a green house (6×6×5m). Nests of 2 types were fastened to cardboard sheets which were then mounted onto the observation box. 1. Elderberry sticks that had been drilled (9mm diameter) and planed lengthwise, were covered with a glass plate to expose the boring; and 2. Glass tubes with plastic inserts were taped to cigarette filters to facilitate handling (8mm diameter) (Fig. 1). The end of the glass tube that served as the nest entrance was dipped in black India ink and inserted into a cork ring to allow the bee secure footing (Torchio 1972). Nests were darkened with paper slip covers until cell construction began. Removal of slip covers after the onset of nesting did not appear to affect females, though no females nested in uncovered nests. A small swamp cooler mounted above the wooden box maintained temperatures below 40° C in order to avoid egg-larval mortality due to heat buildup.

Commercial *Helianthus annuus* L. and 3 garden variety composites (Cosmos, Bachelor's Button, Callendula) were provided as pollen and nectar sources in beds of approximately equal size. Because of its usefulness in similar studies of other megachilids (Parker & Tepedino 1982, Frohlich 1983) *Oenothera hookeri* T. & G. was used as nest partition material. A tape recorder, otoscope, and stopwatch facilitated within nest observations.

As nests were completed, most were removed and replaced. Completed nests were incubated at 30° C and used to study aspects of larval development and behavior. The glass plates on the elderberry sticks were removed prior to incubation and replaced with clear plastic food wrap. The plastic inserts of the glass tube nests were also removed and provisions containing eggs were cut away and placed separately in BEEM® capsules, commonly used in electron microscopy. As each egg eclosed, the emergent instar was marked with a tiny spot of pink fluorescent Day-Glo® powder applied with a watchmaker's forceps. Disappearance of spots indicated molting and new marks were made. Larvae were inspected several times a day and various behaviors associated with each instar were observed

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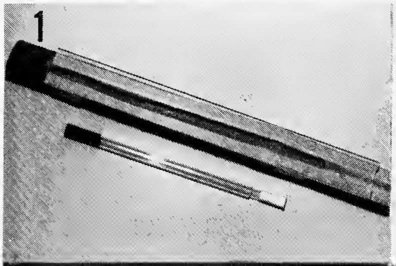

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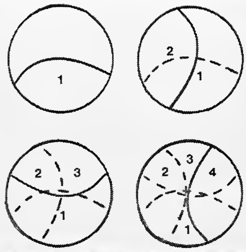

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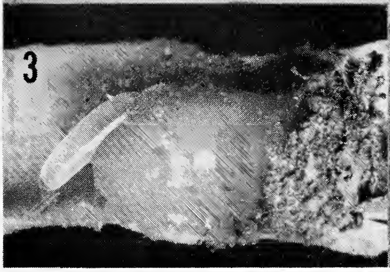

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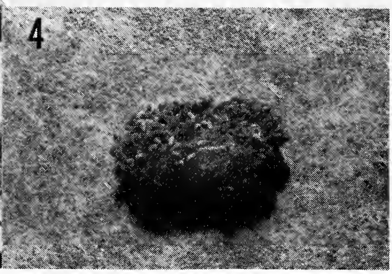

Figure 1. Glass covered stick and glass tube with plastic insert used for nests.

Figure 2. Schematic drawing showing construction of a partition. Whole leaf pieces are added in sequence (starting with No. 1) and are sealed to the nest wall, each subsequent piece partially covering the previous piece.

Figure 3. Egg in late embryogenesis, attached to provision.

Figure 4. Cocoon containing prepupal larva, showing incorporated fecal pellets.

with a dissecting microscope fitted with fiber optics lighting (to reduce heat load). Larvae that died and examples of each instar were preserved in picroformalin.

RESULTS

Within-Nest Biology

Females began nesting in the greenhouse 4 June 1981, within 3 days after release. The following is a composite account, in temporal sequence, from selection and preparation of a new nest to nest closure. Each activity discussed was observed for several different females.

Nest Selection — Preparation. Before beginning cell construction females investigated both types of potential nest substrates. Sticks and glass tubes that were not covered (darkened) in some way were either ignored or only casually inspected. Usually before preparing her nest a female would sit quietly at the back of the stick or just inside the entrance for a few minutes to an hour. Once a choice was made, extraneous pith particles were picked up with the mandibles and jettisoned outside of the nest during flight. Females did not make the nest walls completely smooth but cut away gross irregularities with the mandibles and removed large pith particles. As many as 24 pith removal trips were observed before nest initiation. During this period of preparation females were especially sensitive to any activity around the nest site. On several occasions females abandoned nests when an observer approached the nest entrance. In general nesting *E. pugnata* were very wary of intruders.

Partition Building. Basal and apical partitions of each cell were constructed similarly and were composed of the same materials so construction details of each will be considered together.

After preparing her nest site for cell construction the female left the nest to retrieve a strip of *O. hookeri* leaf. The bee landed on the plant, straddling the leaf, and quickly cut, while walking backwards, a thin strip ½ to ¾ as long as her body, and returned to the nest. After entering the nest with the unmodified leaf in her mandibles the female masticated it into a shiny ball which was pressed into the back wall, or along the floor where the cell was to be initiated. From the leaf material a thin ring of moist chewed leaf was formed around the inner circumference of the tunnel. Three to 6 trips were usually required to complete the ring. The female then left and returned with a large oval-shaped leaf piece that was carried beneath the body by all 6 legs and the mandibles.

The mandible and front legs were used to spread and position the leaf piece along a portion of the chewed ring thus closing a portion of the circle (Fig. 2). The outer edge of the unmodified leaf confluent with the ring was chewed into the ring and the 2 were sealed. The female also used her head in an extremely fast jackhammer-like motion to tamp the ring and leaf pieces together. The clypeus and proximal outer surfaces of the mandibles appeared to be the point of impact. Subsequent leaf pieces were brought in and fastened to the ring in the same manner until the base of the cell was covered (Fig. 2). Three or 4 oval-shaped leaf pieces were required to form the base of the partition. After the leaf pieces were positioned more masticated *Oenothera* strips were used to form a second ring in the same position as the first thus further sealing the leaf pieces to the walls.

Once the second ring was in place the female continued to add to it by placing more masticated *Oenothera* on the inside of the ring and chewing and spreading it toward the center with the mandibles until a thin layer of moist leaf pulp covered the whole leaf pieces. Next, moist soil particles (not mud) were collected and placed at the base of the partition. These clods were cut into many tiny slivers which were taken singly or in groups and pressed into the pulpy partition with the mouthparts. These were then tamped in with the head as before. *Oenothera* and soil particles were retrieved alternately until the partition approached its ultimate size.

As the partition increased in thickness the periods of tamping with the head grew longer. During the last half hour of partition construction tamping often lasted as long as 5 minutes and became combined with a grooming behavior. Before tamping the female groomed the posterior portion of the abdomen with her hind legs and collected a droplet of fluid that was passed to the middle legs and then the front legs. The fore tarsi with the secretion were then used to wipe down the face and antennae; especially the clypeal and mandibular areas that came in contact with the partition during tamping. Possibly the act of tamping or packing at this point not only shaped and defined the partition but incorporated a secretion as well.

After the last leaf pulp and soil were added the concave surface of the partition was further modified. The female laid on her back and groomed the posterior portion of the abdomen and again passed a droplet of liquid to the middle and fore-legs. This time the secretion was placed between the mandibles and chewed vigorously. The female then chewed and licked the outer surface of the partition. As this was finished, provisioning ensued. No threshold or rudiment of an apical partition was laid down prior to provisioning.

Provisioning. The female first backed into the cell with a load of pollen carried on the abdominal scopa. Deposition of the first pollen load began about 3 mm in front of the basal partition and was spread backwards with the feet in the kicking motion. The pollen was removed first by the hind legs rubbing together toward the middle of the sterna. Pollen remaining on the venter between the fore and mid-legs was scraped off initially by the mid-legs and then the fore-legs. Both pairs of legs then transferred the pollen to the hind legs where it was deposited by rubbing the legs together in a "hand washing motion." Pollen removal by the legs was aided by a complementary telescoping motion of the abdomen and elevation of sternal hairs. As the legs brushed pollen from the side, toward mid-sternum and backwards, the abdomen contracted so that the tarsi came in contact with the entire surface of the abdomen. The abdomen then elongated and the contraction-brushing motion began again.

The first load of nectar was brought in on the second provisioning trip. The female entered head first and picked up the pollen left on the first trip with her mouthparts, mixing nectar and pollen into a moist paste that she spread over the concavity in the basal partition. She then went to the nest entrance, turned around outside on the nest face, backed in, and kicked any pollen remaining from the first deposition toward the partition. Before pollen deposition this time the female arched her body into a 'U' shape, with head and abdomen as its highest points. Front legs and hind legs were placed approximately halfway up opposite walls of the nest, while mid-legs rested on the floor. The abdomen was arched and was backed into the cavity of the basal partition. Pollen removal then proceeded as before and the load fell into the concavity or onto the floor in front of the partition. On subsequent trips the female entered head first, swinging her head back and forth as she approached the provision, picking up stray pollen with her mouthparts. The dry pollen from the previous trip was then chewed and mixed with nectar to form a paste which she molded into a loaf with her mandibles. Pollen was then deposited atop the growing provision and the sequence was repeated.

Prior to nectar regurgitation, the bee usually cleaned her face and antennae, removing pollen with her front legs and passing it to her hind legs, where it was deposited along the sides of the abdomen. She also stopped just in front of the entrance and preened again before embarking on the next foraging trip.

Once the pollen loaf was approximately ⅓ its ultimate size the female used the abdomen tip to plunge a shallow hole in the loaf after each pollen deposition. This hole was then filled with nectar on the next trip and masticated. Dry pollen was deposited on it and a new hole was formed with the abdomen tip. This behavior continued until the provision was about ⅔ its ultimate size whereupon the female tended to sprinkle pollen evenly over the entire surface. Nectar was also deposited more uniformly and the whole surface was chewed after each trip, incorporating pollen and nectar.

On the last few pollen trips the bee used her face to flatten the vertical surface of the pollen loaf, using a motion similar to the tamping during partition construction.

Oviposition and Cell Closure. Once the cell was provisioned the female collected an unmodified *Oenothera* strip. She masticated it into a moist ball and wiped down the floor in front of the provision, picking up loose pollen. As when making the basal partition she used the leaf pulp to form a ring around the inner circumference of the tunnel close to the edge of the pollen loaf. Two or 3 leaf gathering trips sufficed; the ring was the initiation of the apical partition.

The leaf pulp ring completed, the female made 3 or 4 more foraging bouts each time returning with only nectar. On returning from the first bout the bee plunged her mouthparts deeply into one side of the face of the provision and continued to do so in an extremely fast up and down fashion for several seconds. With the mandibles moving in a cutting fashion much of the provision was pushed to the side opposite the female. After the next trip the other side of the pollen loaf was worked in a similar fashion until the front half of the entire provision had been thoroughly kneaded. At the end of the final foraging bout the female regurgitated a large quantity of nectar onto the middle of the provision face and plunged her mandibles in an around its center until a small wet hillock was formed. The front half of the provision was thoroughly wetted with nectar and appeared much darker in color than the back half. This completed, the female turned around at the entrance, backed in and oviposited.

As she backed into the cell, she inserted her ovipositor into the upper half of the hillock, appearing to anchor to the provision. A series of pumping motions forced the egg onto the hillock where it appeared to sink into the nectar. When the egg was about halfway extruded from the female the pumping motions ceased and she pulled away, leaving the anterior portion of the egg free and at about a 45° angle (Fig. 3). During oviposition the female remained fairly rigid with the exception of the abdominal pumping motion and a slight rocking of the body. The head was cocked downward somewhat and the antennae wiggled slightly. The whole process lasted about 60 seconds.

Immediately after oviposition the female left the nest and returned with leaf material. Most often this was a large oval-shaped piece that was sealed to the leaf pulp ring. An occasional female returned with *Oenothera* strips and added to the ring but most often the entrance to the cell was immediately closed by adding the oval-shaped pieces. Once the cell was closed, the apical partition was constructed in the same manner as the basal partition.

In almost all nests at least 1 partition, not associated with a provisioned cell, was constructed in the front of the nest to form a vestibular and an intercalary cell. This partition was constructed in the same manner as partitions defining provisioned cells, i.e., soil, leaf pulp, and whole leaf pieces were incorporated. The nest plug made to close the entrance was also constructed of the same material as partitions but was considerably thicker. The behaviors involved in plug construction were identical to those involved in partition formation. In addition to size, the closing plug differed from partitions in that it was often a series of partitions interspersed with soil and leaf pulp placed one atop the other. The outside surface of the plug was also different in that it contained much more soil than partition surfaces. Often what appeared to be pure soil was found on the outside surface of the plug, although leaf pulp was still used as the binding matrix.

Usually *E. pugnata* built 1 cell a day, but occasionally some females began provisioning a second cell. In the greenhouse *E. pugnata* provisioned cells in the morning when pollen was available and built partitions and plugs in the afternoon and early evening hours. Cell provisioning took 3.5 hours on the average. The number of pollen-nectar trips per cell varied from 36–44. Nectar and pollen deposition took roughly the same amount of time; nectar deposition = 38.7 sec. (standard deviation, sd = 12.3), pollen deposition = 32.4 sec. (sd = 6.6). Foraging trips ranged from 2 min. 28 sec. to 9 min. 22 sec. and averaged 4 min. 59 sec. (sd = 1 min. 38 sec.). Plug and partition construction took approximately the same amount of time as provisioning so that a nest with 1 cell, 1 intercalary partition and a plug took about 7 hours to complete. Approximately 15 *Oenothera,* 15 soil, and 3–4 large oval leaf collecting trips were required per partition. Plug construction required roughly twice those numbers. Collection of oval leaf pieces took longer than collection of *Oenothera* strips ($\bar{x}$ = 1 min. 23 sec., sd = 49 sec. vs $\bar{x}$ = 40 sec., sd = 9.4 sec.) and soil collecting trips were shortest of all ($\bar{x}$ = 22.5 sec., sd = 7.7 sec.).

In most cases females constructed nests in hollow sticks. However, when undrilled sticks, with shallow (5 mm) starter holes drilled in the side, were placed in the greenhouse for use by another bee 2 *E. pugnata* widened the cavities and nested therein.

Development

Egg Hatching. The egg, which was attached to the provision by its posterior ¼, was opaque when deposited but gradually became translucent as it developed. It measured 1–1½ mm wide anteriorly and posteriorly, 3–4 mm in length, and was straight (Fig. 3). Embryogenesis took an average of 5.1 days at 30°C (Table 1) and some structures became grossly visible through the chorion approximately 1 day before eclosion.

Eclosion usually took from 10 to 12 hours and became evident with the appearance of a clear fluid-filled area in the region of the posterior attachment. At this time the dorsal vessel, spiracles and major tracheal branches were visible. As the fluid increased in the posterior pole the embryo exhibited undulating waves that passed from anterior to posterior and perhaps aided in concentrating the fluid in the posterior region. Thus, the chorion was stretched very tightly over the head of the enclosed embryo. After fluid disappeared from the posterior pole the embryo appeared to remain quiescent for a short time. Fluid then began to collect at the anterior pole of the egg, accompanied by undulating waves moving in the opposite direction (posterior to anterior). As the chorion became tightly stretched over the posterior embryo a longitudinal-lateral split in the chorion became visible at the level of the spiracles. This rupture divided the chorion into upper and lower halves. As the pressure and peristaltic waves receded the lower half of the chorion slipped from the larva and came to lay directly between it and the pollen mass under most of the body (except the head). The top half of the chorion including that surrounding the head seemed to dissolve. If the larva swallowed any portion of the chorion it was not evident. As eclosion continued the larva came to lay directly on top of the pollen mass, with all segments touching it, and began to feed.

Feeding Stages. The second stadium was short (Table 1) and the second instar fed differently than the other instars. The larva remained nearly motionless with the head in direct contact with food in an area of the provision that was considerably higher in fluid and nectar content than other areas. As the larva fed, a back and forth motion of the head was apparent and it appeared to suck up fluid like a small pump. The mouthparts were partially buried in the provision but almost no movement was detectable in that area during feeding.

The actual process of molting was not observed but larvae marked with powder on the dorsal side of the body were noticed lying on the old exuvium that bore the powder mark after a molt. It appeared then that the entire old integument was sloughed off and not dissolved away. The instars molted in the same manner so that after molts the body was attached to old exuviae which in turn were attached to the provision.

Ingestion of solid food, aided by the mandibles, began in the third stadium. Subsequent instars fed in a similar manner but the last instar consumed the bulk of the provision. As the larva fed, bidentate mandibles shovelled food into the mouth and appeared to be aided by a pumping motion of the head capsule. As the head capsule retracted the mandibles pulled the food in and as the head capsule extended the mandibles opened outwardly. Larvae tended to feed in bouts of approximately 5 minutes, stopping to swallow and pass food into the gut with a series of peristaltic waves between feeding bouts. As the provision was consumed the larva began to turn from white to yellow and the pollen-filled gut became visible.

The third instar began feeding in the place where the second instar fed. The fourth instar fed in the same place, hollowing out a cavity beneath itself. By the middle of the fourth stadium many larvae had become detached from the provision but were much more mobile and continued to feed. Regardless of position (attached, detached with venter on floor, detached with dorsum on floor) the last 3

Table 1. Life history and developmental times (days) for stages.

Stage	$\bar{x}$	sd	range	n
Oviposition to Eclosion	5.1	1.0	4–7	12
Eclosion to Solid Food	1.2	.4	1–2	12
Solid Food to First Defecation	6.5	1.9	5–9	8
First Defecation to Cocoon Spinning	14.9	2.1	10–18	19
Cocoon Spinning to Complete Cocoon	3.7	.5	3–4	11
Oviposition to Complete Cocoon	26.6	1.5	24–28	7

instars appeared to feed in a similar manner: with the body of the larva extended, the mouthparts were planted on the provision, then the body closed into a 'C' shape and several mouthfuls of food were taken in while contracting, forming a trough on the provision. The body then extended and the process was repeated in the same groove cut previously or adjacent to it so that the whole provision was systematically consumed. Feeding continued into the last stadium after the onset of defecation and lasted up to about 3 days before cocoon spinning. The time from the first ingestion of solid food (3rd instar) to first defecation (last instar) averaged 6.5 days (Table 1). The 3rd stadium averaged 1.6 days.

Defecation. Defecation began a few hours after molting into the last larval instar. The midgut in the early instars was a blind sac, not continuous with the hindgut. At the molt to the last instar the gut was connected and defecation was possible. The last instar was also distinguishable from other instars by its longer body setae.

Most of the feeding and growth took place during the last stadium. The average length of time from first defecation to the onset of cocoon spinning was 14.9 days (Table 1).

Feces were small, squat, yellow cylinders and were deposited away from the provision while feeding continued. As the provision was nearly consumed the cell began to fill with pellets and the larva smeared fresh feces on the walls instead of depositing them behind it. Defecation continued for about 3 days after feeding ceased up to the time the cocoon was spun. Most of the pellets were incorporated into the cocoon.

Cocoon Spinning. Before fecal pellets were spun together a web-like matrix was laid down on the walls. The larva pressed its salivary lips onto various points of the walls and partitions and deposited a small droplet of material from which a short strand of silk was pulled and anchored elsewhere. The apical partition was covered with many more strands than the walls or basal partition. Most of the strands were attached anteriorly to the apical partition which was also that portion of the cell where most of the fecal pellets had been deposited. The larva anchored a pellet by holding it with the mandibles, depositing a small drop of material with the mouth, pulling away and attaching the other end to another pellet, leaf hair or portion of the wall. As the salivary component was daubed onto various structures by the salivary lips, the labium appeared to be split so that the silk was pulled through as if being threaded, and a steady pressure was maintained. The fecal pellets were spread evenly across the anterior portion of the cell and when all were anchored a cavity lined by white threads covering the entire cell had been formed. During this time the larva showed much mobility and agility, moving freely about the cell and turning completely around several times as necessary.

Once the fecal pellets were spun together more tiny strands were laid down within the cavity until a fairly dense network of threads that would be the template for the cocoon was formed. The cocoon was composed of one thin transparent and cellophane-like layer. The larva deposited the layer in one of two ways. Either a single thread was grasped with the mandibles and a clear liquid was exuded as the head moved up and down the strand or the mandibles separated 2 or more strands, depositing the liquid between them, moving the head back and forth until the layer dried. A few fecal pellets were incorporated into the matrix and flattened and spread out. No recognizable nipple was formed anteriorly. Instead, an area somewhat more transparent and of similar thickness to the rest of the cocoon was formed (Fig. 4). The average time from initiation of cocoon spinning to completed cocoon was 3.7 days (Table 1).

Pupation and Adult Emergence. On 27 July 1981, 10 overwintering larvae were placed in an incubator at 30° C in order to observe pupation. Average time from incubation to pupation was 9.7 days (sd = 4.3, range = 7–18, n = 9). The transformation from overwintering larva to adult took an average of 22.3 days (sd = 2.9, range = 20–27, n = 6), with males completing development prior to females. Pigmentation changes were first observed in the eyes which turned yellow in approximately 11 to 13 days. At 13 to 14 days both compound eyes and ocelli had turned dark brown. Wing buds became evident and turned yellow at 11 to 14 days. Mouthparts began to darken at 15 days and had usually turned black within 16–16½ days. Coloration of general body regions started at 16 days and began with patches of integument at the bases of hairs on the vertex, frons, thoracic terga and abdominal sterna. Hairs quickly turned dark and pigmentation spread to the remaining portion of the head and thorax followed by the abdomen. Generally proximal portions of appendages changed color first with distal portions of the legs changing color last. From 16 to 20 days the body remained dull black while wings darkened. A shiny appearance to the body and hairs did not appear until just prior to ecdysis. Bees emerged from cells shortly after wings had darkened and proboscides had been retracted.

DISCUSSION

The incorporation of glandular secretions into nest linings, widespread in the Apoidea, is believed to have evolved as a mechanism to protect larvae and provisions from dehydration and/or the microbial consequences of excessively humid environs. Batra (1972, 1980), Cane (1981), and Eickwort et al. (1981) have discussed the inclusion of salivary and/or Dufour's gland components into cell linings and provisions of the 'short tongued bees' (Colletidae, Halictidae, Andrenidae) and the Anthophoridae. While the phenomenon has likely figured prominently in the evolution of these groups, little or no attention has been directed toward similar behaviors in the Megachilidae. Indeed, the evolution of the megachilidae has been viewed in a different framework. Eickwort et al. (1981) see the bulk of the megachilids (Megachilinae) as having evolved from a soil dwelling ancestor that developed the ability to gather foreign materials (leaf pieces, mud, resin, etc.) to line cells as an alternative to glandular secretions in overcoming the constraints of humidity. While Eickwort et al.'s (1981) hypothesis of nesting evolution in the Megachilidae is interesting, more recent evidence points to the fact that glandular secretions are important features of megachild nesting biologies. Parker and Tepedino (1982) observed the application of salivary secretions to bare walls of *Osmia marginata* Michener nests. Frohlich (1983) observed the incorporation by *Osmia bruneri* Cockerell of an abdominal secretion into the provision, and also noted the application of a salivary secretion to partitions. *Dianthidium ulkei ulkei* (Cresson) also incorporates an opaque viscous substance, originating from the abdomen, into resinous cell walls and spreads the material over bare areas of the cell (Frohlich and Parker, in prep.).

Since the twig nesting megachilids probably arose from soil nesting megachilids (Eickwort et al. 1981) and since the Megachilidae is distantly related to the other soil nesting families (Michener 1974) we propose that the Megachilidae have retained the habit of using glandular secretions to line cells. It seems likely that a waterproof layer of some sort is necessary to maintain the humidity of the cell within tolerable limits. Lining cells with leaves in soils that are particularly moist would have little effect on reducing humidity and controlling fungal growth nor would lining pre-existing cavities such as twigs prevent dehydration. It is important, therefore, that we thoroughly examine the behavioral, and more importantly chemical, components of nesting in order to gain an understanding of the role of nest architecture in evolution.

The paucity of information available on the nesting biologies of other species of *Eumegachile* make it difficult to confirm (or refute) Mitchell's (1981) recent revision of the old genus *Megachile* on the basis of behavior or nest architecture. The available data does confirm the separation of *Eumegachile* from *Megachile,* since the nest architectures of the two are radically different. *Eumegachile pugnata* nests are similar to, though somewhat more elaborate than, known nests of other species in the subgenus. Krombein (1967) reported that *E. inimica inimica* Cresson makes unlined cells with partitions of agglutinated sand a little larger than the inner circumference of the nest. *Eumegachile inimica sayi* Cresson also uses a single leafcutting as a partition but covers it with leaf pulp, incorporating five pebbles (Krombein 1967). *Eumegachile policaris* Say lays more than one egg per provision, makes partitions and plugs composed of leaf pulp and two layers of small compressed leaflets with no soil or pebbles, and constructs no vestibular or intercalary cells. No other biologies in the subgenus *Sayapis* are known and no biologies or nest architectures are known in the other subgenera of *Eumegachile.*

The manner in which *E. pugnata* constructs individual cells renders its adoption as a potential pollinator of commercial sunflower somewhat problematical under certain circumstances. *Eumegachile pugnata* construct cells that are separated from each other by partitions and are not surrounded by a leaf envelope. This is unfortunate because *E. pugnata* is susceptible to a chalkbrood fungus, *Ascosphaera aggregata* Skou, the treatment of which in other bees takes advantage of nest architecture. The disease sometimes decimates populations of the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius), which construct cells that are completely leaf lined. During treatment, nests are opened, individual cells are separated as discrete leaf lined units, treated, and stored (Parker and Torchio 1980). When *M. rotundata* emerge only egress from individual cells is necessary and adults are not required to chew through cells containing dead larvae with infectious spores. Since *E. pugnata* are protected only by a thin cocoon and no leaf lined envelope, removal from the nest would cause excessive mortality. This "loose cell" management is also used to control various *M. rotundata* parasites. In the case of *E. pugnata* parasites could emerge from individual cells and reparasitize other cells without leaving the nest.

A second point that will have to be considered in commercial pollination is the fact that *E. pugnata* incorporates a fair amount of nectar into the provision. If growers are going to increase bee populations, sunflower cultivars that provide adequate nectar will have to be available.

Finally, one trait that makes *E. pugnata* a good candidate for sunflower pollination is its habit of provisioning cells early in the day. Male fertile sunflower cultivars dehisce overnight and in the early morning. Thus, the greatest amount of pollen is available during the time that *E. pugnata* are provisioning and pollinating flowers.

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ANTHICIDAE OF THE GREATER ANTILLES, AND A NEW SPECIES FROM VENEZUELA (COLEOPTERA)[1]

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Thirteen of the 29 species that are known or reported from the Greater Antilles appear to be endemic. Five *(Anthicus darlingtoni, hispaniolae, macgillavryi, soledad* and *subtilis)* make up the subtilis-group, which does not seem to have near relatives on the mainland. Three others stand quite isolated in their genera: *Acanthinus schwarzi* in an almost exclusively neotropical genus, *Anthicus blackwelderi* and *russoi* in a world-wide genus that contains many diverse elements. *A. blackwelderi* is counted among the endemic species because it has different color patterns on the islands that it is known to inhabit; the form of the internal sac of the male genitalia is very different from that of possible relatives on the mainland. *A. russoi* is probably not properly placed in *Anthicus,* and is unlike any anthicid known to me in several details; Menozzi's (1930) evidence that it is a myrmecophile with a native ant makes local origin seem logical.

The 5 other endemic species are similar to mainland New World species. *Mecynotarsus hispaniolae* and *jamaicanus* belong to the elegans-group, which has species from Florida to Central America. *Notoxus bipunctatus* and *jamaicus* have been assigned to the monodon-group (Chandler 1978), which ranges from Canada to northern South America. Finally, *Anthicus antilleorum* seems to have originated in the Greater Antilles and spread to the Virgin Islands and Bahama Islands; its nearest relatives are found around the southern Caribbean.

Within the 13 endemic species, there is inter-island variation in color pattern in 3: *Anthicus antilleorum, blackwelderi* and *soledad;* in each instance the Jamaican population is different from that of

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the adjacent island of Cuba (and Hispaniola in *antilleorum* and *blackwelderi*).

Two of the other 16 species listed are based on records that cannot be verified: *Acanthinus ebeninus* on an old specimen with a "Cuba" label, and *Amblyderus* sp. on some specimens from Puerto Rico that cannot now be located. Ten are shared with continental areas of the New World: *Acanthinus angusticollis, concinnus, quinquemaculatus* and *scitulus, Anthicus pallidus, Sapintus similis* and *teapensis, Thicanus texanus,* and *Vacusus holoxanthus* and *vicinus.* These may have reached the Greater Antilles without human help, but *Vacusus holoxanthus* is found mainly from Chile to Bolivia, and *Acanthinus scitulus* seems not to have been present in the lowland localities that were extensively collected in the 1930's, so is probably of recent introduction. Finally, 4 species of *Anthicus* are of Old World origin: *floralis* and *formicarius,* which are almost cosmopolitan; *tobias,* which is expanding its range in several parts of the world; and *crinitus.*

Two large genera, the world-wide *Tomoderus* and the New World *Ischyropalpus,* are conspicuous by their absence. The latter genus, at least, should have been collected if it was present; mainland species are often abundant on blossoms. That the fauna has not been completely sampled is indicated by the addition of a species of *Mecynotarsus* from Hispaniola through the recent collecting of J. and S. Klapperich.

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A critical part of the material reported here was collected by Philip J. Darlington, Jr. in the 1930's. I wish to thank Dr. Darlington and subsequent curators of the M. C. Z. for permission to retain these specimens until they could be studied in comparison with continental faunas. The second large lot came from the collecting of Richard E. Blackwelder and Edward A. Chapin, and was made available by the U. S. National Museum; it was collected in the same period. The largest recently collected lot originated in the collecting of J. and S. Klapperich in the Dominican Republic, and was made available by Dr. M. Branucci of the Naturhistorisches Museum in Basel.

Key to Greater Antilles Anthicidae

1. Prothorax with an anterior horn that extends over the head 25

— Prothorax without a horn 2

2. Sides of mesosternum curved outward to form a broad plate, with a variably developed fringe of setae along its edges 15

— Mesosternum with sides diagonal and nearly or quite straight, without fringe setae 3

3. First visible abdominal sternum with a transverse, pubescence-lined invagination behind each hind coxa. Elytral pubescence double, the under layer more appressed, diagonal 24

— First visible abdominal sternum without invaginations. Elytral pubescence usually single, double in *Anthicus pallidus* 4

4. Elytral pubescence double, undercoat more diagonal. Pale, somewhat flattened, elytra with dark brown midband and suture, markings usually isolating a pale zone in basal and apical fourth of each elytron; head truncate. 2.25–2.35 mm. Hispaniola, Puerto Rico . . . . *Anthicus pallidus* Say

— Elytral pubescence simple 5

5. Vertex of head somewhat produced, edge nearly straight from middle to weak temporal angles (Fig. 11). Uniform pale brown, somewhat shiny, elytra sometimes with a weak median cloud. Ca. 2.6 mm. Hispaniola, Puerto Rico . . . . *Thicanus texanus* (LaFerté)

— Base of head from truncate to evenly rounded 6

6. Base of head truncate, temporal angles narrowly rounded 7

— Base of head rounded, temporal angles broadly rounded or not evident 10

7. Head microreticulate between punctures. Rufescent to brown, elytra usually brown except across base. Elytral pubescence very short and inconspicuous. 2.9–3.2 mm. Jamaica . . . . *Anthicus formicarius* (Goeze)

— Head smooth and shiny between punctures 8

8. Elytral setae sparse and as long as width of a femur, subdecumbent. Rufescent, shiny, elytra with dark markings that

usually isolate a common pale spot in apical third. 2.5–3.2 mm. Puerto Rico, Virgin Islands .... *Anthicus crinitus* LaFerté

— Elytral pubescence shorter than width of a femur; dark elytral markings not enclosing a common pale spot in apical area 9

9. Elytral pubescence short and even, the erect tactile setae extending well above the decumbent setae. Prosternum with uniformly distributed punctures and pubescence in front of coxae. Elytra pale at base and usually in an obliquely oval spot in apical third of each. 2.0–2.3 mm. Jamaica, Cuba, Hispaniola, Virgin Islands and Bahama Islands; elytra usually lacking posterior pale spots in Jamaican population .... *Anthicus antilleorum,* sp. n.

— Elytral pubescence longer and less decumbent, the tactile setae barely evident among the setae. Prosternum with front half of portion in front of coxae smooth, back half bearing some coarse punctures and setae. Uniformly dark (Jamaica) or elytra pale across base and at apex, the posterior marking rounded in front (Cuba, probably Hispaniola). 2.27–2.55 mm. ....*Anthicus blackwelderi,* sp. n.

10(6) Rufescent or paler, with pale appendages; elytra usually with suture and whole apical half black except for a round, very pale spot on each in apical third. 2.6–3.0 mm. ♂ tegmen with apex knob-like, lacking lateral tufts of setae. Jamaica, Virgin Islands .... *Anthicus tobias* Marseul

— Elytra usually with a complete or interrupted dark midband and an oblique pale subapical band, never with a round pale spot on each in apical third. ♂ tegmen pointed, with a tuft of setae on each side. *Anthicus* subtilis-group 11

11. ♂ front tibiae excavated in apical 2/5. Elytral midband often complete. 2.11–2.24 mm. Cuba. .... *Anthicus macgillavryi* Buck

— ♂ front tibiae simple 12

12. ♂ tegmen gradually tapered to apex, slender. Elytral markings dark, all connected along suture, including a dark zone across base. Ca. 2.5 mm. Hispaniola .... *Anthicus hispaniolae,* sp. n.

— ♂ tegmen not evenly tapered to apex................ 13

13. ♂ tegmen very bluntly truncate at apex except for a small median point. Elytral midband complete in Cuban specimens seen, interrupted at suture in Jamaican specimens. 2.22–2.53 mm. Cuba, Jamaica .... *Anthicus soledad,* sp. n.

— ♂ tegmen with sides slightly constricted beyond middle 14

14. Antennae unusually long and slender. Elytral midband reduced to a pale brown triangle with point toward suture, on each side. 2.47–2.76 mm. Hispaniola .... *Anthicus subtilis* LaFerté

— Antennae not so slender. Elytral midband interrupted at suture, but mark truncate toward suture on each side. Elytra slightly inflated. 2.02–2.42 mm. Hispaniola .... *Anthicus darlingtoni,* sp. n.

15(2) Pronotum with a pair of small bumps near anterior edge of disc. Fringe setae of mesosternum closely appressed to mesepisterna. Rufous, elytra black or brown with basal fourth rufous in a well-demarcated zone; appearing glabrous and subopaque. 2.6–3.2 mm. Jamaica, Puerto Rico, Virgin Islands .... *Anthicus floralis* (L.)

— Pronotum without such bumps. Fringe setae of mesosternum at least slightly raised from surface of mesepisterna 16

16. Sides of prothorax not constricted, almost evenly tapered from widest part, near front, to basal impressed line 17

— Sides of prothorax at least slightly constricted anterior to basal impressed line 18

17. Shiny, only erect tactile setae very obvious; luteous to rufous, elytra with apex and an interrupted submedian band dark. 2.3–2.8 mm. Jamaica, Cuba, Hispaniola, Puerto Rico, Virgin Islands .... *Vacusus vicinus* (LaFerté)

— Shiny but with surface partly obscured by appressed pubescence; tactile setae short and inconspicuous. Moderately slender, entirely tannish. 1.8–2.0 mm. Jamaica .... *Vacusus holoxanthus* (Fairmaire & Germain)

18(16) Pubescence fine, silky, moderately dense, appressed, covering all of elytra. Dull rufescent to brown, elytra with dark midband and apex, markings usually connected along suture 19

— Pubescence very sparse, or dense pubescence confined to postbasal transverse impression of elytra 20

19. ♂ fifth visible abdominal sternum excavated on disc; lobes of visible sternum 6 moderately broad. 2.6–3.2 mm. Cuba, Puerto Rico ......*Acanthinus quinquemaculatus* (LaFerté)

— ♂ fifth visible abdominal sternum simple; lobes of visible sternum 6 narrow. 2.4–3.0 mm. Hispaniola ....*Acanthinus concinnus* (LaFerté)

20(18) Elytra with a dense patch of white pubescence in postbasal transverse impression. Dark brown, shiny, otherwise glabrous with erect tactile setae; head triangular, it and pronotum longitudinally strigose. Ca. 2.8 mm. Cuba? ....*Acanthinus ebeninus* (LaFerté)

— Elytra without patch of dense pubescence in postbasal transverse impression 21

21. Head and prothorax strongly sculptured 22

— Whole dorsal surface smooth, shiny, punctures fine and indistinct, setae very short, sparse and inconspicuous, only erect tactile setae evident 23

22. Dark brown with quadrate yellowish white mark laterally in cuticle of postbasal transverse of elytra; head unusually large, it and prothorax with some longitudinal striations. 2.0–2.8 mm. Jamaica, Cuba ....*Acanthinus angusticollis* (LaFerté)

— Head and prothorax rufescent, elytra rufescent at base, with a complete luteous band in postbasal impression, brown behind. Head and prothorax rugose-punctate. 2.4–2.8 mm. Cuba......................*Acanthinus schwarzi* Werner

23(21) Rufescent, elytra paler with brownish to almost black markings, at least in narrow, interrupted bands at basal and apical thirds, to dark with postbasal impression and a narrow postmedian band pale. Prothorax with a strong constriction that continues weakly across dorsum. Edge of mesosternal shelf visible from above, in front of elytral humeri. Head narrower than semicircular behind eyes. 2.0–2.9 mm. Cuba ... . *Acanthinus scitulus* (LeConte)

— Pale rufescent, elytra pale rufescent at base, dark brown on humeri and behind postbasal transverse impression. Prothorax weakly constricted, almost evenly globular from basal impressed line to collar. Only fringe setae of mesosternum visible from above. Ca. 2.0 mm. Hispaniola .... *Anthicus russoi* Krekich

24(3) ♂ fifth visible abdominal sternum shallowly dished out on disc, the excavation flanked with some erect setae. Ca. 2.0 mm. Jamaica, Cuba, Hispaniola, Puerto Rico, Virgin Islands .... *Sapintus teapensis* (Champion)

— ♂ visible sternum 5 simple. Ca. 2.7 mm. Jamaica .... *Sapintus similis* Werner

25(1) Each side of prothoracic horn with 3 teeth, the apex about equal to a tooth. Visible abdominal sternum 1 without a pubescence-lined invagination behind each hind coxa. Length ca. 2 mm. *Mecynotarsus* elegans-group 26

— Each side of prothoracic horn with 3–7 teeth, the apex considerably broader than any tooth. Visible abdominal sternum 1 with a pubescence-lined invagination behind each coxa. Prothoracic horn with a few ventrolateral pits. *Notoxus* monodon-group 27

26. Elytra slightly inflated. Pubescence cinereous but with some intermixed ferrugineous scales on disc of pronotum and basal half of elytra; elytra piceous at base, in a postmedian band, and in a large posterior triangular marking on each. Jamaica .... *Mecynotarsus jamaicanus* Werner

— Elytra strongly inflated. Pubescence cinereous, with diffuse slightly darker to pale rufescent markings on disc of pronotum, dull brown on elytra from base along a broad zone to an apical pale cordate mark, and in a feeble slightly postmedian band and subapical band delimiting the cordate mark. Markings very weak in some individuals. Hispaniola .... *Mecynotarsus hispaniolae,* sp. n.

27(25) Dark elytral markings usually including some on sides that curve inward toward suture at apex. Tip of ♂ aedeagus truncate. Jamaica..................... *Notoxus jamaicus* Pic

— Dark elytral markings not including any on sides behind an irregular transverse midband. Tip of ♂ aedeagus deeply split. Puerto Rico .... *Notoxus bipunctatus* Chevrolat

DESCRIPTION OF SPECIES

Measurements are given in 0.01 mm as head: length from vertex to clypeofrontal suture over width across eyes and behind; prothorax: length including collar over width at collar, maximum, at constriction, and across base; elytra: length over width at humeri where 45° angle would touch them, and maximum. Total length as given is the sum of head, prothorax and elytra.

Anthicus antilleorum, sp. n.

Fig. 9, 19.

2.01–2.24 mm, rufescent, the legs luteous, elytra with a brown midband, the base and an oblique apical mark on each luteous. Head quadrate, antennae moderately thick toward apex; elytra somewhat inflated, even in fully winged individuals. Pubescence moderately short, almost appressed, the tactile setae evident above the setae.

Holotype ♂, 2.11 mm. Head 39/46,42; eyes 16/13, 32 apart, 16 from base, which is straight, the temporal angles narrowly rounded; sides almost straight behind eyes. Disc slightly flattened, with moderately large, deep punctures ca. 3 apart, except on midline of front; pubescence almost appressed, moderately conspicuous. Antennae ca. 77 long, 7 thick at segment 10, segments 7–11 forming a feeble club that is thicker than segment 1. Prothorax 47/24,44,32, its sides just perceptibly concave at usual level of constriction; anterolateral portion narrowly curved. Punctures strong, denser than on head, ca. 2 apart. Elytra perceptibly swollen, 125/53,73; punctures strong, ca. 3 apart; setae 5 long, slightly curved, almost appressed; tactile setae 5, suberect, slightly curved. Legs unmodified. Apical margin of visible abdominal sternum 5 just perceptibly convex.

Holotype: ♂, CUBA: Baraguá (IV-25-28, at light, C. F. Stahl) in MCZ. Paratypes: CUBA: Baraguá (same data, 6; II-10-26, L. C. Scaramuzza), Soledad nr. Cienfuegos (Apr. 1936, P. J. D.; V,VI-'39, C. T. Parsons), Cayamas (Mar.-May, E. A. Schwarz), Camagüey Prov.: Monte Imias nr. California (at light, June 7, 1959, M. W. Sanderson). HISPANIOLA: REP. DOM.: Bani (65m), Boca Chica (10m), and Ocoa (475m), all J. & S. Klapperich, 1971-73. Paratypes in MCZ, USNM, Basel Museum and collection of FGW. Not designated as paratypes: JAMAICA: Morant Bay (Chapin and Blackwelder, 4). VIRGIN ISLANDS: Tortola (BVI, Brandywine Bay, J. F. G. Clarke, 1). BAHAMA ISLANDS: Cat Island (Bennets Harbour, E. B. Hayden & L. Giovanolli, 2).

The specimens from Jamaica are darker than those from Cuba and Hispaniola, only one of them having the posterior pale elytral mark. The pubescence may be less appressed but the specimens are so abraded that they were identified with difficulty. This species is probably most closely related to *A. pauxillus* Champion, *panamensis* Werner, and *margaritae,* sp. n., from Guatemala, Panama, and eastern Venezuela, respectively. The color pattern is similar. The ♂ genitalia are similar, but the simple internal sac provides few clues to relationship. *A. panamensis* has the tegmen step-tapered.

Anthicus margaritae, sp. n.

Fig. 8, 20.

1.90–2.20 mm, of form of *Anthicus panamensis* Werner and *antilleorum,* sp. n., differing from both species in having the head broader behind the eyes and gradually widened to the narrowly rounded temporal angles. Tegmen of ♂ genitalia convexly tapered as in *antilleorum,* but with the apex slightly more pointed. Anterolateral angles of prothorax quite narrowly rounded, as in the above 2 species, differing mainly in this feature from *A. exiguus* Champion.

Holotype ♂, 1.92 mm; head 33/44,40; eyes 16/14, separated by 29,15 from base. Punctures of head ca. 3 apart, on slightly convex disc. Antennae 75 long, 7 thick at segment 10. Prothorax 46/20,42,31. Elytra slightly swollen but with very distinct humeri, 113/51,65. Punctures slightly sparser than on head, intervals smooth and slightly convex; setae ca. 9 long, not quite so decumbent as in *antilleorum,* tactile setae 9 and erect.

Holotype: ♂, VENEZUELA: I. Margarita: Puerto Fermin (12.48, Marcuzzi), in CASC, San Francisco. Paratypes: VENEZUELA: I Margarita: Puerto Fermin (same data, 10), Juan Griego (3.48, 2). Sucre: Carupan (9.48, 2). I am indebted to K. S. Hagen for the loan of these specimens, and for some additional specimens without labels. Paratypes in CASC and collections of KSH and FGW.

Anthicus blackwelderi, sp. n.

Fig. 10, 13, 21.

2.27–2.55 mm, of aspect of a *Vacusus* species, head truncate, prothorax without a constriction, and elytra subparallel. Jamaican individuals brown, with slightly paler legs, antennae and palpi. Cuban individuals with pale marking at base and apex of elytra. Moderately coarsely punctured.

Holotype ♂, 2.34 mm. Head 44/51,47; eyes 19/15, 35 apart, 20 from base, which is truncate with a slight impression at midline, the temporal angles narrowly rounded; disc slightly flattened, smooth, with strong punctures ca. 4 apart except on midline of front; setae decumbent. Antennae ca. 97 long, 7 thick at segment 10, which is slightly longer than thick. Prothorax 49/16,40,31, with even punctures denser than on head, ca. 2 apart, about as wide as intervals. Elytra 141/56,73, with feeble omoplates, as deeply punctured as head and prothorax, punctures ca. 3 apart; setae decumbent, 8, slightly curved; tactile setae 4, suberect. Underside of thorax with punctures slightly smaller than above; front part of prosternum, anterior to coxae, smooth in front half, with some punctures and suberect setae in back half. First visible abdominal sternum finely punctured, rest punctulate. Visible sternum 5 with its apex gently convex, as in ♀; 6 with no indication of even an emargination; last visible tergum shiny, its edge beaded, almost concealed by the tergum before it, which is densely short-pubescent and has an almost evenly rounded apex, as in ♀.

Holotype: ♂, JAMAICA: Kingston (no date, Chapin & Blackwelder) in USNM. Paratypes: JAMAICA: Kingston (C & B, 4; P J D, 1), Morant Bay, Gordon Town, Trinityville, Bath St. Thomas, Blue Mts. (nr. 4500′, P.J.D.). Paratypes in USNM, MCZ and FGW collection. Not designated paratypes: CUBA: Oriente Prov.: coast below Pico Turquino (1); Soledad nr. Cienfuegos (2). HISPANIOLA: Rep. Dom.: Constanza (1♀). The Constanza specimen has very reduced dark elytral markings, with rounded posterior emargination. Even teneral Jamaican specimens have uniformly colored elytra.

Anthicus russoi Krekich
Fig. 5, 22.

Anthicus russoi Krekich in Menozzi 1930: 93 (type-locality: Moca, Rep. Dominicana).
Stricticomus russoi: Bonadona 1981: 275.

♂, Jarabacoa, 2.20 mm, very smooth, shiny, appearing somewhat glabrous except for long, erect tactile setae; body and basal 36 of elytra pale rufescent (abdomen brown in another specimen); humeri and apical area of elytra brown. Head semicircular behind eyes; prothorax evenly swollen in profile at level of widest portion.

Head 42/45,39; eyes prominent, 17/13, 27 apart, 20 from base. Disc evenly convex, punctures ca. 4 apart, small but distinct on front, very fine behind; setae ca. 1, decumbent, almost invisible, tactile setae erect, 7, fine. Antennae 105 long, 7 thick at segment 10, gradually thickened, with moderately conspicuous suberect curved setae ca. 4 and erect, nearly straight tactile setae ca. 7. Prothorax 47/18,36,25,28; portion anterior to strong basal impressed line almost globular, rising 11 above line from top of base to top of strong collar. Elytra 131/50,67; humeri well defined, omoplates slightly swollen; postbasal transverse impression well indicated but with punctures and pubescence like rest of elytra; punctures very fine, ca. 5 apart, setae decumbent, fine, ca. 1, barely visible, tactile setae erect, nearly straight, 11. Mesosternum extremely smooth, flat, with lateral expansion 15 wide and reaching almost to epipleura of elytra, bearing a fringe of slightly curved setae ca. 11 long, partly visible from above, the lateral and posterolateral setae lapping onto sides of elytra and mesepisterna. Metasternum, abdomen and legs with sparse, decumbent setae ca. 4 long, slightly denser on tibiae. Visible sternum 5 with disc evenly convex, its apex shallowly emarginate and bearing several long setae; 6 ca. 11 wide, divided into almost parallel, deeply separated lobes, which are deeply grooved mesally. Last visible tergum thin, nearly flat. Wings apparently absent. Cuticle very translucent, some parts almost transparent.

Records: HISPANIOLA: REP. DOM.: Jarabacoa (530m, 23.I.1972), and Boca Chica (10m, 6.X.1971), both on single ♂ specimens, collected by J. & S. Klapperich, and in the Basel Museum. These specimens agree in general with the original description, which may have suffered from being translated from German into Italian, and finally from my translation to English. The original figure is not helpful. Professor M. Princippi informs me that there is a specimen of *russoi* in the Menozzi Collection at the Istituto di Entomologia of the Università di Bologna. This must be the holotype, since the species was described from a single specimen.

I am leaving *russoi* in *Anthicus* for lack of a better place to put it. The mandibles and gonopore armature are different from *Acanthinus*, and the mesothorax differently designed from *Formicilla*. In that genus the setae on the sides of the mesothorax arise from a ridge above the side of the expanded mesosternum. Bonadona has placed it in *Stricticomus,* an Old World group characterized by the shape of the prothorax. While this is a convenient way to split up the numerous species of *Anthicus,* the division has not been defined on a phylogenetic basis.

Anthicus subtilis-group

Five species of *Anthicus* in the Greater Antilles form a very distinctive group. The males have a unique tuft of long setae on the sides of the tegmen and the species share enough external features that two of them are indistinguishable in the female sex. Of the five, two have been taken only on Hispaniola, one only on Cuba, one on Hispaniola and Cuba, and one on Cuba and Jamaica, the last with some geographical variation on the two islands. All three species on Hispaniola are at least partly sympatric, as indicated by the labels, as are two on Cuba.

Anthicus subtilis LaFerté

Fig. 1, 18.

Anthicus subtilis LaFerté 1848: 135–6 (type-locality: LaFerté states it as Colombia, collected by Moritz, but the specimens probably originated in the Greater Antilles).

2.47–2.76 mm, pale rufescent, legs, antennae and palpi dull luteous, tibiae obscurely darker at base, elytra with pale brown median marking widely interrupted at suture and more or less triangular with a mesal point, and a narrow, usually paler, diagonal subapical band. Pubescence short, fine, almost appressed, dulling the generally shiny surface; punctures fine and not very evident except on base of pronotum. On the elytra the pubescence in this and the other species of the subtilis-group is slightly diagonal over most of the surface, to ca. 45° in the postbasal transverse impression and nearly transverse on rear of the weak omoplates.

♂, Ennery, Haiti, 2.66 mm. Head 44/53,47, almost semicircular behind prominent eyes, with a slight impression at midline. Eyes 22/16, 35 apart, 16 from base. Disc evenly convex, shiny, with small, well-defined punctures ca. 5 apart, and more numerous very fine punctures on intervals, punctures collectively ca. 1 apart. Setae fine, silky, decumbent. Antennae unusually slender, segments 16/7, 9/5, 11/5, 15/5, 16/5, 16/5, 15/5, 14/6, 14/7, 13/7, 17/6, base to apex. Prothorax 54/20,44,33,35, with well-defined collar and slight constriction. Collar without dense pubescence ventrally. Disc evenly convex, punctures ca. 1 apart, finer and with intervals nearly flat on anterior 1/3, larger and grading to finely rugulose in region of basal impressed line. Elytra 169/64,86, widest near middle, tapering to moderately narrow apex; omoplates distinct, transverse impression weak. Surface almost evenly covered with fine, slightly elevated punctures ca. 2 apart, intervals flat; setae fine, appressed, ca. 3, tactile setae suberect, 7. Setae of 2 slightly different lengths and thicknesses, the longer and thicker slightly less appressed and discernible with backlighting. Punctures and setae of impression no different from those of adjacent areas except for the setae being more perpendicular to the midline. Legs slender, not modified. Visible sternum 5 simple, its apex truncate.

The median dark elytral markings on this individual are 37 long, separated by 30 across suture, and 9 from side margin; subapical band ca. 11 wide, paler than median marks, slightly oblique, extending forward along suture for ca. 18, pale and evanescent laterally, to 7 from margin. All of the specimens have rather similar markings, and none has the median markings connected across the suture.

Records: All individuals are fully winged and apparently capable of flight. HISPANIOLA: HAITI: Ennery (nr. 1000′ (4♂, 5♀), Camp Perrin (nr. 1000′, 2♂), N.E. foothills of La Hotte (3000′, 1♂). REP. DOM.: Villa Altagracia (1♂), Pto. Plata (25 km. S. of, 2♀), San José de las Matas (1–2000′, 1♀). CUBA: Loma (Pico) del Gato (Sierra Maestra, Oriente Prov., 2♂), Soledad nr. Cienfuegos (1♀). Almost all collected by P. J. D.

I am applying LaFerté's name to this species largely on the basis that his description matches it quite well and that he particularly noted unusually slender antennae. He had two specimens to study, one in the Dejean collection and one in his own, the source of both being a series in the museum at Berlin, and ultimately the collecting of Moritz. I have seen the specimen in the LaFerté collection and compared it with West Indian material, but did so before I realized that there are several species in the subtilis-group. I have never seen a specimen of this group from a continental area. According to W. Horn's Entomologische Sammlungen, C. Moritz collected in both Colombia and Puerto Rico in the 1830's. It is likely that some labels got mixed.

Anthicus darlingtoni, sp. n.

Fig. 3, 17.

Generally similar to *subtilis* but smaller, 2.02–2.42 mm, head slightly truncate and with more distinct punctures, antennae not so slender, elytra more rounded at apex, median elytral markings usually darker and barely narrowed mesally, and subapical band very faint. Some individuals, including the holotype, lack wings and have the elytra slightly inflated.

Holotype ♂, 2.06 mm. Head 36/46,41, subtruncate with broadly rounded temporal angles. Eyes 17/13, 31 apart, 15 from base. Disc evenly convex, shiny, with evenly distributed punctures ca. 1 apart, small but well defined; diameter of punctures, including downcurved borders, about equal to intervals. The larger punctures described in *subtilis* are barely larger than those on the intervals. Antennae not unusually slender, segments 13/6, 7/5, 9/5, 10/5, 11/5, 11/5, 11/5, 11/5, 11/6, 10/7, 16/7, base to apex. Prothorax similar to *subtilis,* 44/16,41,27,31. Elytra 126/49,69, similar but apex more rounded and impression weaker. Fully winged individuals are more similar. Surface slightly more deeply punctured, punctures ca. 2 apart; setae similar, ca. 4, tactile setae ca. 7. Legs not modified. Apex of visible sternum 5 very feebly excavated. Median elytral markings 29 long, separated by ca. 18 across suture, 4 from side margin; subapical band much paler, barely a cloud, ca. 11 wide.

Holotype, ♂, HAITI: Etang Lachaux (under 1000′, Oct. 26-27, '34, P. J. Darlington, WL) in MCZ. Paratypes: HAITI: Etang Lachaux (same data, 2 WL ♂, 1 WL ♀), Camp Perrin (nr. 1000′, 1 F ♂, 1 WL ♂, 2 F ♀), Damien (2 F ♀), Port-au-Prince (1 WL ♂), Miragoane (2 WL ♀), Ennery (nr. 1000′, 2 WL ♀), Mt. La Hotte (Tardieu, 3000′, 1 WL ♀), Kenskoff (nr. Port-au-Prince, 4–6000′, 1 F ♀). All specimens were collected by P. J. Darlington between September and November, 1934.

In at least two localities this species is sympatric with *subtilis,* but it appears to have a narrower range. Six of the specimens have full wings (F) and 11 are entirely wingless (WL).

Anthicus hispaniolae, sp. n.

Fig. 2, 16.

Larger than *subtilis* and the other species of the group, 2.68–3.11 mm, and with more extensive and darker markings on the elytra, these tending to be connected along the suture but not along the sides. Most of the head and prothorax brown, elytra with base to transverse impression, a midband and an oblique subapical band brown, these connected at least narrowly along suture; subapical band paler in part of the series. Rest of elytra, legs, palpi, antennal segments 1 & 2, and usually labrum, mandibles except for tips, and head adjacent to antennal insertions luteous. Dark midband and subapical band not reaching side margins. Underside and abdomen pale brown. Head and prothorax densely, finely punctured. Tegmen of ♂ genitalia very slender and tapering almost evenly to narrow tip.

Holotype ♂, 2.68 mm. Head 42/56,49. Eyes 25/18, 36 apart, 15 from base, which is subtruncate with a shallow median impression, the temporal angles broadly rounded. Disc evenly convex, shiny, but punctures ca. 2 apart and broader than intervals. Antennal segments 1–2 pale, 1 heavier than usual; segments 18/11, 9/5/ 12/5, 13/5, 15/5, 17/6, 15/6, 14/6, 13/7, 13/7, 18/7, base to apex. Prothorax 52/22,47,37,42; punctures very dense, 2 apart, intervals very narrow, especially in back half. Elytra 175/69,95, with distinct omoplates and postbasal impression; punctures small, ca. 2 apart, intervals flat and about as wide as punctures; setae moderately dense, decumbent, 4, part slightly less decumbent, 5; tactile setae ca. 6. Legs simple; visible sternum 5 truncate.

Holotype, ♂, REP. DOM.: Constanza to Jarabacoa (2–4000′, Aug., '38, P. J. Darlington) in MCZ. Paratypes: REP. DOM.: same data (2♂), foothills of Cordillera Central (S. of Santiago, 1♂). HAITI: N.E. foothills of La Hotte (2–4000′, 1♂). The last locality is almost the same as where one *subtilis* was collected. All collected by P. J. Darlington in Oct., 1934, and June and Aug. 1938. All specimens are fully winged, and apparently capable of flight.

Anthicus soledad, sp. n.

Fig. 4, 14.

Generally similar to *subtilis* but smaller, 2.22–2.53 mm, elytral markings darker, median elytral markings nearly or quite a complete band in Cuban individuals, interrupted at suture in those from Jamaica. Head slightly more truncate and deeply punctured, antennae not unusually slender. Unique in having the apex of the ♂ tegmen nearly truncate, with a median point. Cuban specimens are so similar to *macgillavryi* Buck that females cannot be identified.

Holotype ♂, 2.33 mm. Head 40/49,44, subtruncate with broadly rounded temporal angles, slightly impressed at middle. Eyes 19/14, 33 apart, 16 from base; surface similar to *subtilis* but with fine but distinct punctures ca. 2 apart, most slightly narrower than intervals, with gradually downcurved borders. Antennal segments 13/6, 7/5, 9/5, 11/5, 12/5, 13/5, 14/5, 13/5, 13/6, 11/7, 16/6, base to apex. Prothorax similar, 47/18,39,27,33. Elytra 145/55,79, shiny, punctures distinct, ca. 3 apart and almost as wide as intervals; setae ca. 4 long, tactile setae 6. The midband on this and other Cuban specimens is complete, slightly paler at suture; subapical band broad and dark, connected to midband at sides and narrowly at suture, leaving a diagonal mark on each elytron and apex pale; base onto omoplates somewhat darkened. Jamaican individuals lack the basal darkening, have the midband interrupted at the suture, and the subapical band connected to it only at the sides. Legs unmodified. Apex of visible sternum 5 feebly excavated.

Holotype, ♂, CUBA: Soledad nr. Cienfuegos (Oct. 21, '26, P. J. Darlington, F) in MCZ. Paratypes: CUBA: Soledad (2 F ♂), Cayamas (5 R ♂). JAMAICA: Rio Cobre (5 mi. above Spanishtown, 1 F ♂, 1 R ♂, 1 WL ♂), Ocho Rios (1 WL ♂), Blue Mts. (Whitefield Hall, nr. 4500′, 1 R ♂), Milk River (1 F ♂). Five of the males are fully winged (F), 7 have reduced wings (R), and 2 are wingless (WL). In addition 5 fully winged females from Jamaica are identified with this species but not included as paratypes: Whitefield Hall (2), Milk River (2), and Mandeville (1, dead in light globe). Paratypes in MCZ, USNM and collection of FGW.

Anthicus macgillavryi Buck
Fig. 12, 14.

Anthicus macgillavry Buck 1960: 69–70 (type-locality: Manicaragua, CUBA, but holotype is a ♀ and not conclusively identifiable as the species redescribed here).

2.11–2.24 mm, extremely similar to sympatric *soledad* individuals on Cuba, ♂ differing in having the front tibiae excavated in apical 2/5 and in having the tegmen of the genitalia slightly constricted beyond middle, similar to *subtilis* and *darlingtoni*. Elytra with dark midband complete in all specimens identified.

♂, Soledad, 2.20 mm. Head 36/48,41; eyes 18/15, 31 apart, 13 from base; antennal segments 13/7, 8/5, 9/4, 11/5, 13/5, 13/5, 13/5, 12/5, 12/5, 11/7, 17/5, base to apex. Prothorax 47/17,40,27,31; elytra 138/56,75; setae ca. 4, tactile setae 5. Front tibiae gradually thickened from base to 6 thick at 16 from base, zone beyond thickest portion moderately abruptly thinned to slightly more than 4 in a gently concave, flattened zone ca. 6 wide, this lined with moderately dense, pale, decumbent setae. Front tarsi not modified. Apex of visible sternum 5 feebly excavated.

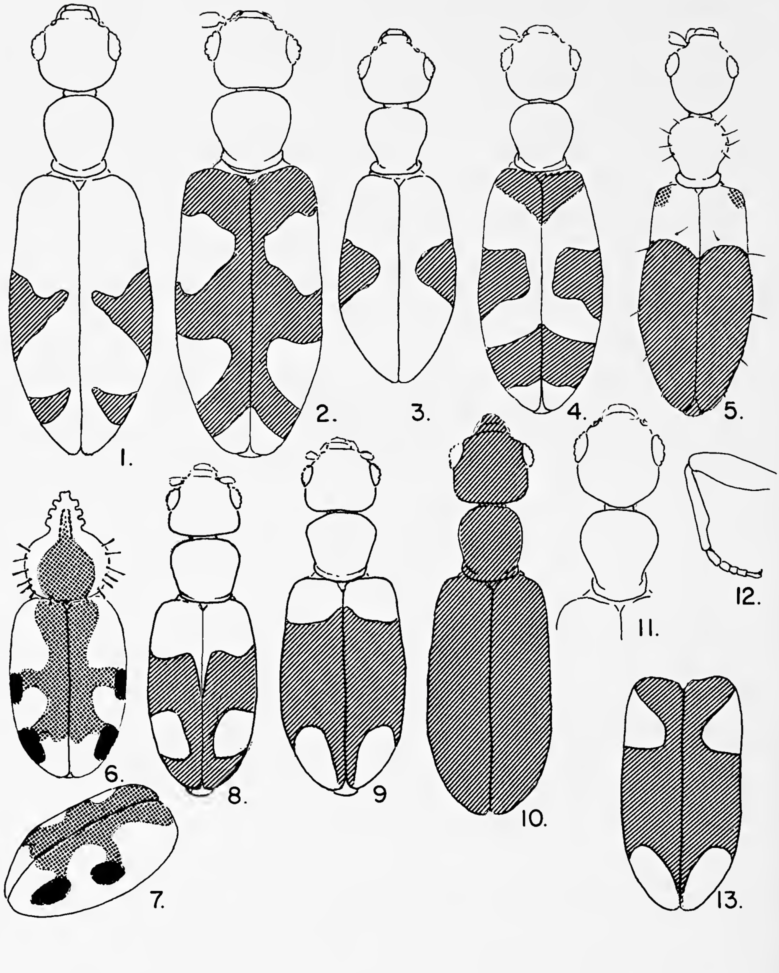
Records: CUBA: Soledad, nr. Cienfuegos (5 F ♂, 5 WL ♂), Baraguá (at light, 1 F ♂), Cayamas (2 F ♂, 6 R ♂), Limones (1 WL ♂). Of the 20 specimens identified, 8 have full wings, 6 reduced wings, and 6 are wingless.

This species is more abundant than *soledad* on Cuba, so is the more likely one to be associated with Buck's name. The holotype and all 15 paratypes sent from the Amsterdam collection are females, so no part of the type series can be included in the records.

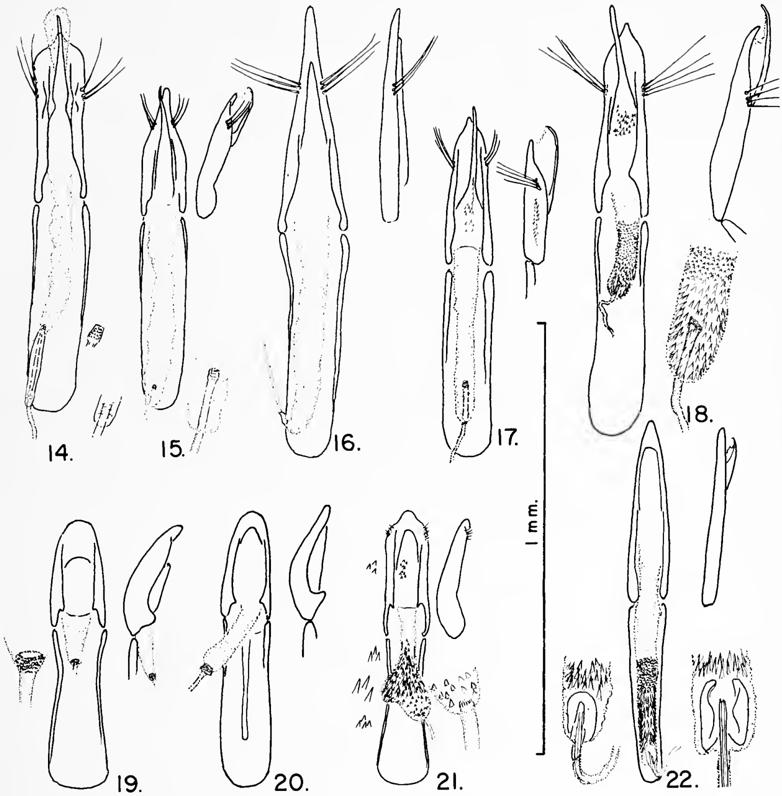
Mecynotarsus hispaniolae, sp. n.
Fig. 6, 7.

1.56–2.04 mm (elytra plus prothorax including horn). Brown, appendages rufescent, surface largely concealed by appressed scales, which are cinereous but with a median rufescent cloud on the pronotum and dull brown markings on the elytra. The darkest of the elytral markings are lateral, one rounded and close to middle, the other larger, oval and subapical, both isolated from sides by a broad cinereous zone. Paler brown markings extend from the omoplate area to the level of the front of the subapical mark, with vague connections to both sets of dark marks. The background color of the elytra is slightly rufescent dorsally. Prothorax with a sparse fringe of long, erect, flattened, slightly clavate setae, on sides and onto base. Elytral scales of 2 different widths, the wider ca. 1½ times as wide, the 2 widths tending to be in alternate rows and the wider just perceptibly elevated.

Holotype: 2.04 mm; head 39/45,45; eyes small, 12/9, their curved scales ca. 1.5; 29 apart, 12 from base of head. Upperside of head flat, with sparse setae and some 12 long, suberect setae and well-developed erect, flattened setae on horn outline, 10–14 long. Prothorax 39 long, 82 with horn, 63 wide; horn 31 wide at widest, 12 thick. Marginal setae 9 long, the ones on base slightly shorter. Horn



Figures 1–13. Fig. 1. *Anthicus subtilis*, described specimen. Fig. 2. *A. hispaniolae*, holotype. Fig. 3. *A. darlingtoni*, holotype. Fig. 4. *A. soledad*, holotype. Fig. 5. *A. russoi*, described specimen. Fig. 6. *Mecynotarsus hispaniolae*, holotype. Fig. 7. Same specimen, oblique lateral view of elytra. Fig. 8. *Anthicus margaritae*, holotype. Fig. 9. *A. antilleorum*, holotype. Fig. 10. *A. blackwelderi*, holotype. Fig. 11. *Thicanus texanus*, Barahona, Rep. Dom., forebody. Fig. 12. *Anthicus macgillavryi*, front leg of described ♂. Fig. 13. *A. blackwelderi*, elytral markings of Cuban population, from coast below Pico Turquino.



Figures 14-22. ♂ genitalia of *Anthicus* spp., in ventral view, most with tegmen in left lateral view, details of internal sac and gonopore armature to sides. Fig. 14. *A. soledad,* paratype, Soledad, Cuba. Fig. 15. *A. macgillavryi,* Soledad, Cuba. Fig. 16. *A. hispaniolae,* paratype. Fig. 17. *A. darlingtoni,* paratype, Damien, Haiti. Fig. 18. *A. subtilis,* Villa Altagracia, Rep. Dom. Fig. 19. *A. antilleorum,* paratype, Cayamas, Cuba. Fig. 20. *A. margaritae,* paratype, Carupano, Venez. Fig. 21. *A. blackwelderi,* paratype, Kingston, Jam. Fig. 22. *A. russoi,* Boca Chica, Rep. Dom.

with a well-developed crest of 2 ridges, these up to 8 apart, and with 3 strong teeth on each side. Underside of horn with a sparse brush of suberect, anteriorly directed simple setae 10 long. Elytra 122/65,87, strongly inflated, punctures ca. 3 apart but obscured by dense scales ca. 4 long; no tactile setae discernible. Hind tibia 47 long, tarsus 61, front tarsus 29.

Holotype, ♀, REP. DOM.: Las Salinas b. Bani (10.X.1979, J. & S. Klapperich) in Natural History Museum, Basel, Switzerland. Paratypes: 2 ♀, same data, Basel and FGW collection.

Relationships: The species of *Mecynotarsus* in the elegans-group seem assignable to at least 3 subgroups. The first, already noted (Werner 1962), has the sutural area of the elytral apex pale, this zone restricted anteriorly by oblique dark bands. To this group belong *elegans* LeConte, *intermixtus* Werner, *jamaicanus* Werner, and probably *falcatus* Chandler. In this group the male genitalia are distinctive, the phallobase bearing rounded lateral lobes. The male antennae are not expanded and the prothoracic horn is relatively narrow.

A second subgroup has the markings at the tip of the elytra based on a pale sutural mark and lateral spots, with a narrow extension from the oblique subapical bands tending to reach the very apex on each side, where there may be a tiny development of a pit in the male. This subgroup contains *balsasensis* Werner and *salvadorensis* Werner. These 2 species have a distinctive pale strip through discal clouding on the pronotum. Werner (1962) indicates that the phallobase is simple but Chandler (1977) states that there are lateral lobes in *salvadorensis*. Very small size of the genitalia makes interpretation difficult. The antennae are simple in the male and the horn is relatively narrow.

Finally, a third subgroup has each elytron pale at the apex, with a convex anterior border to the pale zone. The most distinctive feature is expansion of the intermediate antennal segments in the male, and simple phallobase of the male genitalia. The prothoracic horn is broader than in the other 2 subgroups, and any clouding on the pronotum lacks a median pale stripe. This last subgroup contains *nevermanni* Werner, *alvarado* Chandler, and *vafer* Chandler, with *sexnotatus* Champion assignable to it on male characters but having the elytral markings so reduced that they are difficult to interpret.

M. hispaniolae is probably a member of this third subgroup, but no males have been collected. However, the more posterior dark mark on the elytra shows no sign of a posterior excavation, as is present in *alvarado* and *vafer.* The distinctive erect setae on the sides of the prothorax are matched in *alvarado* and approached in *vafer,* but are also approached in *salvadorensis* in the second subgroup. No other species has such differences between the broad and narrow scales, but there is some difference in *vafer, alvarado* and *salvadorensis;* the tendency may be more a function of denseness of scales than relationship. The long setae on the underside of the horn are matched in *vafer* and hinted at in some others in the third subgroup, *salvadorensis* in the second, and *intermixtus* in the first. The setae on the horn, and matching setae on top of the head, as well as the erect setae on the top of the head that outline the horn, probably have an adaptive value in keeping sand grains out of the space between head and horn when the beetle is digging. Degree of development might very well be habitat-related.

CHECKLIST OF SPECIES AND GREATER ANTILLES RECORDS

Acanthinus angusticollis (LaFerté) 1848: 120–1. Werner 1966b: 747–9, fig. 1, 3, 6, synonymy. Southern Brazil to northern South America. Introduced? CUBA: Bahia Honda, Camagüey, Cayamas, Havana, Santa Clara. JAMAICA: Kingston.

Acanthinus concinnus (LaFerté) 1848: 123. Werner 1970a: 123, fig. 7, 21. Bolivia to eastern Mexico. Introduced? CUBA: on ship from Cuba. HISPANIOLA: Rep. Dom.: Boca Chica, Colonia (1000 m), Haina, San Cristobal (35 m), San Francisco Mts., San José de las Matas, Trujillo Valdes (Boni), Villa Altagirica.

Acanthinus ebeninus (LaFerté) 1848: 117. Werner 1970a: 119, fig. 17.

Pseudoleptaleus cubanensis Pic 1917: 8 (type-locality: Cuba). Venezuela and Colombia; reported from Guatemala without exact locality (specimen not seen). CUBA: only the Pic specimen, without specific locality.

Acanthinus quinquemaculatus (LaFerté) 1848: 115–6. Werner 1970a: 121–2, fig. 6, 20. Bolivia to eastern Mexico. Introduced? CUBA: Sabanilla. HISPANIOLA: Rep. Dom.: Boca Chica, Colonia (1000 m). PUERTO RICO: Flamboyant, Puerca Bay.

Acanthinus schwarzi Werner 1967: 1232, fig. 10, 23. Probably endemic. CUBA: Cayamas, Pinar del Rio, Soledad nr. Cienfuegos.

Acanthinus scitulus (LeConte) 1852: 94–5. Werner 1970b: 724–5, fig. 20–22, 34.

Formicilla cubana Pic 1944: 9–10 (type-locality: Cuba).

Formicillia gracillipes (sic): Buck 1960: 64, in part, Cuban specimens.

Honduras to southeastern U.S.A. Probably a recent introduction. CUBA. Hormiguero, Pinar del Rio. Through the courtesy of Ben Brugge, of the Zoological Museum of Amsterdam, I have examined most of the specimens reported by Buck. His specimen from Colombia belongs to *Acanthinus leporinus* (LaFerté). HISPANIOLA: Rep. Dom.: Boca Chica (10 m).

Amblyderus sp. Wolcott 1936: 210. PUERTO RICO: Ponce (on *Randia mitis* and other flowers). Identification was provided by H. S. Barber, but specimens cannot now be located. The blossom association makes the identification suspect, since the usual association of *Amblyderus* is sand dunes.

Anthicus antilleorum Werner. Native. Also in Virgin and Bahama Islands. CUBA, HISPANIOLA.

Anthicus blackwelderi Werner. Probably endemic. JAMAICA, CUBA, HISPANIOLA.

Anthicus crinitus LaFerté 1848: 204–5. Werner 1975b: 472–3, fig. 2, 5. Old World, becoming cosmopolitan. HISPANIOLA: Rep. Dom.: Bani, Mao Val-Verde, San Cristobal, St. Domingo, all near sea level. PUERTO RICO: Fortuna A. E. S., La Parguera, Ponce.

Anthicus darlingtoni Werner. Endemic. HISPANIOLA.

Anthicus floralis (L.) 1758: 420. Werner 1964: 233–4, fig. 18, 71. Cosmopolitan. JAMAICA: Trelawney. HISPANIOLA: Rep. Dom.: San Cristobal, St. Domingo. PUERTO RICO: Ponce.

Anthicus formicarius (Goeze) 1977: 705. Werner 1964: 234–5, fig. 19, 72. Cosmpolitan. JAMAICA: St. Andrew.

Anthicus hispaniolae Werner. Endemic. HISPANIOLA.

Anthicus macgillavryi Buck. Endemic. CUBA.

Anthicus pallidus Say 1826: 245. Werner 1964: 230–1, fig. 1, 2, 64, synonymy. Coastal areas, Florida to northern South America; Lesser Antilles. Probably native. CUBA: Maisi in Oriente Prov. HISPANIOLA: Haiti: Grande Anse. Rep. Dom.: Barahona. PUERTO RICO: Bayamon.

Anthicus russoi Krekich. Probably a myrmecophilous endemic. HISPANIOLA.

Anthicus soledad Werner. Endemic. CUBA, JAMAICA.

Anthicus subtilis LaFerté. Endemic. CUBA, HISPANIOLA.

Anthicus tobias Marseul 1879: 125. Werner 1964: 235, fig. 12. Old World, becoming cosmopolitan; Virgin Islands. JAMAICA: Gordon Town, Morant Bay, Spanish Town. HISPANIOLA: Rep. Dom.: Boca Chica, San Cristobal, Santo Domingo, all near sea level.

Mecynotarsus hispaniolae Werner. Endemic. HISPANIOLA.

Mecynotarsus jamaicanus Werner 1962: 84, fig. 3, 10. Probably endemic. JAMAICA: Kingston.

Notoxus bipunctatus Chevrolat 1877: ix. Chandler 1978: 35, fig. 26, 57. Probably endemic. PUERTO RICO: Alsina, Anaso District, Coama Springs, Ponce, Rio Piedras, San Juan.

Notoxus jamaicus Pic 1913: 8–9. Chandler 1978: 36, fig. 27, 57. Probably endemic. JAMAICA: Alligator Pond Bay, Bull Run in St. Andrew Parish, Milk River, Morant Bay, Santa Cruz, Spanish Town, Trelawney.

Sapintus similis Werner 1983: 420. Mexico to Panama. Introduced? JAMAICA: Spanish Town.

Sapintus teapensis (Champion) 1890: 249. Southeastern Mexico to southern Brazil. Introduced? CUBA: Baracoa, Cayamas, Vinales. HISPANIOLA: Haiti: Desbarrière-Mt. La Hotte, Port-au-Prince. Rep. Dom.: Bani, Haina, La Romana, Monte Cristi, Puerto Plata. JAMAICA: Orange Bay, Santa Cruz, Spanish Town. PUERTO RICO: Tortuguero Lake.

Thicanus texanus (LaFerté) 1848: 301. Werner 1975a: 290, synonymy. Southeastern U.S.A. to eastern Texas, primarily coastal. Probably native. HISPANIOLA: Rep. Dom.: Barahona, Lake Enriquillo. PUERTO RICO: Ensenada.

Vacusus holoxanthus (Fairmaire & Germain) 1860: 3. Werner 1961: 808–9; 1966a: 219, synonymy.
Vacusus jamaicanus Werner 1961: 809.
Chile to southern Brazil. Probably introduced. JAMAICA: Gordon Town, Milk River, Morant Bay, Spanish Town.

Vacusus vicinus (LaFerté) 1848: 157–8. Werner 1961: 799–801, synonymy. Southern U.S.A. to Venezuela. Lesser Antilles. Introduced? CUBA: Baraguá, Camagüey, Cayamas, Havana, Hormiguero, Jatabonica, Manicaragua, Soledad nr. Cienfuegos. HISPANIOLA: Rep. Dom.: Bani, Boca Chica, Mao Val-Verde, San Cristobal, Santo Domingo. JAMAICA: Bath St. Thomas, Clarkstown, Milk River, Morant Bay, Santa Cruz, Spanish Town, Trinityville. PUERTO RICO: Ensenada, La Guanica, Lajas, Mayagüez, Sabena Grande, Salinas. VIRGIN ISLANDS.

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NEST ARCHITECTURE AND BROOD DEVELOPMENT TIMES IN THE PAPER WASP, *POLISTES EXCLAMANS* (HYMENOPTERA: VESPIDAE) *

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One of the distinctive features of social insects is that they rear their brood in nests. In the Vespidae these nests are typically constructed of paper; they have one or several layers of cells, and may have an outer envelope of paper (Jeanne 1975). Nest architecture has been interpreted as a means of minimizing vulnerability to nest predators, particularly ants (Jeanne, 1975; 1979). Another factor that may contribute to nest design is a limitation on efficient food distribution to larvae when there are many cells in a single layer. For example if foragers tend to land on one part of the nest and then begin feeding the nearest larvae, unequal food distribution would result. The purpose of this study was to examine the influence of cell location on brood development times of *Polistes exclamans* Viereck. Also examined were the roles of time of year, numbers of workers, and larvae per worker as factors influencing development times. *P. exclamans* was chosen as a study organism because all cells are in one layer, without an envelope; nests are approximately circular, and have a single off-center pedicel usually located towards the top of the nest. Cells near the pedicel are the oldest. These features make nests of *P. exclamans* among the more simple types of nests. In central Texas nests of *P. exclamans* vary greatly in size, reaching an upper limit of about 500 cells (Strassmann, personal observation).

METHODS

Three nests representing small, average and large nests were chosen for observation at Brackenridge Field Laboratory of the University of Texas at Austin, Texas. These nests appeared to be

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generally representative of their size classes. In 1978 nest 83 (44 cells) and nest 22 (220 cells) and in 1979 nest 27 (345 cells) were observed (Fig. 1). Contents of cells were scored every other day on a cell map, and numbers of females associated with the nest were marked and counted. Nest 22 was observed from 12 June to 14 August; nest 83 was observed from 19 June to 14 August; and nest 27 was observed from 6 June to 18 August. From mid June to mid August mean daily termperatures changed very little. Average monthly temperatures were 23.5° C for June, 24.7° C for July and 24.8° C for August (30 year averages for Austin, Texas, National Weather Service). When an adult emerged from a cell an egg was laid in it so all cells contained brood. In the rest of this paper the nests will be referred to as the small (nest 83) medium (nest 22) and large (nest 27) nest.

For the purposes of analysis the medium and large nests were divided into 4 regions, and the small nest was divided into 3 regions (Fig. 1). The regions were chosen by first mapping development times of brood in every cell on a cell map, and then choosing regions that were homogeneous within themselves and as different as possible from other regions. This technique maximized the probability that differences among regions would be found. On all nests region 1 is the oldest, directly in front of the nest pedicel. Region 2 is the center of the nest. Regions 3 and 4 are edge regions. The medium nest may appear in the figure to have two lobes to it but they were actually contiguous. The cells were deformed somewhat due to contact with 1 inch chicken wire mesh which ran down the center of the nest.

Large sample sizes, normal distribution of data and nearly equal variances allowed us to use parametric statistics in this study. Because of its size the small nest was omitted from some of the analyses. All statistical analyses were performed using Statistical Analysis System (SAS) or Statistical Package for the Social Sciences (SPSS).

RESULTS

Average development times of eggs varied from 9 to 14 days depending on the nest (Table 1). Eggs took significantly longer to develop on the small nest (small compared to medium nest $t = 5.45$,

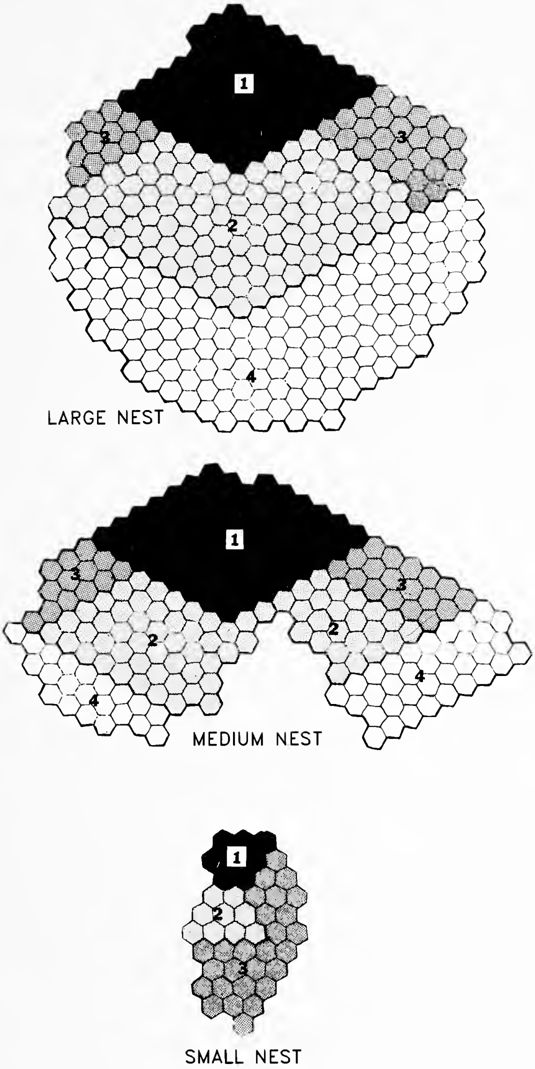

Figure 1. Cell maps of nests in the study indicating nest regions.

df=381, p <0.001; small compared to large nest, t=8.55, df=542, p <0.001). There were no differences in egg development times between the medium and large nests (t=0.57, df=839, n.s.). Average larva development times varied from 13 to 18 days depending on nest (Table 1). The small nest and the large nest did not differ in average larva development times (t=0.68, df=343 n.s.). However they both had longer larva development times than did the medium nest (small compared to medium, t=4.84, df=322, p <0.001; medium compared to large, t=8.89, df=611, p <0.001). Pupa development times averaged 13 days on all nests, and there were no significant differences among the nests.

Development times of eggs, larvae and pupae did not vary significantly from one region of the nest to another on the small and medium nests (Tables 2–4, Fig. 2). In the large nest both eggs and larvae developed most quickly in region 1 (the oldest part of the nest), and most slowly in the edge regions 3 and 4 (Tables 2–4, Fig. 2). In no case did region of nest explain more than 10% of the variance in development time.

Date did not have a consistent effect on development times. Eggs developed more slowly towards the end of the season in the large nest, and more quickly towards the end of the season in the small nest (Table 5). There was no change in egg development time with date in the medium nest. Larva development time increased with date in both the large and the medium nest, and decreased with date in the small nest (Table 5). Development times of pupae did not change with date in the large nest, but decreased with date in the medium and small nests (Table 5). Date explained 35% to 51% of the variance in larva development times depending on nest. It explained smaller percentages of the variance in egg and pupa development times except on the small nest (Tables 2–4).

Interaction between date and region of nest was examined using a 2-way ANOVA (Tables 2–4). There was a significant (p <0.05) interaction between date and region of nest for egg and larva development times in the large nest that explained 7% and 5% of the variance respectively (Tables 2–4). This interaction thus explains a trivial amount of the variance in development compared to that explained by date.

The effect of numbers of females tending the nest was found to be quite variable. Looking only at the medium and large nests, it

TABLE 1. Average brood development times per nest.

	X	S.D.	N
Egg development time			
Small nest	13.81	5.67	43
Medium nest	9.58	4.67	340
Large nest	9.43	2.92	501
Larva development time			
Small nest	18.18	3.71	28
Medium nest	13.39	5.09	296
Large nest	17.39	6.03	317
Pupa development time			
Small nest	12.74	2.18	19
Medium nest	13.05	4.31	218
Large nest	13.00	3.83	268

TABLE 2. ANOVA of the effects of date and location in nest on egg development times.

	Main Effects		*Interaction*
	Location in nest	Date	Location in nest × date
Small nest			
Sum of squares	68	648	76
F	2.1	1.31***	1.5
df	2	3	3
% of variance explained	5	48	6
Medium nest			
Sum of squares	56	1184	319
F	1.0	16.3***	1.5
df	3	4	12
% of variance explained	1	16	4
Large nest			
Sum of squares	105	100	278
F	4.5**	3.2*	3.2***
df	3	4	11
% of variance explained	3	2	7

df = degrees of freedom, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

was found that egg development time increased with number of females on the large nest and decreased on the medium nest (Table 5). Larva development times increased with numbers of females on both large and medium nests. Pupa development time decreased with increasing numbers of females on the large nest, and did not change significantly on the medium nest (Table 5).

Partial correlations of development time with date were calculated controlling for numbers of females, since numbers of females increased with date. Development times of larvae increased significantly ($p < 0.01$) with date on the large and medium nests when numbers of females were controlled for (Table 5). Development times of eggs decreased with increasing numbers of females on the medium nest when date was controlled for. Development times of larvae and pupae decreased with increasing numbers of females on the large nest when date was controlled for.

The ratio of larvae to females on the large nest was 3.11 ± S.D.2.05, and on the medium nest it was 1.23 ± S.D.0.47. Development time of larvae was slower when there were more larvae per female on the large nest ($r=-0.13$, $p<0.03$, $N=317$). The correlation was in the same direction on the medium nest, but was not significant ($r=-0.10$, $p>0.1$, $N=296$) perhaps because there averaged more females per larva.

DISCUSSION

The results presented here do not offer strong support for the hypothesis that location of brood affects development rates. Centrally located brood developed no more quickly than did edge brood. Feeding efficiency does not appear to be limiting the size of nests. Foragers arriving on the nest with prey typically share it with 3 or 4 other females who each visit many larvae (Strassmann, unpub.). The result seems to be even distribution of food. Though the largest nest did show a significant region effect for egg and larva development, it explained less than 7% of the variance. Perhaps an even larger nest would show a more marked effect. West Eberhard (p. 38, 1969) suggested that 7 pupae in the center of a nest she observed and 8 pupae towards the edge of the nest had long and short pupal periods respectively because of differences in larva nutrition. She suggested that better-fed larvae in the center of the nest would have longer pupa development periods. This study does

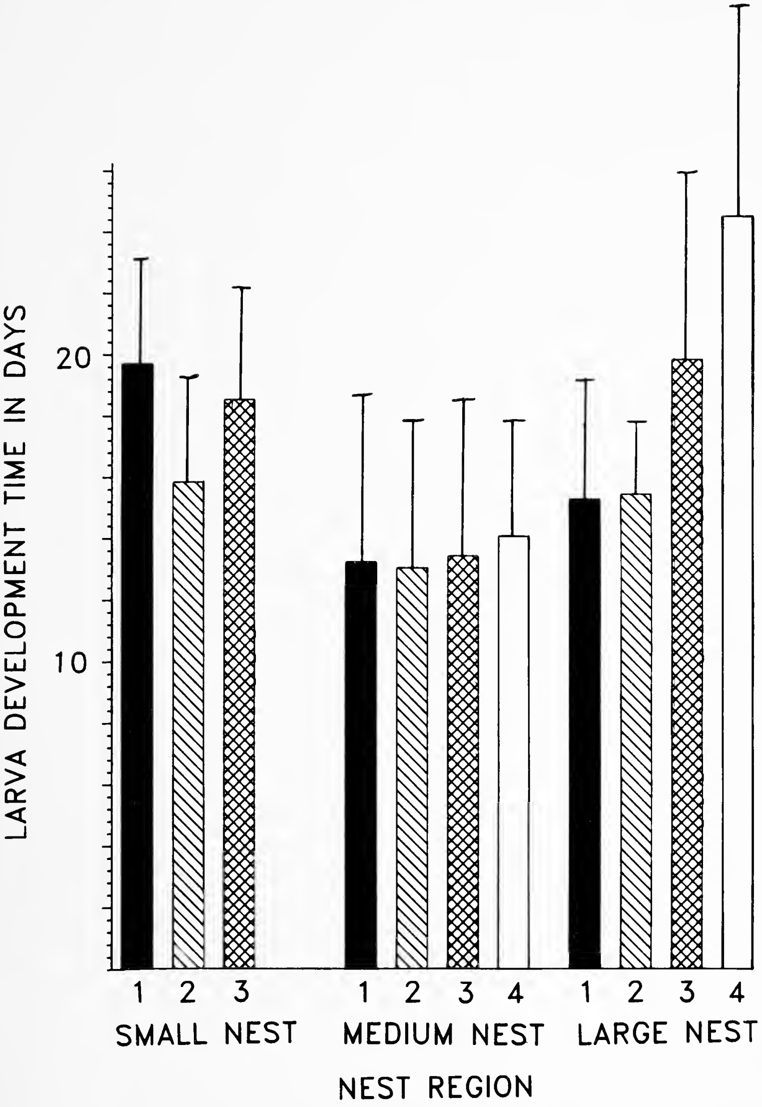

Figure 2. Development times of larvae in different regions of each nest. Bars indicate means and lines indicate standard deviations.

TABLE 3. ANOVA of the effects of date and location in nest on larva development times.

	Main Effects		*Interaction*
	Location in nest	Date	Location in nest × date
Small nest			
Sum of squares	25	148	22
F	1.4	5.6	1.3
df	2	3	2
% of variance explained	7	40	6
Medium nest			
Sum of squares	35	2631	49
F	0.7	37.0***	0.3
df	3	4	11
% of variance explained	1	35	1
Large nest			
Sum of squares	821	5842	568
F	19.4***	138.1***	5.0***
df	3	3	8
% of variance explained	7	51	5

df = degrees of freedom, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

not support her conclusions.

High mean daily temperatures characterized the entire period of this study, essentially eliminating temperature as a variable. The slight increase in temperature over the season would be expected to speed up development if it had any effect at all. The increase in development time with date may best be explained by a gradual seasonal decrease in abundance of prey. Later in the season larvae may take in less nutrition per day, which results in longer times spent as larvae. Also there is usually a gradual increase in size of adults over the season in *P. exclamans* (Strassmann, unpub.). Larvae destined to become larger adults may require longer feeding periods. In *P. metricus* midsummer workers are as large as queens (Haggard and Gamboa, 1980). These large workers were larvae when worker to larva ratios were at their maximum (Haggard and Gamboa, 1980).

Development times of larvae were shortest on the medium nest which had the fewest larvae per worker. There are probably advan-

TABLE 4. ANOVA of the effects of date and location in nest on pupa development.

	Main Effects		*Interaction*
	Location in nest	Date	Location in nest × date
Small nest			
Sum of squares	7	33	3
F	1.1	11.1**	1.1
df	2	1	1
% of variance explained	8	39	4
Medium nest			
Sum of squares	21	333	180
F	0.4	4.8**	1.0
df	3	4	10
% of variance explained	1	8	5
Large nest			
Sum of squares	57	278	105
F	1.4	5.0	0.8
df	3	4	9
% of variance explained	2	7	3

df = degrees of freedom, *p <0.05, **p <0.01, ***p <0.001

tages to flexibility in development time of larvae which allow more time for development when food is limiting, either because there are fewer females to harvest it, or because of a general scarcity of prey in the environment.

Data on development times were found in the literature for 4 populations of *P. fuscatus*, and 1 each of *P. hunteri, P. annularis, P. gallicus* and *P. exclamans* (Table 6). Development times varied from 10 to 25 days for eggs, from 15 to 25 days for larvae and from 13 to 22 days for pupae (Table 6). *P. exclamans* in this study falls towards the faster end of this range, particularly for pupa development time. All reports of pupa development times averaged over 18 days except Rabb's study of *P. exclamans* in N. Carolina. *P. exclamans* was studied in the most southern climate, so it is possible that the differences are due to temperature. There is a trend in *P. fuscatus* towards shorter pupa development times in more southern populations. *P. exclamans* and *P. annularis* are the only two members of the subgenus *Aphanilopterus* represented here. It is possible that *Aphanilopterus*, which generally has larger nest sizes and more adults tending

TABLE 5. Correlations between development time, date and number of females on the nest.

	Correlation with date	Correlation with number of females	Correlation with date controlling for number of females	Correlation with number of females controlling for date	N
Egg development time					
Small nest	–0.31*				43
Medium nest	–0.07	–0.15**	0.13**	–0.18***	340
Large nest	0.10*	0.10*	0.01	0.04	501
Larva development time					
Small nest	–0.58**				28
Medium nest	0.46***	0.40***	0.25***	–0.04	296
Large nest	0.65***	0.30***	0.96***	–0.93***	317
Pupa development time					
Small nest	–0.59**				19
Medium nest	–0.15*	–0.11	–0.11*	0.05	218
Large nest	–0.04	–0.16**	0.25**	0.29***	268

*p <0.05; **p <0.01; ***p <0.001

the nest, also has faster development times (Strassmann, unpub.). This is not contradicted by the very long development times reported by Jeanne for *P. annularis* since these were early spring data, and are therefore not strictly comparable. Another factor that may result in selection for fast pupa development times is that nests of *P. exclamans* are very vulnerable to predation, and to loss of the nest due to death of all workers (Strassmann, 1981). Short pupa development times may reduce the probability of nest loss. But this

TABLE 6. Brood development times for other species of *Polistes*. Means plus or minus standard deviations are given. For *P. gallicus*, the range is given in parentheses.

Species	location	egg	N	larva	N	pupa	N	reference
P. fuscatus	Michigan	13.0 ± 2.9	36	15.3 ± 3.4	58	22.2 ± 4.9	124	West Eberhard, 1969
P. fuscatus	Iowa	10.2 ± 2.13	122	17.6 ± 7.1	105	19.2 ± 2.3	96	Klahn, unpub.
P. fuscatus	N. Carolina	14.8	5	15.5	4	18.5	6	Rabb, 1960
P. variatus	Wisconsin	11.5 ± 1.9	395	17.2 ± 3.2	192	19.9 ± 1.6	192	Morgan, unpub.
P. hunteri	N. Carolina	14.0	6	17.2	6	17.4	8	Rabb, 1960
P. annularis	Virginia	24.9 ± 4.4	96	25.4 ± 5.2	42	19.7 ± 1.4	15	Jeanne, unpub.
P. exclamans	N. Carolina	13.4	8	19.7	6	14.7	6	Rabb, 1960
P. gallicus	Italy	10 (6–15)	201	16 (9–23)	117	13 (9–21)	106	Pardi, 1951

may also be the case for the other species of *Polistes* where data on nest failure rates are not available.

Polistes has slightly longer development times than other social wasps. *Paravespula vulgaris, Dolichovespula sylvestris* and *Vespa crabro* all have summer egg development times of about 5 days, larva development times of 10 to 15 days and pupa development times of 11 to 15 days (Spradbery, 1973). The shorter development times in these species as compared to *Polistes* may be due to the much larger colony sizes found in these species, as well as their ability to eat a greater variety of arthropods and carrion.

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We thank Christi Steinbarger and Dana Meyer for help with field work, and Bill Mueller and Colin Hughes for their comments on the manuscript. This research was supported by NSF Postdoctoral Fellowship #SPI-7914902 and NSF #DEB80-05739 to JES.

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NEW SPECIES OF THE ANT GENUS MYOPIAS (HYMENOPTERA: FORMICIDAE: PONERINAE)

By Robert B. Willey[1] and William L. Brown, Jr.[2,3]

The work reported upon here began in the early 1950's as a revision of genus *Myopias,* including as a synonym *Trapeziopelta.* For a year or more it served as the trial focus of RBW's doctoral thesis research, until his interests shifted into other channels, and he laid the revisionary work aside. Meanwhile, WLB's interest in the revision continued, but he had no opportunity at that time to do much more than supervise the drafting of a set of illustrations by artist Nancy Buffler—many of which are now offered here—and to make some of the dissections of mouthparts, etc.

As WLB's work on the reclassification progressed for over 25 years through the tribes of subfamily Ponerinae, much new material was added to what had been available for the original *Myopias* study, and additional new synonymies and new species were discovered, as well as valuable information on the larvae, males, distribution and bionomics of species new and old. Even the status of *Myopias* as a genus apart from *Pachycondyla* came into question. Although in some ways it would be best if the old findings to which we both contributed could simply be incorporated in the reclassification part dealing with tribe Ponerini *s. str.,* there seemed in this course no convenient way to recognize the legitimate claim of RBW to authorship based on the considerable amount of work he had done on *Myopias* in 1955.

The compromise reached sees the larger *Myopias* review, with keys to species and discussions of synonymy, biology, etc. to be included in Brown's forthcoming Part VII of "Contributions toward a Reclassification of the Formicidae," while descriptions of the new species included in various drafts of our joint manuscript of the

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1950's are presented here, together with a few notes on variation, on bionomics, and on the distribution of certain species. Figures of some old species are included with those of the new ones.

COLLECTIONS AND COLLECTORS, WITH ABBREVIATIONS

The main collection used is that of the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (MCZ), for *Myopias* based mainly on collections by Eric Mjöberg, Edward O. Wilson, James W. Chapman, William L. Brown, Jr. and Philip S. Ward. Secondary sources were the British Museum (Natural History) in London (BMNH), collected by Barry Bolton and others, and the Australian National Insect Collection at Canberra (ANIC), collected by Robert W. Taylor and others. For the collectors named above, only surnames are cited in the text. Our thanks go to all who provided us with specimens.

The drawings provided here were mostly done during the mid-1950's by Nancy Buffler. Fig. 4 is by James S. Miller. We are also grateful for a copy set of Edward Wilson's wonderful New Guinea field notes of 1955, which have yielded most of what we know about *Myopias* bionomics, here published for the first time.

MEASUREMENTS AND RATIOS

Where series were available, measurements were usually taken on the largest and smallest (worker) specimens in each locality-series. The measurements and indices are mostly those standard in ant taxonomy for the past 30 years.

TL	(total length) axial length of body, including closed mandibles; summed ML + HL + WL + petiole L + length of gaster.
HL	(head length) maximum measurable length of head as seen in dorsal full-face view, using the anterior edges of the frontal lobes as the anterior reference point, and the posteriormost point or points of the cranial outline as the posterior reference point.
HW	(head width) maximum measurable width of head, not including the eyes, as seen in dorsal full-face view.
CI	(cephalic index) HW × 100/HL.
ML	(mandibular extension) maximum measurable distance be-

	tween the most distal apex of the closed mandibles and the anterior edges of the frontal lobes, as seen in same (dorsal full-face) view from which HL is taken.
MI	(mandibulo-cephalic index) ML × 100/HL.
MLO	(mandibular outside length) maximum absolute chord length of left mandible measured from lateral insertion to apex.
CLL, CLW	(length, width of median clypeal lobe) as measured in dorsal full-face view.
SL	(scape length) chord length of antennal scape, excluding radicle.
SI	(scape index) SL × 100/HW
EL	(eye length) maximum measurable length of facetted part of eye.
WL	(trunk length) diagonal length of trunk as measured from side view, from anterodorsal slope of pronotum (excluding cervix) to most posterior extremity of propodeum.

Myopias gigas, new species
(Figures 1, 12)

Diagnosis, worker: A very large species of the *M. loriai* group, even larger than *M. loriai*, with proportionately longer mesonotum and petiolar node, and with the head dorsally, trunk dorsum and pleura of posterior section of trunk sharply and regularly striate; body otherwise prevailingly smooth and shining. Funicular segment II very long, longer than I.

Worker, holotype: TL 16.9, HL 2.50, HW 2.60 (CI 104), ML 2.26 (MI 90), SL 2.62 (SI 101), EL 0.45, WL 4.61, petiole L 1.7, hind femur L 3.7, hind tibia L 3.16 mm.

This, the largest known species of *Myopias*, has the broad, posteriorly narrowed head of the *loriai* group; long, slender, curved mandibles and rather large eyes with many fine facets. A scape, when held straight back as seen in full-face view, surpasses the posterior border of the head by nearly 2½ times the apical scape width. The posterior border of the head is transverse and nearly straight, varying from very feebly concave to subsinuate in slightly different views. As in *M. loriai,* the median clypeal lobe is apically biconvex, with a shallow median notch; the lobe is shorter and broader than in *M. loriai,* and tapers slightly from base to apex.

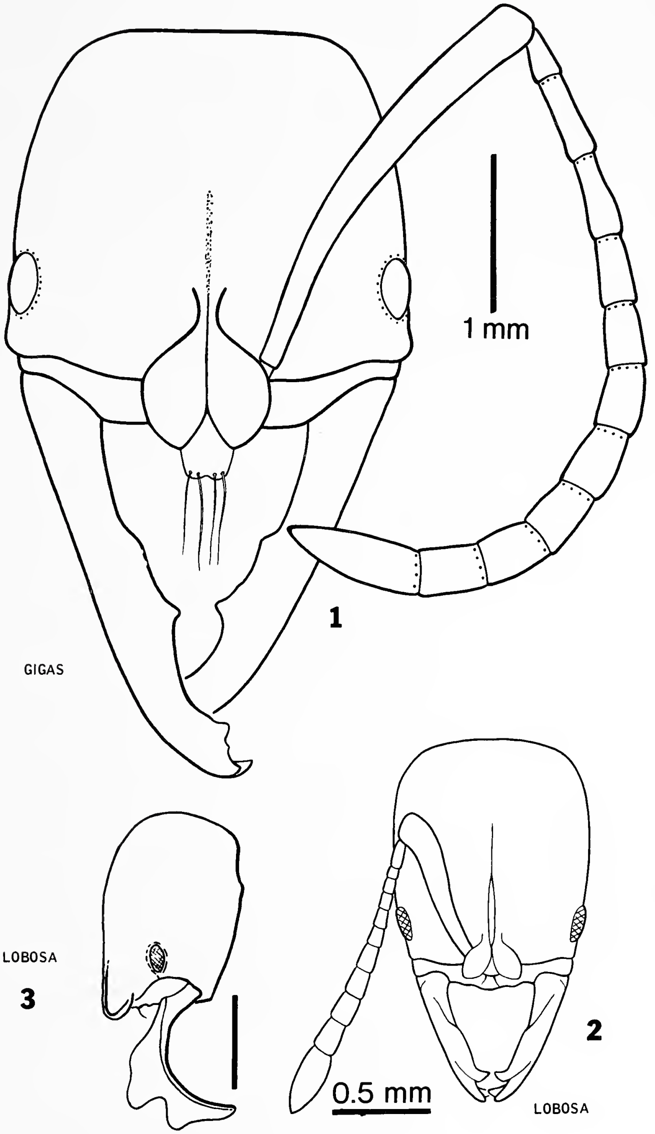
Antennal funicular segment II is longer than I, III and all other funicular segments except the apical, and it is 2.5 times longer than its maximum (apical) width. No differentiated antennal club.

Labrum with a sharp erect tooth at the apex of each labral lobe; no median labral tubercle. Palpi concealed, not seen. Mandibles as shown in Figure 1; apical tooth followed closely basad by 2 coarse denticles and a blunt tooth; middle tooth followed basad by a low, rounded basal angle. Strix (mandibular groove) well-developed from base to apex.

Trunk long and robust; mesonotum longer than in *loriai,* but wider than long (L/W ~ 0.7). Metanotum present as a deeply impressed groove, widening laterad on each end. In side view profile, pronotum strongly convex, although transversely impressed just in front of the raised, cariniform posterodorsal margin; mesonotum feebly convex and sloping downward behind, but its anterior margin raised slightly above the posterior pronotal margin, especially (as in the type) when the two somites are flexed against each other. Promesonotum (without cervix) and propodeum subequal in length; propodeum broadly convex from front to rear, with its declivity steeper than its dorsum, but passing into dorsum through a gentle curve. Mesopleural suture distinct and complete, moderately deeply impressed (more distinct than in *M. loriai*). Propodeal spiracle elongate and oblique, its opening about 2½ times longer than wide.

Petiole (Fig. 12) loaf-shaped, longer than broad and longer than high; exact shape of subpetiolar process, if any, not determined because the extreme anterior end of the segment is hidden by the coxae. Gaster long, gently downcurved, with a distinct constriction between first and second segments; dorsally viewed, second segments longer and a little wider than first. Sting long and strong, distinctly upcurved.

Dorsum of head completely finely and regularly striate in a longitudinal direction, the striae mesal to and behind the eyes tending to curve slightly outward. Dorsum and declivity of trunk similarly striate, but in a transverse direction, arching on pronotum. Sides of trunk behind pronotum with similar, oblique striation, continued from the propodeal dorsum through a curve. Remainder of head, body and appendages smooth and shining, including mandibles, cervical border of vertex and sides of pronotum. Coarse, spaced,



Figs. 1–3, *Myopias* spp., heads of workers, sculpture and pilosity omitted. Fig. 1, *M. gigas* holotype in full-face view. Fig. 2, *M. lobosa*, paratype in full-face view. Fig. 3, *M. lobosa*, another paratype in side view. Scale bars for Figs. 2 and 3 are 0.5 mm.

piligerous punctures are conspicuous in smooth areas, particularly the sides of the head, mandibles, femora and tibiae, petiole, and normally exposed surfaces of gastric terga.

Pubescence appressed and decumbent, generally very sparse, except on antennal flagella, coxae, tarsi, flexor surfaces of fore tibiae, flexor surfaces of mid femora, extensor surfaces of mid tibiae, and apex of hypopygium. Rather abundant erect or suberect, fine, tapered hairs, from short to over 0.5 mm long, occur on almost all normally exposed surfaces of body and appendages. Color deep reddish brown, appendages mainly clear light red.

Holotype (MCZ) a unique worker from Dobodura, Papua New Guinea (P.J. Darlington leg.).

This magnificent species is even larger than *M. loriai,* and has very different sculpture, but the two forms are obviously closely related. Because of the long mandibles and large size, we guess that *M. gigas* may be a millipede predator, but we have no direct evidence of feeding behavior for this species.

Myopias julivora new species
(Figs. 5, 22)

Diagnosis, worker: Similar to *M. tenuis,* but larger (HW 0.80–1.01), with relatively longer mandibles and antennae, MI > 65, scapes overreaching posterior border of head (when held straight back, full face view) by about their own apical width to nearly twice their apical width; all antennomeres longer than broad. Shafts of mandibles approximately straight over middle half of their length.

Worker, holotype: TL 6.2, HL 1.04, HW 0.94 (CI 90), ML 0.73 (MI 70), MLO 1.01, SL 0.90 (SI 96), EL 0.09, WL 1.74, hind femur L 1.00, hind tibia L 0.94 mm.

Worker, paratypes (n = 6 of 34 representing 7 colonies from 6 localities, including largest and smallest specimens): TL 5.8–6.7, HL 0.91–1.14, HW 0.81–1.01 (CI 88–90), ML 0.62–0.83 (MI 66–73), MLO 0.86–1.14, SL 0.86–1.09 (SI 96–108), EL 0.06–0.10, WL 1.66–1.93, hind femur L 0.89–1.15, hind tibia L 0.87–1.12 mm.

Description limited to details not covered in diagnosis and measurements. Median frontal sulcus extends approximately to middle of HL, followed posteriad after a gap by a shallow pit marking location in queen of anterior ocellus; this pit is usually absent in *M. tenuis,* but is occasionally faintly indicated there. Compound eye essentially reduced to a single convex lens, but at high magnifications, traces of an ommatidial grid can be made out; reduction approaches the state in *M. tenuis,* but does not go quite so far. Median clypeal lobe trapezoidal, widest near apex (CLL 0.12, CLW 0.16 mm), but by optical illusion may seem as long as or longer than wide; free corners rounded; anterior margin straight, convex, or even slightly sinuate. Basal oblique mandibular groove (strix) sublateral in origin, difficult to see in dorsal view, but distinct with its ventrolateral extension in side view. Submedian tooth situated in seventh tenth of the shaft length, counting from base. Basal angle obsolete.

The upturned tooth on each labral lobe and 3,3 palpal segmentation formula are as in *tenuis.*

Trunk formed much as in *M. tenuis;* promesonotum subequal in length to propodeum; side view outline rather low and weakly convex, with a distinctly, but not deeply, impressed metanotal groove; propodeal dorsum only feebly convex, and sometimes very feebly impressed near midlength. Petiolar node slightly longer than broad, about as broad as long, or slightly broader than long, in different series (as in *M. tenuis* also), summit convex, slightly higher behind.

Gaster with first segment strongly rounded above, tergum rising caudad; segment II distinctly constricted in front at juncture with its acrotergite; about as high at maximum height as segment I, and slightly wider. As seen from above, anterior margin of segment I straight or feebly convex; shallowly concave in Vanimo worker (and queen). Sting long (extruded up to 0.6 mm), sharp, upcurved.

Sculpture prevailingly smooth and shining; punctures minute and widely spaced, more numerous and coarser on head, especially in Vanimo worker and queen, and on propodeum, but even here still obscure. Pilosity of uneven length, fine, tapered, erect to suberect hairs, mostly 0.05 to 0.30 mm long; pubescence decumbent to suberect, very dilute on anterior dorsum of head, but more abundant on antennae and legs, especially extremities.

Color averaging lighter than in fully pigmented *M. tenuis* workers, light to medium brownish red to dark brownish red, light orange brown in some workers, possibly callow. Appendages usually lighter, more yellowish, than basic body color.

Worker variation, as mostly discussed already above, involves mainly size-related features and shape of clypeal lobe, distinctness and density of the obscure puncturation, length and degree of apical taper of petiolar node, size and pigmentation of compound eyes, length of antennal scapes, and depth of body color.

Queen, dealate (from type nest series, Wilson No. 905), TL 7.1, HL 1.10, HW 0.97 (CI 88), ML 0.74 (MI 67), MLO 1.02, SL 0.96 (SI 99), EL 0.26, WL 2.03 mm. Combined measurements for the largest queen specimen (above), another queen from the type locality, colony No. 1048, and a smaller queen from near Vanimo, are: TL 5.6–7.1, HL 0.93–1.10, HW 0.84–0.97 (CI 88–90), ML 0.63–0.76 (MI 67–72), MLO 0.87–1.03, SL 0.87–0.96 (SI 99–104), EL 0.22–0.26, WL 1.78–2.03 mm.

The queen differs from accompanying workers by the usual ponerine characters, and is also darker in color, prevailingly piceous, or even blackish in the Vanimo specimen. On trunk, centers of scutum and scutellum are infuscated, while marginal areas of these and other sclerites are lighter and more reddish. Appendages lighter, more yellowish.

Male unknown.

Described from material representing seven separate collections from six localities in Papua New Guinea. Holotype (MCZ) from Wilson's colony No. 905, lower Busu River, Huon Peninsula, Papua New Guinea, 3 May 1955, a nest in rain forest in a small *Zoraptera*-stage rotten log, in a part of the log somewhat raised off the ground, containing one queen, about 30–40 workers, and brood of all stages, with pupae predominating. Abundant remains of millipedes were found in the brood chamber and galleries leading away. One fresh millipede corpse was among larvae; the prey all seemed to belong to one kind.

Another colony (Wilson No. 1048) also came from the lower Busu River tract, 15 May 1955, from cavities in an old, hard polypore fungus growing on a large *Passalus*-stage log, containing a queen and about 75 workers, plus abundant brood of all stages, without notable preponderance. Half of a freshly dead millipede was found with the brood; the midden remains were collected (but later lost with the nest residue in alcohol).

A worker and a dealate queen were found in lowland (40 m) rain forest next to the quarry at Km 2 on the Bewani Road, near Vanimo, West Sepik District, Papua New Guinea, 27 February 1981, leg. Brown (No. 81–48). The nest was in a small rotten stick lying on the ground, and contained larvae as well as the remains of small millipede prey. (Paratypes in MCZ, BMNH, ANIC, etc.)

In addition, single strays come from three widespread localities: Dobodura, March to July 1944, leg. P. J. Darlington, Jr.; Iora Creek, 17 km. S. of Kokoda at 1400 m, leg. Ward (No. 1831) rotten log, montane rain forest; Baiyer River, Western Highlands, about 1200 m, 6 July 1974, leg. S. Peck, berlesate B-281. The last specimen is the largest one of the species seen; it is also the darkest in color, has somewhat coarser punctures than usual on the head, and has the longest scapes, so that it might be thought transitional to *M. media,* but the form of the mandibles and clypeal lobe is typical for *julivora.*

The name of this species derives from the Latin *julus,* a millipede, and *vorare,* to devour. The new species is close to the very variable *M. tenuis,* but seems constantly distinct from it, even where the two species occur in intimate sympatry, as they do in the Busu River tract. For relationship to *M. media,* see under that species below.

Myopias media new species
(Figs. 6, 23)

Diagnosis, worker: member of *tenuis* group, very similar to *M. julivora* in habitus, color, etc., but larger, head wider, with more robust and more strongly curved mandibles, the submedian tooth situated closer to the midlength (at the seventh twelfth from base along MLO). Antennae long; scapes overreaching posterior border of head (when held straight back) by nearly twice their apical width.

Worker, holotype: TL 7.6, HL 1.25, HW 1.24 (CI 99), ML 0.93 (MI 74), MLO 1.26, SL 1.27 (SI 102), EL 0.13, WL 2.20, hind femur L 1.40, hind tibia L 1.35 mm.

Details additional to diagnosis: Viewed at apparent full-face, posterior border of head feebly convex, almost straight, but even a slight tilting of the cranium forward yields a concave border, and an increase in HL to 1.30, so that from this view, CI would be about 95. Anterolateral corners of head more prominent (at a lower level of focus), so that, excluding eyes, head is widest just behind clypeus. Median frontal sulcus continuing past mid-HL to include anterior clypeal pit. Eyes as in *M. julivora*, but relatively a little larger, and with remnants of facetting a bit more evident. Median clypeal lobe very obviously broader than long (CLL 0.13, CLW 0.20), with weakly concave sides, nearly straight apical margin, and one free corner rounded, the other rectangular. Mandibles thicker, particularly in the stretch between the obsolescent basal angle and the submedian tooth, which is also feebly convex mesally (concave or straight along mesal margin in *M. julivora*). Labrum toothed as in *M. julivora*.

Sculpture as in *M. julivora*, but small, widely spaced punctures (diameter 0.01–0.02 mm) are perhaps more distinct on head and trunk. A small patch of longitudinal costulation lies below spiracle on side of propodeum (as in *M. julivora*). Posterior corners of propodeum less broadly rounded, tending more towards angularity, both in side and dorsal views, than in *M. julivora*, and both the pilosity and pubescence seem to be less copious and a trifle longer.

Color deep brownish red; legs yellowish red; antennae and mandibles dark yellowish brown.

Holotype and only known specimen (MCZ) a stray collected from rotten wood at Joangeng, a village in the Mongi River Watershed of the Huon Peninsula, Papua New Guinea, at about 1500 m, 7–8 April 1955, in montane rain forest, leg. Wilson, No. 752.

We describe this species with some misgiving because it is based on a unique, and because it is so similar to *M. julivora*, especially to the largest (Baiyer River) specimen of the lattter. The mandibles, however, differ enough that we feel inclusion of the big Joangeng specimen in *M. julivora* would unduly strain the concept of that species. Further collections will of course help to demonstrate whether our decision is correct or not. The name *media* refers to the size of the body, intermediate in the *tenuis* group between *M. tenuis* and such large forms as *loriai* and *gigas*.

Myopias concava new species
(Figs. 4, 18)

Diagnosis, worker and queen: A medium-sized, stout-bodied species with head slightly broader than long, widest just behind eyes. Median labral tooth absent, but an erect apical tooth on each labral lobe. Eyes of worker large and multifacetted, occupying more than a quarter of the length of the sides of the head. Posterior margin of head weakly concave; sides convex. Median lobe of clypeus distinct but very short, rectangular. Mandibles short and stout, each with 2 small teeth at apex, 2 large blunt teeth basad of these, and an obtusely rounded basal angle. Antennal scapes overreaching posterior margin of head. Trunk compact, promesonotum and propodeum subequal in length, forming separate weak convexities meeting at a distinct and depressed metanotal groove. Petiolar node massive, subcuboidal, broader than long. Anterior face of gastric segment I weakly concave as seen from dorsal view. Integument prevailingly smooth and shining, but with abundant, coarse piligerous foveolae, sometimes contiguous on head, and tending to become elongate on first two gastric terga. Color brownish red.

Worker, holotype: TL 7.1, HL 1.25, HW 1.31 (CI 105), ML 0.71 (MI 57), MLO 1.26, SL 1.11 (SI 85), EL 0.33, WL 2.16, hind femur L 1.25, hind tibia L 1.20 mm.

Worker, paratypes (n = 6 of 42 from 4 colonies, including largest and smallest specimens): TL 6.5–8.6, HL 1.17–1.43, HW 1.21–1.47 (CI 100–105), ML 0.67–0.81 (MI 53–66), SL 1.00–1.24 (SI 83–88), EL 0.30–0.40, WL 2.00–2.46 mm.

Head broader than long, with sides convex, broadest immediately behind eyes, and narrowed slightly in front of eyes; posterior border broadly and shallowly concave. (The head can be lengthened slightly by tilting it forward from the full-face plane; this has the effect of foreshortening the mandibles and deepening the concavity of the posterior margin, and of course decreasing CI.) Eyes large and convex, with about 18–19 ommatidia in the longest diagonal row, each eye occupying nearly 3/10 of the length of its side of the head, situated about 2/3 its own length from mandibular insertion.

Clypeal lobe distinctly projecting but short, rectangular, more than twice as broad as long, with parallel sides, a nearly straight anterior margin, and subrectangular free corners (in Wau Creek series, anterior margin weakly convex, free corners more rounded). Labrum with the transverse ridge feebly sinuate in front view, lacking a median tubercle; labral lobes each with a small upturned apical tooth. Maxillary palpi each 3-merous; basal segment broadest, with one subapical lateral sensillum; apical segment with a single apical sensillum. Labial palpi each with 3 subequal segments; basal segment with 2 adjacent submedian sensilla; II with one subapical lateral sensillum; III with the same, plus 2 apical sensilla.

Mandibles stout, gently bowed, each with two small teeth at apex, a blunt tooth near apical quarter of ML, a large, blunt submedian

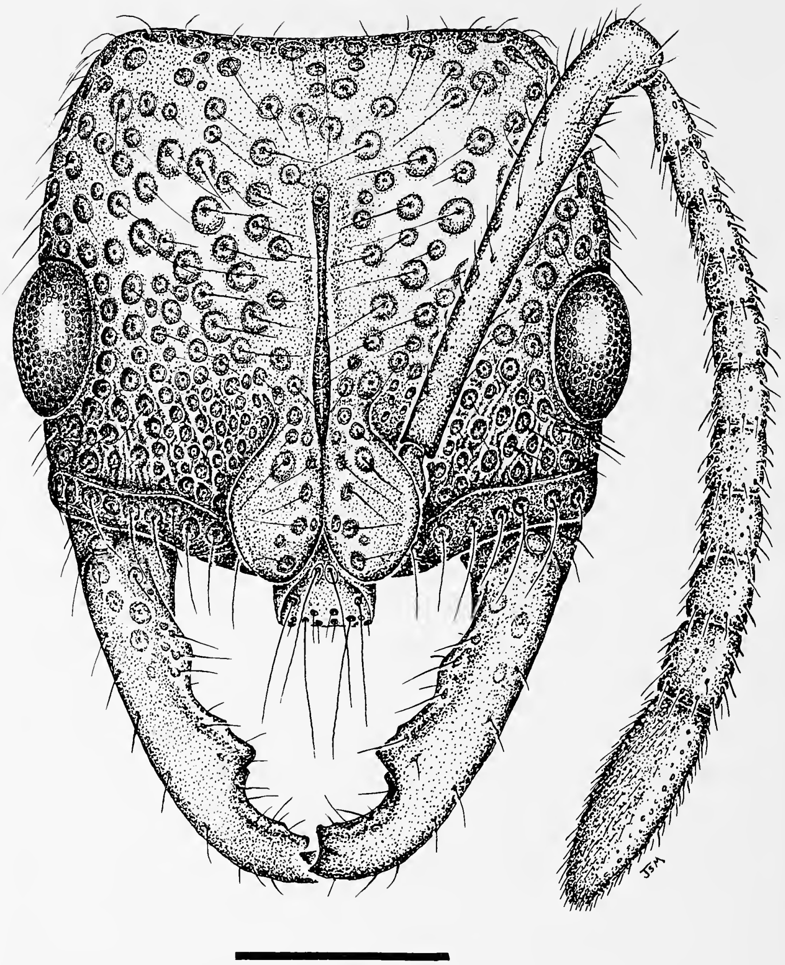


Fig. 4, *Myopias concava*, head of worker paratype in full-face view. Scale bar is 0.5 mm.

tooth, and a distinct but rounded basal angle. Oblique groove at base continued as a broad lateral-marginal groove (strix) to apex.

Median frontal sulcus of head extends to or nearly to posterior quarter of head length. Scapes gently curved, moderately incrassate apicad, overreaching posterior border by more than their apical width when head is viewed full-face. Funiculus relatively slender, all segments longer than broad; apical segments not forming a club;

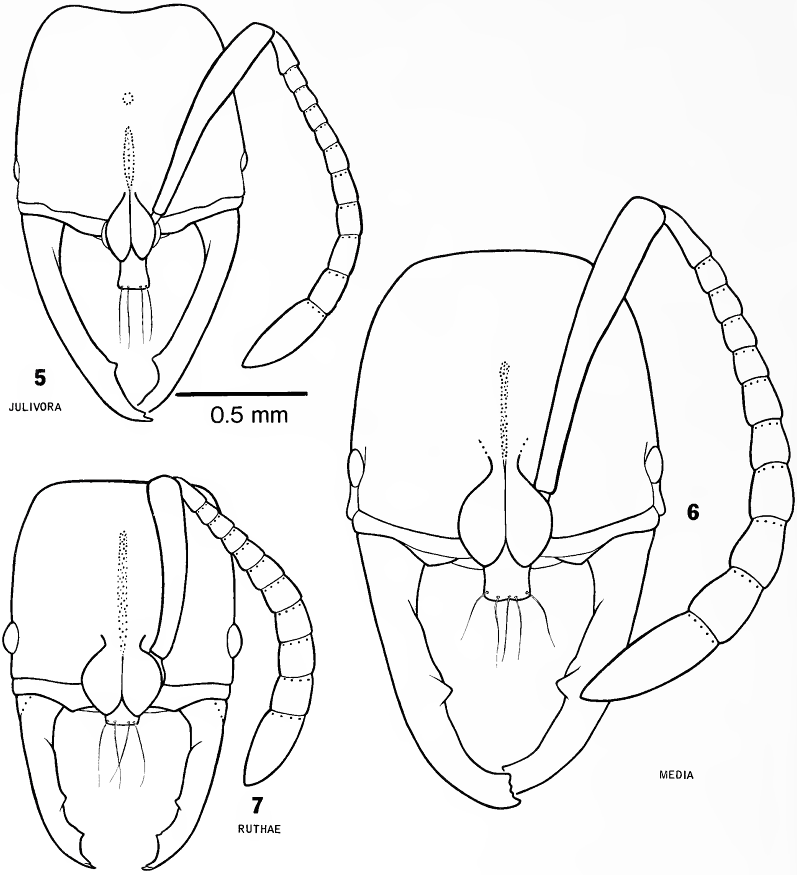
pedicel (funiculus I) longer than II as 4:3.

Trunk robust, with a weakly convex dorsal profile as seen from the side; propodeum subequal in length to promesonotum; mesonotum convex, about half as long as propodeal dorsum, and separated from it by a distinct but only moderately impressed metanotal groove. Propodeal dorsum only very feebly convex, passing into declivity through a rounded obtuse angle. Declivity almost flat, with bluntly subangular lateral edges, densely punctate in upper 2/5, smooth and shining below this.

Petiolar node massive, subcuboidal, slightly higher and broader behind than it is long (disregarding sternital keel); front and rear faces flat, vertical, dorsal face gently convex and sloping slightly anteriad. Sternite forming a sharp, recurved (hooklike) anterior subpetiolar process, followed by a short concavity and then by a long, low, feebly convex keel.

Postpetiolar segment (gaster I) wider than long (roughly about as 4:3) and very slightly wider than gaster II; anterior face abruptly vertical, its dorsal margin gently concave as seen from above. Gaster II (ignoring acrotergite normally covered by gaster I) longer than I, but still not quite as long as wide. In side view, these two segments are about equally high. Apical gastric segments short, as usual; sting very long (and is found extended up to 1.1 mm in some paratype workers), gently upcurved. Gonostylus (in paratypes) long, 2-merous.

Body basically smooth and shining, but sown with deep, conspicuous, piligerous foveolae, mostly round or oval on the head (here 0.03 to 0.09 mm in diameter), trunk and petiole, becoming more elongate axially on first two gastric terga. Foveolae on head smaller and more crowded, forming oblique chains interspersed with costulae between eyes and frontal lobes, but those caudad of eyes larger, forming vague, oblique chains, separated on the average by their diameters near the cephalic midline, but smaller and more crowded., often subcontiguous laterad and caudad. Foveolae more widely spaced on trunk and petiole, especially near midline and on sides of pronotum; metapleura with a few coarse longitudinal-oblique costae. Petiole and postpetiole (first gastric segment) with smaller, crowded foveolae on sides and ventrad, but on second gastric segment, the foveolae become very sparse apicad and ventrad, the surfaces here virtually smooth, except for a crowded band of small foveolae along the apical margin. Apex of gaster, antennal scapes,



Figs. 5–7, *Myopias* spp., heads of workers in full-face view, sculpture and pilosity omitted. Fig. 5, *M. julivora* paratype. Fig. 6, *M. media* holotype. Fig. 7, *M. ruthae* holotype, All to same scale; bar is 0.5 mm.

mandibles and legs prevailingly smooth, with spaced piligerous punctures.

Body and appendages clothed with numerous fine, tapered, decumbent to subdecumbent hairs, mostly each issuing from a foveola, and nearly all 0.10 to 0.25 mm long (up to 0.30 mm on anterior clypeal lobe).

Color rich, deep brownish red; legs a little lighter reddish.

Worker variation; apart from size, mainly involves slight differences among nest series in the shape of the median clypeal lobe (convex vs. straight apical margins), density and size of individual foveolae of sculpture, and depth of coloration.

Queen, dealate, from holotype nest series, Wamuki: TL 8.2, HL 1.37, HW 1.50 (CI 109), ML 0.80 (MI 58), SL 1.20 (SI 80), EL 0.45, WL 2.61. Four additional queens range downwards in size slightly from this (Collection Nos. 887 (n = 3) and 990 (n = 1) from Busu River, the smallest having HW 1.33. A female from the Wau Creek series is ergatoid, but has HW about 1.50; this specimen lacks ocelli, but has small, blackened forewing stumps. The queens resemble the workers except in the caste difference usual for ponerines.

Male unknown.

Described from material from four separate nest series, all from what is now Papua New Guinea: holotype from Wamuki, 800 m, on the Mongi River watershed, Huon Peninsula, 19–20 April 1955 (Wilson No. 844; MCZ). No. 844, a colony containing one queen and about 20 workers, was taken from a *Zoraptera*-stage rotten log in hill rain forest. Two colonies came from the area between the lower Busu and Bupu rivers, near Lae, at the base of the Huon Peninsula, in lowland rain forest (Wilson Nos. 887 and 990). No. 887 was a nest in a small *Passalus*-stage log, 28 April 1955, and included at least three queens. No. 990 was in a small (10 cm diameter) rotten log with interior crumbling, but bark intact. It held 50–60 workers, two queens, eggs, larvae up to half-grown (no larger larvae) and one cocoon. The brood chamber contained an unidentified insect larva, also an adult (cucujoid?) beetle that was still alive and feebly moving; this beetle could possibly have fallen or walked in during excavation of the nest. (Unfortunately, the residues from Wilson's collections were eventually lost.)

The fourth collection comes from Wau Creek, at about 1200 m elevation in a "Stage III" [rotten] log (leg. D.H., A.C. and A.H. Kistner, No. 1213); it contained at least 10 workers and a more or less ergatoid queen.

This very distinct species shows some affinities with the *tenuis* group in the presence of upturned teeth on the labral lobes and lack of median labral tooth, but it is different in its robust build, very prominent foveolate sculpture, shorter mandibles, and the concave anterior face of the first gastric tergum, which gives the name *concava.*

Myopias chapmani new species
(Figs. 10, 26)

Diagnosis, worker: A modest-sized member of the *tenuis* goup; head large, nearly square, with sides almost straight and nearly parallel; posterior margin concave. Eyes small but distinctly facetted. Mandibles rather short and stout; antennal scapes distinctly overreaching posterior border of head. Trunk robust, with broad and deeply impressed metanotal groove; propodeal dorsum less than twice as long as mesonotum. Node of petiole higher and wider than long, convex above. Gaster distinctly constricted between first and second segments. Sculpture predominantly smooth and shining, with spaced, indistinct punctures, especially on head, but sides of propodeum obliquely costulate, subopaque; dorsal propodeal surface finely roughened in part, and bearing a few, coarse, indistinct grooves and punctures, as well as a weak impression just caudad of its midlength. Color light ferruginous red.

Worker, holotype: TL 5.7, HL 1.12, HW 1.07 (CI 96), ML 0.57 (MI 51), MLO 0.87, SL 0.95 (SI 89), EL 0.11, WL 1.77, hind femur L 1.06, hind tibia L 1.00 mm.

Worker paratypes (21 from type nest series) range downward from the size of the holotype to the smallest individual, which has TL 5.2, HL 1.03, HW 0.98 (CI 95), ML 0.54 (MI 52), MLO 0.81, SL 0.86 (SI 88), EL 0.11, WL 1.63, hind femur L 0.94, hind tibia L 0.86 mm.

Head massive, sides only feebly convex, widest at posterior edge of eyes and tapering almost imperceptibly to rather abruptly rounded posterior corners; posterior border moderately concave across its middle half. Eyes almost round, with about 17 or 18 facets, each situated nearly twice its own diameter away from mandibular insertion; an indistinct groove extends the dorsal (mesal) orbital groove forward onto clypeal wing. Median clypeal lobe slightly longer than wide (CLL 0.14, CLW 0.13 mm), widest near apex, its anterior margin convex and free corners rounded. Median frontal sulcus wide and deep, extending back to posterior third of HL.

Antennal scapes slender, gently bowed, slightly incrassate apicad, overreaching the posterior border of the head by about the same as their apical width when held straight back in dorsal full-face view of head. Funiculus slender, but with an indistinctly 4-merous club; all antennomeres longer than wide; funiculus I about twice as long as II.

Mandibles robust, rather short, with a sharp apical tooth and a minute adjacent companion tooth; one subapical and one submedian tooth each isolated, blackened and rounded; basal angle present, but low and rounded. Oblique basal groove and its lateral continuation very distinct. Labral lobes each bearing a delicate, upturned apical tooth, practically impossible to see without dissection. Palpi segmented 3,3; basal maxillary palpomere short and broad, last two subequal in length, but apical broader, fusiform, with apical sensillum; labial palpomeres all slender, the apical slightly longer and thicker than the basal two, and with an apical sensillum.

Trunk robust, divided by a broad and deeply impressed metanotal groove into a promesonotal portion and a shorter propodeal portion. Mesonotum convex, rising above pronotum, sloping caudad, nearly 2/3 as long as propodeal dorsum; propodeum weakly convex, but with a feebly impressed area in the posterior half of its dorsum (variably distinct in paratypes); dorsum rounded unevenly into declivity and with a feeble median impression at the point where they meet; declivity more or less flat, with lateral boundaries distinct, almost submarginate.

Petiolar node distinctly higher than long. its curved dorsal face highest behind the midlength; anterior face in side view straight or feebly concave, sloping caudad; posterior face convex in side view, sloping cephalad. In dorsal view, anterior cornuae of node very prominent; node widest behind, with convex sides, slightly wider than long. Postpetiolar (gastric I) segment slightly broader than long; its anterodorsal border feebly concave in the middle; gastric II a little wider than I, but equal in depth in side view after a distinct constriction between the two that is boldly scrobiculate. Sting long and sharp, gently upcurved (found extended up to 0.60 mm in various specimens.

Sculpture mainly smooth and shining, with mostly inconspicuous, separated, piligerous punctures, distributed as follows: on dorsum of head, on each side of midline, numerous small ones, averaging about 0.01 mm in diameter, or smaller, mostly in the space between eye and median sulcus; small punctures distributed sparsely on mandibles, back and sides of head, fore coxae, pronotum, mesonotum, and gastric tergum II. Moderately coarse, often elongate, punctures on propodeal dorsum, petiolar node and first gastric tergum. Antennae and legs largely smooth and shining, but with very fine punctulation, increasing toward extremities. Sides of propodeum with fine, partly broken, oblique costulation, rising caudad, surface here subopaque, giving way on dorsal surface to some partial, roughened microsculpture that renders the surface between coarse punctures only weakly shining. Upper propodeal declivity feebly, finely, transversely strigulose, smooth and shining below.

Pilosity consisting of fine, tapered, erect to suberect setae of uneven length, mostly 0.03 to 0.25 mm long, distributed abundantly over dorsal surfaces of body, venter of head, and gaster, fore coxae, and most surfaces of appendages. Decumbent pubescence is dilute on dorsum of head, directed mesad; more dense on anterior surfaces of mid coxae, and on all tibiae and tarsi.

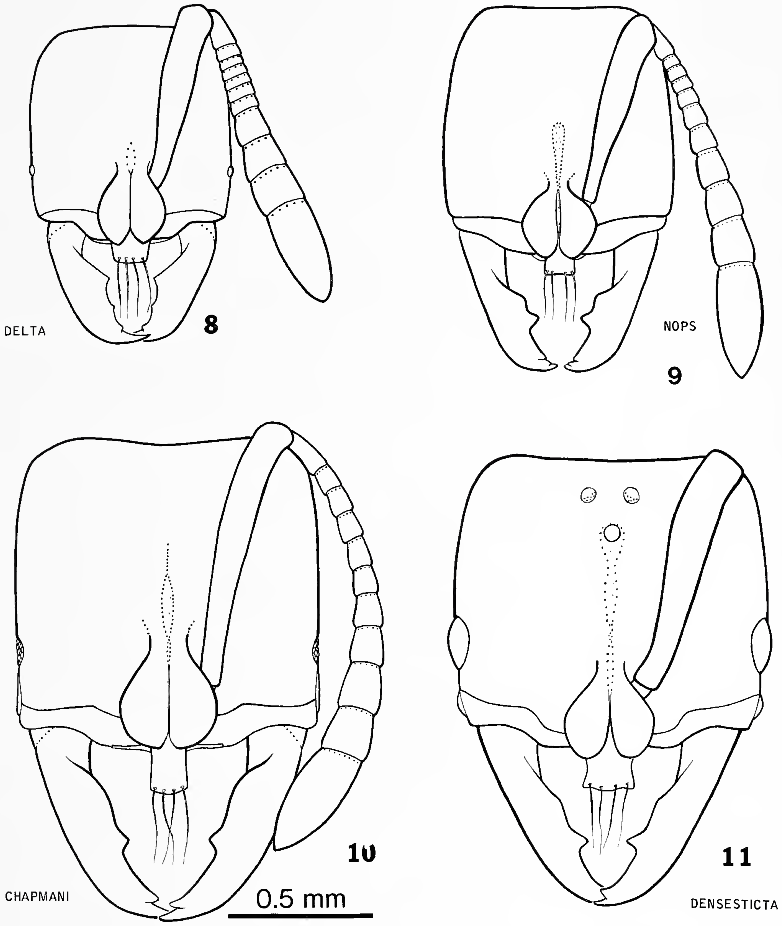
Color rich, light, ferruginous red; appendages slightly lighter.

Worker variation, apart from the slight mensurable spread, is weak. As already mentioned, the feeble impression, or "saddle," in the posterior dorsal surface of the propodeum varies from distinct to almost absent in different workers.

Queen, dealate: TL 5.2, HL 1.00, HW 1.00 (CI 100), ML 0.55 (MI 55), MLO 0.77, SL 0.84 (SI 84), EL 0.23, WL 1.65, hind tibia L 0.81 mm. Notable for size being slightly smaller than for workers of the same colony. Otherwise, differences are those usual between castes in Ponerini. Nota of pterothorax smooth and shining, with dispersed, small punctures. Propodeum more completely and strongly sculptured than in worker, subopaque, finely transversely strigulose, with a short, longitudinal, median sulcus or impression; lower declivity smooth. Color slightly darker than in worker, especially lightly infuscated parts of cranium, pronotum, median scutum, propodeum, petiole, and first two gastric segments.

Male unknown.

Holotype worker (MCZ) and paratypes (MCZ, BMNH, ANIC) from a small nest in a thick fragment of a rotten branch lying on the ground in wet rain forest along Obi Obi Creek, below and just west of Montville, Blackall Range, Queensland, Australia, 20 May, 1951, leg. Brown. The nest contained 20–30 workers, larvae (since lost together with prey remains), and two dealate queens. The forest at the type locality has since been destroyed (*fide* P.J. Darlington,



Figs. 8–11, *Myopias* spp., heads in full-face view, sculpture and pilosity omitted. Fig. 8, *M. delta,* paratype worker. Fig. 9, *M. nops,* holotype worker. Fig. 10, *M. chapmani,* paratype worker. Fig. 11, *M. densesticta,* paratype queen from Kuranda, Queensland. All to same scale.

personal communication). The species is named for the late Dr. James W. Chapman, who collected many *Myopias* series in the Philippines.

Myopias densesticta, new species
(Figs. 11, 29)

Diagnosis, worker and queen: A member of the *M. tenuis* group, similar to *M. chapmani,* but with much more distinct and abundant foveolate sculpture and a shorter, wider median clypeal lobe and shorter antennae. Also, the trunk is not deeply divided at the metanotal groove, the petiolar node is more massive, and the gaster is gently tapered, not sharply constricted, behind the first segment.

Worker, holotype: TL 5.6, HL 1.03, HW 0.97 (CI 94), ML 0.55 (MI 53), MLO 0.82, SL 0.85 (SI 88), EL 0.09, WL 1.62, hind femur L 0.87, hind tibia L 0.83 mm.

Worker, paratypes (n = 3 of 9 from two colonies, including largest and smallest, the holotype): TL 5.6–5.7, HL 1.03–1.07, HW 0.97–1.03 (CI 94–97), ML 0.55–0.56 (MI 51–54), MLO 0.82–0.83, SL 0.85–0.86 (SI 83–88), EL 0.09–0.11, WL 1.62–1.71, hind femur L 0.87–0.89, hind tibia L 0.83–0.84 mm.

In overall size, proportions of head, and mandibles, this species is very similar to *M. chapmani,* but the sides of the head are a trifle more convex, and the basal angle of the mandible is a little less distinct; also the following, more definite differences from *M. chapmani:*

(1) Antennae shorter; scapes overreach posterior border when held straight back by only a slight amount, less than their apical width. Segments II through VIII of funiculus wider than long; I (pedicel) more than twice as long as II.

(2) Median clypeal lobe shorter, wider (CLL 0.08–0.10, CLW 0.16–0.17 mm), with sharply angular free corners terminating the divergent carinae that form the lateral edges of the lobe.

(3) Promesonotum shorter than propodeum; propodeal dorsum about twice as long as mesonotum, and nearly on the same level; both only weakly convex and meeting at a distinct but not deeply impressed metanotal groove, so that the side-view dorsal profile is a nearly smooth, gently convex outline from top of front pronotal incline to top of propodeal declivity.

(4) Petiolar node more massive and more nearly cuboidal, less no-

tably longer than high; seen from above wider than long, but sides convex; widest near midlength.

(5) Second gastric (true abdominal IV) segment narrower and lower than first segment (postpetiole), so that the gaster is gradually tapered caudad of I, and not constricted and recovering after.

(6) Body, especially head, trunk and petiolar node, with deeper and much more distinctly developed foveolate sculpture, the punctures mostly 0.01–0.02 mm in diameter and densely crowded, contiguous on front of head between eyes and frontal lobes, becoming larger, mostly 0.02–0.03 mm in diameter and narrowly separated on posterior half of head, at times with intervening, indistinct, longitudinal strigulosity, and still coarser and more widely spaced on sides and underside of head and near median frontal sulcus (which reaches back to near the posterior quarter of HL). Trunk and petiole with abundant foveolae, mostly 0.02–0.04 mm in diameter, separated on the average by a little more than their own diameters, but more crowded and more elongate on sublateral strips of propodeal dorsum; truncal midline strip partly open, with few foveolae. In general, interfoveolar surfaces smooth and shining, but lower sides of propodeum indistinctly, longitudinally costulate, and sides of petiolar node coarsely and densely foveolate and minutely roughened, more or less opaque. Gaster I smooth, with scattered coarse punctures, and these become fewer and smaller still on gaster II. Mandibles smooth and shining, with scattered punctures. Antennal scapes and legs smooth and shining, but with fine punctulation. Propodeal declivity nearly smooth, but peppered with many small foveolae. Clypeus smooth and shining.

(7) Pilosity and pubescence more abundant than in *M. chapmani,* most notably on mandibles and antennal scapes; decumbent pubescence on head more conspicuous, directed mesad.

(8) Color perhaps averaging slightly darker than in *M. chapmani,* but legs and antennae tending to be lighter, more yellowish red. As in *chapmani,* the palpi are segmented 3,3, and upturned teeth are present, one on each labral lobe. Worker variation is very slight overall. The Koombooloomba series averages very slightly larger, and the compound eyes may be a trifle larger than in the Shipton's Flat colony.

Queen, dealate, a unique taken in rotten wood in a rain forest patch near Kuranda, Queensland, 31 October 1950, leg. Brown: TL

6.7, HL 1.07, HW 1.05 (CI 98), ML 0.52 (MI 49), MLO 0.81, SL 0.85 (SI 81), EL 0.24, WL 1.92 mm.

Male unknown.

Holotype [MCZ] one of six workers from Shipton's Flat, south of Cooktown, Queensland, during June 1958, leg. P.F. and P.J. Darlington. This locality is savannah woodland grading into riparian rain forest (gallery forest), and lies at an elevation of about 300 m. (The Kuranda queen is from a similar elevation.) A pin of three workers comes from Koombooloomba, near the dam of the same name south of Ravenshoe, Queensland, at about 750 m in rain forest, "4/7/71," leg. Taylor and J. Feehan. We have no information about possible prey.

The name *densesticta* refers to the characteristic foveolate sculpture.

Myopias tasmaniensis
(Fig. 16)

Myopias tasmaniensis Wheeler, 1923, Psyche 30:177–179, fig. 1, worker. Type loc: Hobart, Tasmania.

Trapeziopelta tasmaniensis: Brown, 1953, Psyche 60:51, records from Dandenong Range, Victoria, Australia.

Trapeziopelta diadela Clark, 1934: Mem. Nat. Mus., Melbourne, Australia, 8:54–55, pl. 4, f., 7,8, worker, queen. Type loc., Turton's Track, Otway Ranges, Victoria. (Syn. by Brown, 1953).

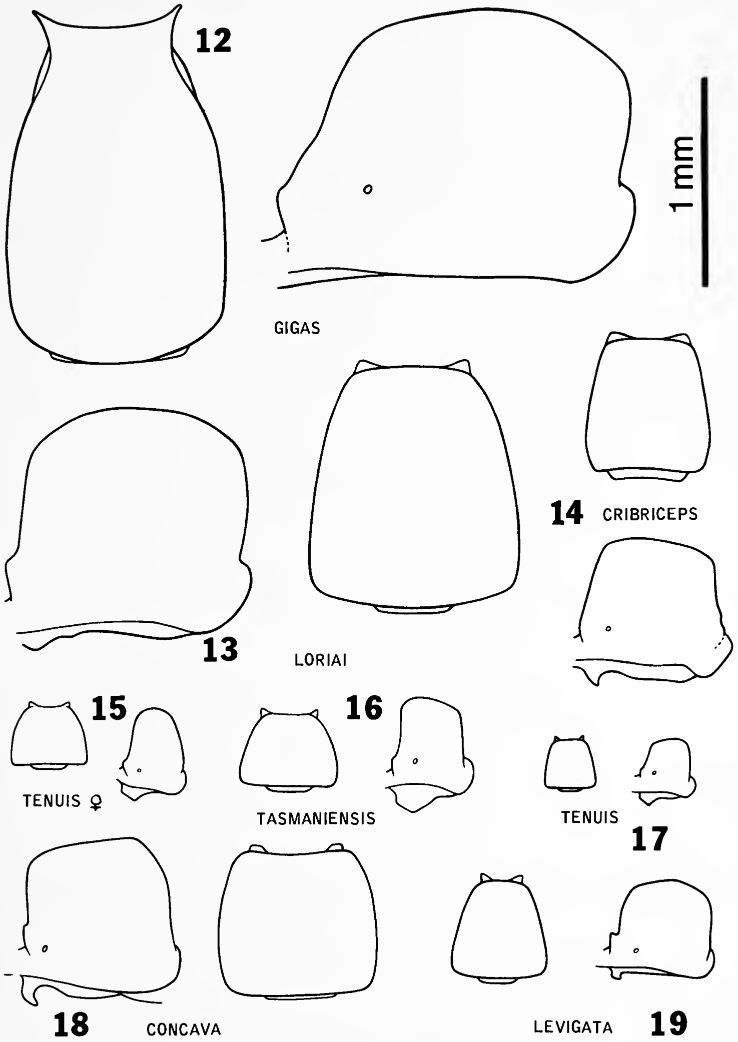
Two collections made by Father Bede Lowery extend the range far to the north in eastern Australia; Minnamurra Falls, near Kiama, New South Wales, nest in soil of very moist forest, behind rock slab set in a vertical bank, 22 Dec. 1959; Cunningham's Gap, southeastern Queensland, at about 600 m in rain forest,. 22 Jan. 1961.

Myopias tenuis new combination
(Figs. 15, 17)

Trapeziopelta tenuis Emery, 1900, Természetr. Füz. 23:313–314, dealate queen. Type loc.: Beliao Island, near Berlinhafen (now Aitape), Papua New Guinea. 1902, 155, worker, Sattelberg, Huon Peninsula, Papua New Guinea.

Trapeziopelta tenuis var. *fulvescens* Emery, 1902:155, worker, dealate queen. Type loc.: Sattelberg, Huon Peninsula, Papua New Guinea. New synonym.

This is the smallest of the known Melanesian *Myopias* species, and also the most common and widespread. The typical form is



Figs. 12–19, *Myopias* spp., petiolar nodes in lateral and dorsal view, sculpture and pilosity omitted, all to same scale. Fig. 12, *M. gigas* holotype worker. Fig. 13, *M. loriai* worker fro Gemeheng, Huon Peninsula, Papua New Guinea. Fig. 14, *M. cribriceps* worker from Bubia, near Lae, Papua New Guinea. Fig. 15, *M. tenuis* queen from Bubia, near Lae, Papua New Guinea. Fig. 16, *M. tasmaniensis* from Olinda, Victoria, Australia. Fig. 17, *M. tenuis* worker from Bubia, near Lae, Papua New Guinea. Fig. 18, *M. concava* paratype worker from lower Busu R., near Lae, Papua New Guinea. Fig. 19, *M. levigata* worker from Nganduo, Huon Peninsula, Papua New Guinea.

small, has slightly convex sides of the head, scapes that just fail to reach (or just barely reach) the occipital border when held straight back, and a median clypeal lobe that is as long as, or slightly longer than, wide at its widest (near apex). The end of the lobe is convex or straight, and the free angles may be rectangular or rounded. Measurements for Papua New Guinea North Coast workers are: TL 2.8–3.7, HL 0.53–0.71, HW 0.45–0.60 (CI 81–91), ML 0.30–0.43 (MI 81–92), MLO 0.40–0.57, SL 0.42–0.58 (SI 87–95), EL 0.03–0.06, WL 0.95–1.25 mm. Workers of a colony series from Salawati Island, at the western end of New Guinea, fall within these dimensions and proportions. Workers from Bisianumu, in the hills above Port Moresby, fit the North Coast dimension range, while a sample from Karema, in the lowlands north of Moresby, tends slightly to exceed the North Coast samples in size.

Samples from the Cape York area of North Queensland average larger than any of the New Guinea series; a large worker from the Black Mt. Road, north of Kuranda, measures TL 4.1, HL 0.74, HW 0.67 (CI 91), ML 0.43 (MI 91), MLO 0.58, SL 0.59 (SI 88), EL 0.04, WL 1.34 mm. The Australian samples often have the laid-back scapes reaching the posterior border of the head, and the posterior border is more distinctly concave. In addition, the median clypeal lobe tends to be wider, often as wide as or wider than long, and the minute punctures, especially on the head, are a trifle coarser and more distinct. Several of these series have sordid yellowish individuals, undoubtedly partly callow, that correspond to var. *fulvescens*.

New locality records: PAPUA NEW GUINEA: Karema, Brown R., rotten log, lowland rain forest, leg. Wilson, No. 552. Bisianumu, near Sogeri, about 500 m, hill rain forest, Wilson Nos. 637, 637A, litter and rotten wood, strays. In the vicinity of Lae (Didiman Creek, Bubia and lower Busu R.), several nests and litter strays, Wilson Nos. 688, 689A, 690, 716, 939, 962, 978, 1037, 1045, 1058, all in lowland rain forest. No. 689 was a small colony in a Zoraptera-stage log, with about ten workers and two queens. No. 716 was a worker carrying an entomobryid collembolan about its own length lengthwise beneath its body, army ant fashion. No. 1037 was a nest in a cavity in the under surface of a hard, barkless log in leaf litter. No. 1045, a nest in a soft *Passalus*-stage log, had peripheral galleries packed with unidentified arthropodan cuticular fragments. Nadzab, dry evergreen forest, Wilson No. 1100. Wau north, on Bulolo road, 650 m, leg. S. Peck, B-278. IRIAN JAYA: near Phillips Petroleum Base Camp, SE Salawati I. (just off western extremity of Vogelkop), swamp forest near sea level, leg. Brown No. 81–189, nest in rotten wood, with at least 15 workers, a dealate queen, a male, about a dozen pupae in tan cocoons, and a few half-grown larvae. AUSTRALIA, N. QUEENSLAND: Black Mt. road N. of Kuranda, 300–600 m, leg. P.F. Darlington, in rain forest, small colony with at least two dealate queens. Mt. Cudmore Range, 11 mi. N. of Ingham, about 210 m, six workers from rotten log in small roadside patch of disturbed rain forest, leg. Taylor, Acc. No. 1706. Mulgrave Forestry Road, 17° 18′S, 145° 48′E, leg. Ward No. 4366, from rotting epiphyte fern on rain forest floor.

From the SOLOMON ISLANDS we have three scanty samples of forms sent from ANIC that could belong to *M. tenuis,* or to sibling species:

(1) A large form, extending some of the tendencies seen in Australian series; HW 0.80, EL 0.09 mm; scapes reaching posterior border of head. Propodeal dorsal profile a little more convex than usual in *M. tenuis.* Color castaneous. Two workers from Guadalcanal I.: Mt. Austen, Feb. 1966, leg. P.M. Greenslade, No. 21095.

(2) A small worker, also from Mt. Austen, Guadalcanal, 14/5/1963, leg. P.M. Greenslade, No. 6076; HW 0.55, EL 0.03 mm; scapes very short, failing to reach posterior border of head by at least the apical scape width; posterior border of head weakly concave. Color yellowish brown. Sides of head straighter and more parallel-sided than in the other Mt. Austen sample.

(3) A worker from San Cristoval I., Humi R. est., N.E. Wainoni, leg. Royal Society Expedition, 1966–1, HW 0.60, EL 0.05 mm; sides of head almost perfectly straight and parallel, posterior border feebly convex; scape fails to reach posterior border of head by about half of apical scape width; mandibles unusually short (ML 0.37, MLO 0.47 mm) and broad; basal angle forming a distinct convexity. Color deep brownish red.

I suspect that the Solomons will eventually yield much more variation in the *tenuis* complex; the available material is simply inadequate as a basis for understanding the complex in this archipelago.

Key to Known *Myopias* Species of Australia, Based on Workers

1. Small, slender species (HW < 0.75 mm); worker compound eye reduced to a single smoothly lenticular dot < 0.05 mm long (in Australia, N. Queensland) .... *tenuis*
   More robust species (HW > 0.75 mm); worker compound eye 0.05 or more long, with 3–5 rows of distinct, raised ommatidia (Figs. 10, 11) 2
2. Second gastric segment lower and narrower than the first and tapering gently apicad, not constricted at base (N. Queensland) .... *densesticta*
   Second gastric segment wider than the first and sharply constricted from its own acrotergite basad 3
3. Antennae shorter, scapes not overreaching posterior border of head when they are held straight back from insertions as head is viewed full-face; small funicular segments (funiculus II-VII at least) broader than long (Tasmania to SE Queensland) .... *tasmaniensis*
   Antennae longer, scapes distinctly overreaching posterior border in full-face view of head; all antennal segments longer than broad, or at least as long as broad .... (S. Queensland: Blackall Range) .... *chapmani*

Myopias ruthae new species
(Figs. 7, 20)

Diagnosis, worker: A modest-sized *Myopias;* head longer than broad, with nearly parallel but gently convex sides and weakly convex posterior border; scapes curved, barely surpassing posterior border; funicular club indistinctly 6-merous. Median frontal groove deep and wide, reaching to the posterior quarter of head length. Median clypeal lobe broad, short, rectangular, widest basad. Labrum without a median tubercle. Eyes fairly large, convex, finely facetted. Mandibles robust, gently curved, with 4 teeth and a low basal angle. Body robust, metanotal groove distinct but weakly impressed. Petiolar node massive, subcuboidal; gaster short and thick. Sculpture of numerous coarse punctures or foveolae, dense and contiguous, or nearly so on most of head and sides of petiolar node; foveolae sparser mesad on vertex, trunk and succeeding terga, the surface here prevailingly smooth and shining. Color piceous, nearly black, with contrasting tan appendages.

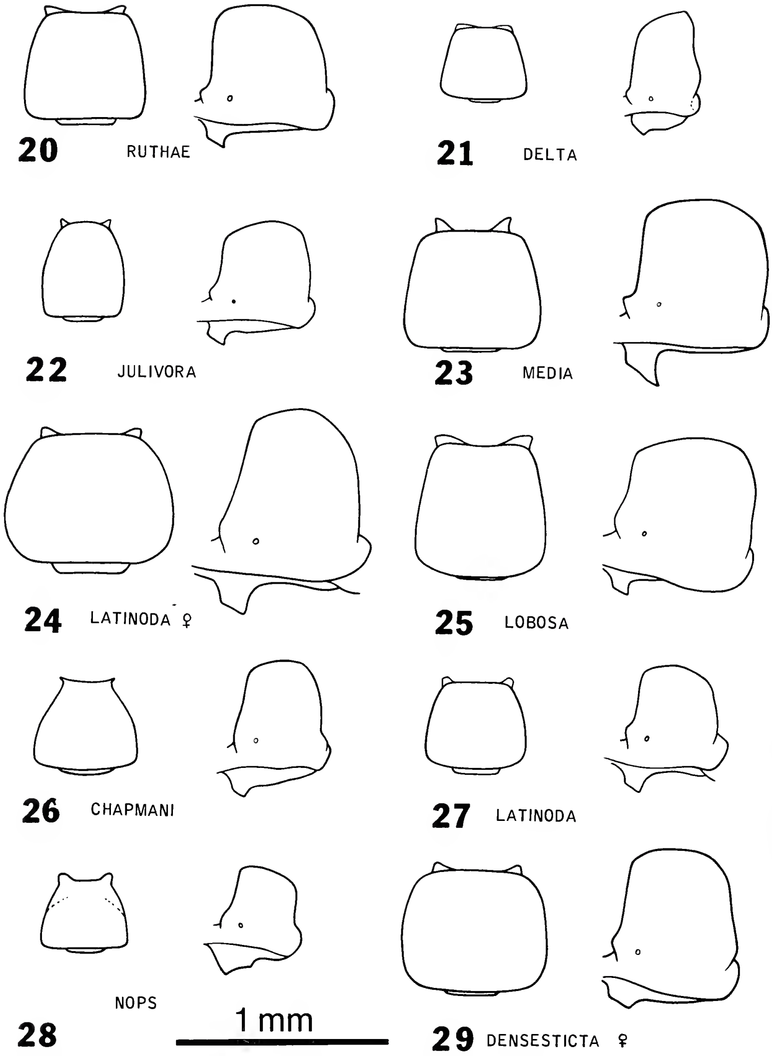
Worker, holotype: TL 5.2, HL 0.96, HW 0.86 (CI 90), ML 0.48 (MI 50), SL 0.73 (SI 85), EL 0.14, WL 1.60, hind femur L 0.80, hind tibia L 0.83 mm.

Description mainly directed at details not fully covered in the diagnosis and figures. Antennal scape broadly curved in basal half, incrassate distad; apical width about 0.12 mm, or slightly less than maximum eye length. Funicular segment I about twice the length of II. Eye with distinct but fine ommatidia, numbering about 11 or 12 units in the longest diagonal row, darkly pigmented. Median clypeal lobe about 0.05 mm long (CLL) and about 0.14 wide (CLW) at apex, about 0.15 mm wide at base where it meets frontal lobes; anterior border straight, free corners subrectangular. In examining the single, intact specimen, no upturned teeth could be seen at the apex of each labral lobe, but a dissection would be needed to make sure that they are really absent. Mandibular armament consists of an acute apical tooth and a small adjacent tooth, then after a gap another large, blunt tooth, another gap and a similar-sized but more acute median tooth, then halfway from this to the base, a low, rounded basal angle. Oblique groove (strix) near dorsal base of mandible distinct, continuing along lateral margin to near apex. MLO 0.77 mm.

Trunk robust, dorsal outline in side view nearly straight, the mesonotum feebly sunken; metanotal groove slightly impressed, but distinct; propodeal dorsum very feebly convex, rounding obtusely into declivity, but sides of declivity forming blunt angles with pleural faces of trunk. Propodeal spiracle small and round, situated at mid height. Petiolar node massive, subcuboidal, slightly wider behind than long; slightly higher than long if one ignores the small, hooklike anterior subpetiolar process; dorsal surface convex in both directions.

First gastric (postpetiolar) segment higher and wider (by about 4:3) than long. Succeeding (gastric II) segment about as wide as the first, and only slightly longer, but slightly thinner dorsoventrally. Sting long and slender, gently upcurved.

Sculpture distinctive, consisting basically of a smooth, shining integument invaded by coarse, mostly umbilicate, piligerous foveolae. The foveolae are densest and smallest (0.02–0.03 mm diameter)



Figs. 20–29, *Myopias* spp., petiolar nodes in lateral and dorsal view, sculpture and pilosity omitted, all to same scale. Fig. 20, *M. ruthae* holotype worker. Fig. 21, *M. delta,* paratype worker. Fig. 22, *M. julivora,* paratype worker from Papua New Guinea. Fig. 23, *M. media,* holotype worker. Fig. 24, *M. latinoda* queen from Maffin Bay, Irian Jaya. Fig. 25, *M. lobosa,* paratype worker. Fig. 26, *M. chapmani,* paratype worker. Fig. 27, *M. latinoda* worker from Maffin Bay, Irian Jaya. Fig. 28, *M. nops,* holotype worker. Fig. 29, *M. densesticta* paratype queen from Kuranda, Queensland.

on anterior and sides of head, where most are contiguous and yield a reticulate-foveolate surface that is subopaque in most lights. This kind of sculpture, a bit more loosely distributed, covers the upper sides and dorsum of trunk and petiole, except for median posterior part of vertex, midline of trunk, and dorsal midline of petiole, which have wide spaces free of most foveolae, and are smooth, shining. Sides of trunk below largely smooth, with sparse foveolae, and posteriorly, low down, with a few fine, longitudinal costulae. Sides of petiolar node foveolate-striate. Gaster with spaced foveolae, becoming smaller (0.02 mm) and sparser caudad, interspaces smooth and shining, but a double band of foveolae along apical margin of second gastric tergum. Mandibles and legs with sparse punctures, generally otherwise smooth and shining; scapes and middle tibiae, and all tarsi, more densely punctulate, but still shining.

Hairs numerous, fine, tapered, suberect to decumbent, mostly 0.04 to 0.25 mm long; those on head and appendages mostly short, while those on clypeal lobe, trunk, petiole, and especially gastric apex are longer.

The species is named for Dr. Ruth Lippitt Willey.

Holotype (MCZ) a unique worker specimen from Bubia, about 13 km NW of Lae, Papua New Guinea, about 20 m above sea level, in high-graded rainforest, 26 March 1955, by E.O. Wilson (MCZ). The worker was foraging under the bark of a large Zoraptera-stage (rotting) log.

This species is distinct from all congeners, but difficult to place to a group. Probably it comes closest to the *tenuis* group than any other so far described, but the longish head, bulging eyes, short scapes and coarsely foveolate sculpture will distinguish it from all *tenuis*-group species.

Myopias lobosa new species
(Figs. 2, 3, 25)

Diagnosis, worker and queen: Head distinctly longer than broad; median clypeal process obsolete; labrum without median tubercle. Mandibles much broadened, each with the two major teeth before the apex exaggerated into triangular lobes; blades of mandibles sharply curved ventrad and rotated so that their blades lie nearly parallel to the sagittal plane of the head at full closure. Antennal scapes very short. Sculpture composed of distinct punctures, fine and densely arranged on cephalic dorsum, with smooth to finely shagreened interspaces.

Worker, holotype and six paratypes from type nest series: TL 6.0–6.3, HL 1.27–1.31, HW 0.98–1.04 (CI 76–82), ML 0.76–0.78 (MI 75–83), SL 0.74–0.77 (SI 75–80), EL 0.22–0.25, WL 2.01–2.09 mm.

Head with gently convex subparallel sides, straight to feebly convex occipital border, and broadly rounded posterior angles. Greatest head width slightly behind midlength. Eyes oval, only feebly convex, their greatest diameter greather than maximum width of scape; about 12–15 fine facets in rows across the short axis; eye separated from anterior corner of head by about 2/3 its own length or slightly more. Frontal sulcus extends slightly beyond midlength of head. Median clypeal process obsolete, represented only by a weak convexity between the frontal lobes with two or three minute piligerous tubercles. Form of mandibles shown in Figs. 2, 3. Scapes reaching roughly to about 3/4 the distance between their insertions and the occipital border; segment I of funiculus distinctly longer than II; II through X increasing rather uniformly in size, so that no club is formed.

Trunk as seen from side forming gentle, subequal promesonotal and propodeal convexities, separated by the impressed metanotal groove. Petiolar node slightly higher than long seen from the side (without subpetiolar process) and very slightly longer than broad seen from above. Postpetiolar segment seen from above about 4/5 as long as broad, slightly shorter than the succeeding segment.

Dorsum of head densely sown with fine, uneven-sized punctures, close together, but interspaces mostly smooth and shining; region posteromesad of compound eyes with densest punctation. Sides and underside of head smooth and shining and with scattered coarse punctures. Mandibles, gastric apex, scapes and legs smooth and shining.

Trunk, petiole, and first two gastric segments with numerous coarse, mostly elongate piligerous punctures. Between punctures the integument is mostly smooth to shagreened on the dorsum, becoming striolate and subopaque on sides and rear of trunk and petiolar node, and to some extent on mesonotum and propodeal dorsum.

Pilosity of fine, tapered, erect hairs, moderate in length and generally distributed. Head with abundant, mesally directed decumbent pubescence over most of the dorsum; scapes and legs with similar pubescence, directed apicad. Color bright to deep brownish-red; mandibles and appendages lighter, more yellowish.

Holotype (MCZ) a worker from a uninidal series of 7 workers and a queen from the Cuernos Mts., near Dumaguete, Negros, Philippine Islands (Chapman). Paratype workers from the same colony (MCZ, BMNH).

Queen, dealate: slightly larger than the worker. Flight sclerites and wing stumps well developed. Petiolar nodes slightly broader than long as seen from above. Mesonotum and propodeum shagreened (finely reticulate) above and with scattered coarse punctures. Ocelli small. Compound eyes large; maximum diameter ca. 1/5 the full head length (HL).

Myopias nops new species
(Figs. 9, 28)

Diagnosis, worker: A modest-sized, depigmented (dull yellowish) species without eyes; sculpture opaque, predominantly densely reticulate-punctulate over head, trunk, node and first gastric segment. Mandibles short and stout, with basal angle distinct, but rounded and close to submedian tooth. Median clypeal lobe distinct, short with subacute free corners and indented apical margin. Antennal scapes just reaching posterior border of head. Petiolar node thick, but tapered apicad, its sternal keel ending behind in an abrupt angle, paired bilaterally as in *Ponera.*

Worker, holotype: TL 4.4, HL 0.85, HW 0.77 (CI 91), ML 0.42 (MI 49), MLO 0.59, SL 0.65 (SI 84), WL 1.30, petiole L 0.45, hind femur L 0.65, hind tibia L 0.64 mm.

The two paratype workers, both dismembered, hardly differ from the holotype by more than the usual error of measurement in the standard dimensions. Since the three specimens of the type series are all incomplete (one lacking head, another without gaster, various legs missing, sculpture in part obscured on holotype), the description is composite.

Head oblong with nearly parallel, weakly convex sides, greatest width a little way anterior to midlength; posterior corners rounded; posterior border straight in full-face view, or perhaps just the slightest bit concave. Median frontal sulcus broad but short, not reaching back to mid-HL. Eyes obsolete, or at least unpigmented and not distinguishable amid the sculpture in strong light at 50×. Antennae with robust scapes that just reach the posterior border of the head when held straight back; funiculus long, with an indistinctly 4-merous apical club; funicular segments II through V short, wider than long; pedicel (I) is 3–4× as long as II; VI-XI longer than wide.

Mandibles short and stout, strongly downcurved, with acute apical tooth and blunt companion tooth, followed after long gaps by two blunt teeth, of which the submedian is followed closely basad by a distinct but rounded basal angle. Labrum without a distinct median tooth, but the two lobes each bear a delicate, upturned tooth at apex. Palpal segmentation not determined. Median clypeal lobe distinct but short, CLL 0.08, CLW 0.12, with indented or concave apical margin and subacute free corners; one side deformed in holotype.

Trunk compact, with a weakly convex dorsal outline (in side view) between steeply sloping pronotal and propodeal declivities; promesonotum distinctly longer than propodeum; mesonotum weakly convex; metanotal groove strong, but only moderately impressed; propodeal dorsum feebly convex overall, but with a very shallow impression near midlength. Position of metapleural suture indicated by a vague sulcus. Propodeal declivity rather abruptly rounded off from dorsum, weakly transversely aciculate above, smooth and shining below, meeting sides of propodeum through bluntly subrectangular curves. Lengths of propodeal dorsum: mesonotum about as 5:3.

Petiolar node thick but higher and broader than long; summit anterior, dorsal face rounded, but meeting steep concave anterior face through an abrupt curve, rounding broadly caudad into posterior face, which is low, flat and smooth. Ventral keel of petiole with a large, obliquely truncate process in front and another, lower, rectangular or obtuse angle farther caudad; this last angle is paired bilaterally with a mate, and together they appear to be homologous with the similar teeth or angles diagnostic of the genus *Ponera*.

Gaster robust; constriction behind first segment deep, broad, scrobiculate. First segment abruptly truncate in front, the front face vertical, flat, smooth and shining; second subequal in length to first, but slightly wider than first.

Head, trunk, and anterior disc of first gastric segment densely reticulate-punctulate and opaque, with a minutely pitted overlay;

sides of trunk, especially mesopleura and metapleura, and sides of node, obscurely striate-punctulate; coxae minutely striate, becoming smooth anteroventrad. Posterior disc of gastric tergum I, and most of II, densely covered with small, round punctures with smooth, shining, but very narrow interspaces, becoming wider behind; undersides of the same two gastric segments with scattered coarse punctures, the interspaces in part minutely roughened (I) or shining. In addition to the other surfaces listed above as smooth and shining may be added the gastric apex, mandibles and femora, all with scattered punctures. Antennae, tibiae, tarsi mostly finely punctulate, but more or less shining.

Pilosity reduced to a mostly pubescence-like vestiture, abundant but not very conspicuous, of appressed to subdecumbent, fine hairs; only the clypeal and paired humeral setae as long as 0.10 mm, but the specimens are badly rubbed, and probably had moderately, abundant, but still fine and short, erect and suberect pilosity, some of which can still be seen at times on scapes, legs, and dorsum of trunk, as well as gastric apex.

Color dull, light brownish yellow.

Queen and male unknown.

Holotype (MCZ) and two paratypes workers (MCZ, BMNH) from Taiwan: Rarasan (probably the same as the mountain now called La La Shan, 24°44′N, 121°26′E, to the southwest of T'ai Pei), 31 July 1933, leg. R. Takahashi. I have no information concerning the habitat, nest site, or prey. This is obviously a cryptic-foraging form, probably living in the soil or in rotten wood. A related undescribed species has been found in Borneo.

The type series was originally three workers mounted on points on a single pin; these were heavily damaged in a laboratory accident, but the species is so interesting that we decided to describe it from the collectively adequate remains. The name *nops* is from a Greek word meaning blind.

Myopias delta new species
(Figs. 8, 21)

Diagnosis, worker and queen: A modest-sized species, completely distinct from all congeners in possessing downcurved triangular mandibles with distinct basal and masticatory borders meeting at a dentiform basal angle. Head oblong, with convex sides and straight posterior border, and broadly rounded posterior corners. Worker eyes reduced to dots. Frontal lobes and median clypeal lobe large; clypeal lobe squarely truncate. Antennae very robust; scapes overreaching posterior border of head; funiculus dominated by a long, thick, 4-merous apical club. Trunk compact, weakly convex, separated into two subequal parts by a distinct but not sunken metanotal groove. Petiolar node short and high, summit posterior and acutely rounded, posterior face vertical and feebly concave. Gaster constricted behind first segment. Integument smooth and shining, with separated minute punctures. Color dark yellowish brown.

Worker, holotype: TL 4.1, HL 0.79, HW 0.70 (CI 89), ML 0.30 (MI 38), MLO 0.54, SL 0.66 (SI 94), EL 0.04, WL 1.27, hind femur L 0.68, hind tibia L 0.61 mm.

Worker paratypes (15 from type nest series) range downward from size of holotype to smallest individual, TL 3.9, HL 0.75, HW 0.68 (CI 91), ML 0.29 (MI 39), MLO 0.49, SL 0.62 (SI 91), EL 0.04, WL 1.20 mm.

Head a little longer than broad, with parallel gently convex sides, straight posterior border, and rounded posterior corners. Frontal lobes broad, median clypeal lobe thick and wide (CLL 0.07, CLW 0.14), squarely truncate at apex, sides slightly convergent towards apex. Median frontal sulcus very short, not extending rearward past constricted ends of frontal carinae.

Mandibles basically of the ordinary ponerine, rather than *Myopias*-like, form, triangular and strongly downcurved, with distinct basal and oblique masticatory margins, each furnished with five coarse, spaced teeth, the most basal of which, corresponding to the basal angle, is subacutely dentiform; apical tooth the largest and most acute; masticatory margins crossing over one another at full closure. Basal oblique groove and its lateral extension (strix) strongly developed.

Eyes small, round and dot-like, with indistinct facets, only 0.03–0.04 mm long, and distant from mandibular insertions by about 0.20 mm. Antenna massive, scape thick, especially toward apex, and overreaching posterior border of head (when held straight back in full-face view) by more than half apical scape width; funiculus with 4-merous club (which takes up more than 0.6 of funicular length) following six short, transverse ring segments (II through VII); pedicel (funiculus I) about 5× length of II.

Labrum without a median tooth, but each of its two lobes bears a delicate, upturned apical tooth. Palpi segmented 3,3.

Trunk compact; aside from the rounded declivities of pronotum and propodeum, the dorsal profile in side view is only weakly convex, with moderate interruptions at premesonotal suture (movable) and metanotal groove; latter is moderately wide and distinctly, but not very strongly, impressed, and it divides the trunk into approximately equal anterior (promesonotal) and posterior (propodeal) halves. Dorsum of propodeum gently convex, about twice as long as mesonotum; declivity of propodeum steeply sloping, its outline convex in side view, but the surface feebly concave, and weakly submarginate above and laterally, as seen from above.

Petiolar node short and high, highest and widest behind at narrowly rounded summit, after which the posterior face drops off sharply and almost vertically. Anterior face nearly as steeply sloping upward, shorter, meeting sloping dorsal face at an obtusely rounded angle. Sternal keel prominent, with a thick, obliquely truncate anterior process, pointed behind, then diminishing convexly caudad (see fig. 21). In holotype and two of the paratypes, the posterior convex portion bears an additional low point or tubercle, but shape of keel is variable in any case.

Gaster robust, distinctly constricted after first segment; segment II about as high as I, and only very slightly wider. Sting long, sharp, upcurved, capable of at least 0.4 mm extension. Seen from above, anterior border of gaster I transverse, straight.

Body smooth and polished, with well-spaced, small (mostly 0.01 mm diameter or less), piligerous punctures, most numerous on dorsum of head and gaster. Antennae, frontal lobes, tibiae and tarsi densely and finely punctulate. Bullae of metapleural glands obscurely striate.

Longer pilosity abundant on body, sparse on antennae and mandibles, and almost lacking on legs; mostly 0.03 to about 0.20 mm long, appressed to erect, but mainly decumbent to suberect on propodeum, node, and first two gastric segments; longest on clypeal lobe, propodeum, node and gastric apex. Pubescence mostly appressed to decumbent, inconspicuous and mesally inclined on anterior half of head, more abundant and conspicuous on antennae and legs.

Color dark yellowish brown or orange brown; legs, mandibles, antennal scapes slightly more yellowish.

Queen, dealate, from holotype nest series: TL 4.7, HL 0.80, HW 0.71 (CI 89), ML 0.34 (MI 43), MLO 0.57, SL 0.70 (SI 99), EL 0.18, WL 1.47 mm.

Showing the usual ponerine differences of caste, and darker, deep brownish red, in color; scutum yellowish brown, with a broad, V- or Y-shaped median fascia of deep reddish brown; mandibles, antennae, legs, and indefinite patches on lateral areas of pronotum and upper mesopleura obscure yellowish brown. Punctures a little coarser and more conspicuous than in workers. An additional dealate queen apparently belonging to this species, taken in 1901 by L. Biró (Hungarian Natural History Museum), comes from Friedrich-Wilhelmshafen (now Madang, Papua New Guinea); it is notably smaller (HL 0.62, HW 0.50 mm.) than either workers or queen from the type colony; and was found in the Hungarian collection placed with the *M. tenuis.*

Holotype (MCZ) and paratypes (MCZ, BMNH, ANIC) from a colony collected in rain forest just west of the lower Busu River, near Lae, Papua New Guinea on 9 May 1955, by Wilson (No. 983). Wilson's notes on this colony are slightly modified:

"A colony of one queen and about 30 workers, with brood at all stages, none preponderant; in a crumbling small *Passalus*-stage log, diameter about 5 inches, held in shape by intact bark. Ants relatively fast, nervous, similar to other [*Myopias*] species. Workers and brood scattered through a number of indistinct galleries and chambers in the crumbling wood. In one chamber near larvae was a fresh, decapitated worker of a small *Leptogenys* species. Around another, large chamber was the kitchen midden, consisting of discarded [*Myopias*] cocoons and numerous remains of *ants,* mostly or entirely myrmicines, including at least two genera (q.v.)." The "q.v." refers to the vial containing the whole colony. Unfortunately, the *Myopias* brood and the midden remains, left in alcohol after an adult sample had been mounted from the vial, was lost in transit by a colleague who had borrowed Wilson's and Brown's *Myopias* collection residues for study.

From the circumstances of the collection as noted by Wilson, it seems likely that *M. delta* is an ant predator specializing on Myrmicinae, but perhaps occasionally accepting ponerines or other subfamilies. We need further collections and field and laboratory observations to confirm this interesting possibility and to learn the details of the *M. delta* behavior and ecology.

The name *delta* refers to the triangular mandibles. This species cannot easily be placed to species group, and the mandibular form even puts generic assignment into doubt. The 3-merous palpi (both sets) and the upturned tooth on each labral lobe probably are derived characters shared with the *tenuis* group, so the triangular mandibular shape may well be secondarily derived from the *Myopias* plan; it seems, indeed, that the dentition of *M. delta* is more easily homologized with that of various *Myopias* species than it is with the run of *Pachycondyla* groups. It thus becomes doubly important to find again the larvae of *M. delta.*

LARVAE OF WRACK COLEOPTERA IN THE FAMILIES CORYLOPHIDAE, RHIZOPHAGIDAE, AND LATHRIDIIDAE*

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Wrack studies in New Hampshire have revealed a number of poorly known beetles. The temporary habitat produced by moist rotting seaweeds presents an environment which allows certain insects to become quite abundant for a short time. After processing with a Berlese funnel the siftings of several square meters of wrack from Odiorne Point State Park, I noted that large numbers of three unfamiliar taxa of beetle larvae were present. Two of these three taxa, *Orthoperus scutellaris* LeConte (Corylophidae) and *Monotoma producta* LeConte (Rhizophagidae), were subsequently reared. The third taxon is associated with *Corticaria valida* Fall, the only adult lathridiid collected in or near this habitat. Generic characters of another described larva of *Corticaria* confirm this placement. Descriptions of these larvae are presented in this paper to aid those workers studying wrack fauna.

All larvae were obtained from beach wrack by the author on June 15, 1982, at Odiorne Point State Park, Rockingham County, *New Hamsphire.* Adults were reared by July 1, 1982. The two reared taxa were processed with a simple program. Plastic boxes with removable tops were supplied with a thin layer of sand, enough water to saturate the sand, and a piece of rotting wrack. A number of the largest larvae of the taxa were separated out, placed in the containers, and left undisturbed except for the occasional addition of water every 3–4 days. Examination of the gut contents of field collected larvae indicated that all three taxa feed on the spores of two species of Fungi Imperfecti, *Helminthosporium* sp. and *Alternaria* sp., which grow on the rotting kelp.

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Orthoperus scutellaris LeConte
(Figs. 1, 2)

There are two apparent taxa of *Orthoperus* found in wrack at Odiorne Point. These run to *Orthoperus s. scutellaris* LeConte and *Orthoperus s. piceus* Casey in the last revision of the family (Casey 1900). I have not been able to separate these two taxa when examining specimens mounted on slides. Both forms are represented in the type series of LeConte for *scutellaris* at the Museum of Comparative Zoology.

Their collection in the same habitat at the same time indicates that the differences observed may be no more than normal variation within the species. All of the reared adults were assignable to the nominate subspecies.

Last instar larva: length 1.5–2.0 mm. Body elongate, slightly flattened dorso-ventrally, white with grey or brown patches in dorsal view. Head slightly declined, two stemmata to each side, setae aciculate, frontal arms of epicranial suture widely V-shaped, epicranial stem absent, gular sutures distinct and widely separated through length to head base; antennae two-segmented, sensorium almost as long as terminal seta; mandibles symmetrical with several teeth at apex, mola well-developed with series of large teeth on margin; sclerites of maxillary base fused, palps two-segmented, mala arcuate and blunt at apex, labial palps of a single segment; hypopharyngeal sclerome elongate, the arcuate anterior cap may be the reduced epipharynx. Thorax and abdominal segments densely covered with short spicules, scattered setae are apically enlarged and truncate, fluting is visible toward the apex, aciculate setae are found only on the lateral margins. Prothorax with large quadrate shield formed by dense clustering of larger spicules; medial longitudinal light area dividing shield lacking spicules; the remaining thoracic and abdominal segments each with dark lateral area formed by dense large spicules, last abdominal segment lacking urogomphi, somewhat explanate, darkened by dense large spicules, with alternating fluted and aciculate setae on margin; abdominal segments 1–7 with large glandular openings on lateroposterior margins of lateral darkened areas. Spiracles annular. Legs well-developed, with five segments, coxae widely separated, tarsungulus with single seta.

The only illustration of an *Orthoperus* sp. was by Perris in 1852 (in Klausnitzer 1978, p. 275). The illustration indicates the general form

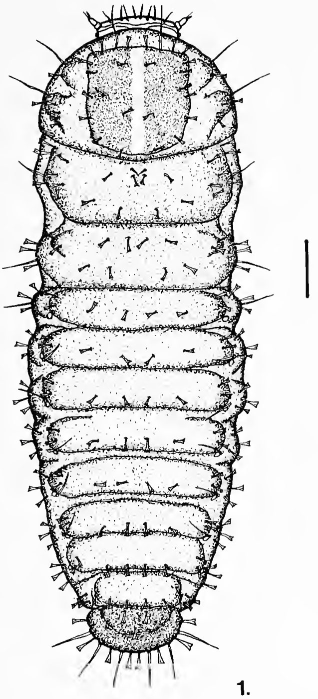
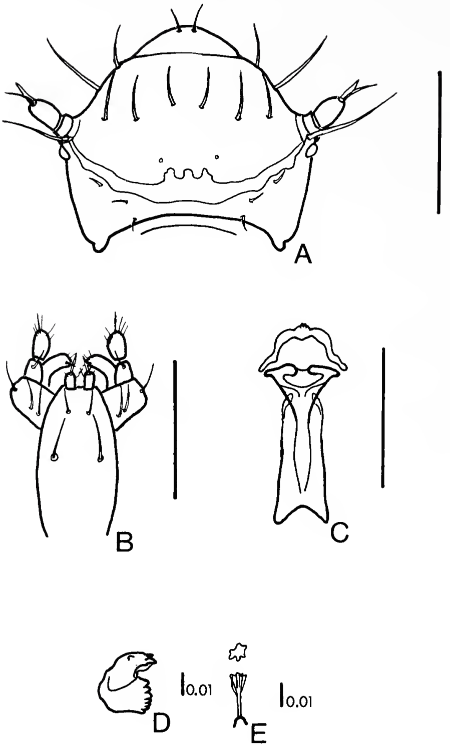


Figure 1. *Orthoperus scutellaris* LeConte, dorsal view of larva; line equals 0.1 mm.

of members of the genus, but differs in many of the fine details. Considering the age of the description, no attempt is made here to contrast it with the description of *O. scutellaris.*

Monotoma producta LeConte
(Figs. 3, 5, 6)

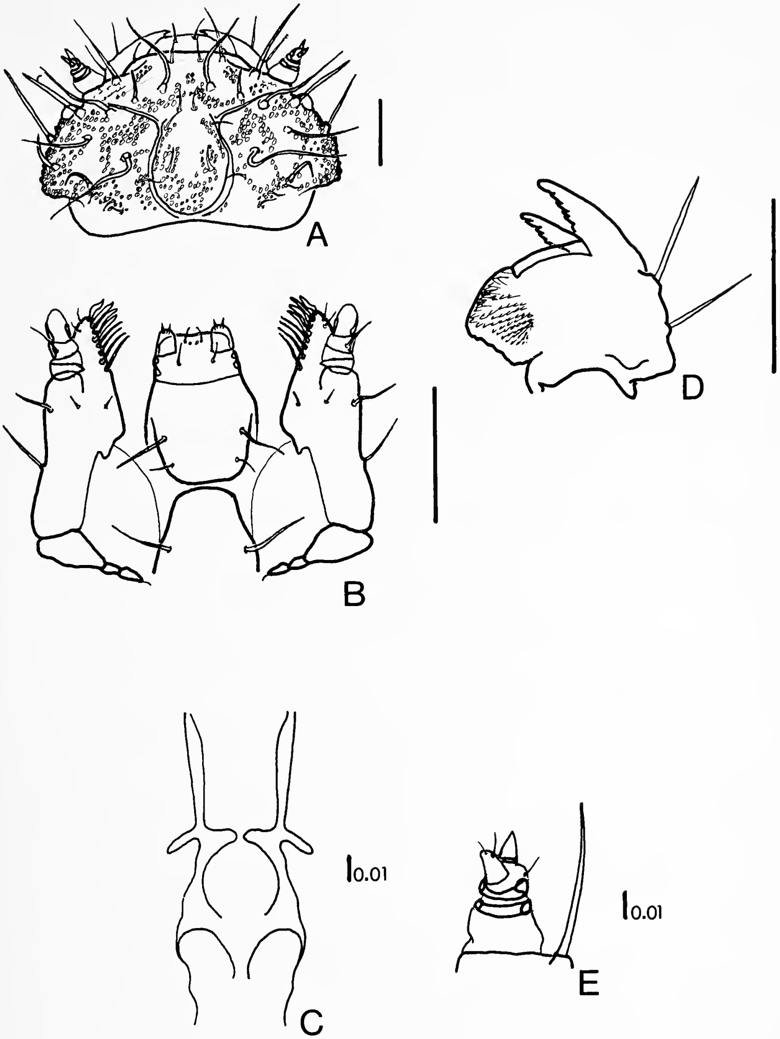
Adults were identified by using the key of Horn (1879), and comparing specimens with the LeConte type. Last instar larva: length 4.0–4.5 mm. Body elongate, flattened dorso-ventrally, whitish, all setae aciculate. Head with patches of darkly sclerotized tubercles, labrum distinct, single stemma on each side, frontal arms of epicranial suture lyriform, epicranial stem absent; antennae three-segmented, sensorium two-thirds length of third segment; maxillary base divided into three sclerites, palps three-segmented, mala bluntly



2.

Figure 2. *Orthoperus scutellaris* LeConte. A, dorsal view of head; B, ventral view of maxillae and labium; C, ventral view of hypopharyngeal sclerome; D, dorsal view of left mandible; E, dorsal and lateral views of enlarged setae. Line equals 0.1 mm unless otherwise indicated.

produced at apex, row of thick setae in inner margin to apex; labium transversely divided, palps one-segmented; mandibles symmetrical, with large prostheca, prostheca and incisor edge of mandible serrate, accessory ventral process present on mandible base, mola with series of fine teeth over surface, two widely separated long setae on outer margin; the area of the hypopharyngeal sclerome and epipharynx very complex, only outline of sclerome is figured. Prothorax with scattered patches of dark tubercles on anterior half, notum with two transverse rows of four multiply tubercu-



3.

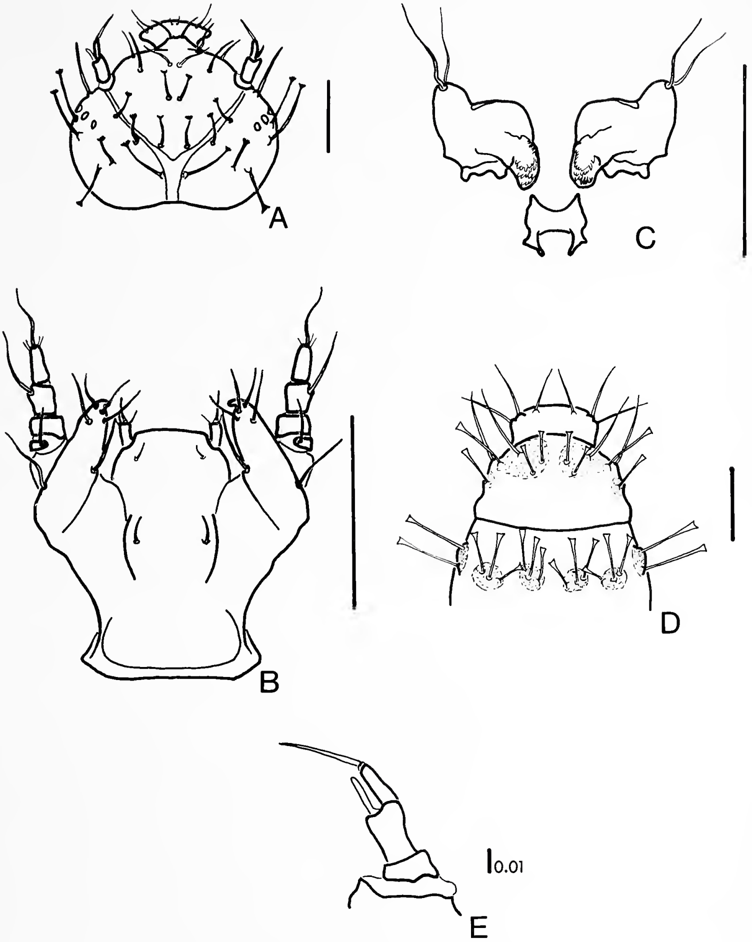
Figure 3. *Monotoma producta* LeConte. A, dorsal view of head; B, ventral view of maxillae and labium; C, ventral view of hypopharyngeal sclerome; D, dorsal view of right mandible; E, dorsal view of right antenna. Line equals 0.1 mm unless otherwise indicated.

late processes, the processes of the posterior row being reduced, basal lateral margins posterior to other lateral tubercles with single tuberculate process, each process bearing a single long seta; the remaining thoracic segments and abdominal segments 1–8 bear dorsally two transverse rows of six multiply tuberculate processes, each process bearing a single long seta, segment 9 possesses an anterior row of three and a posterior row of two processes similar to those of the other segments, lateral margins of all segments with 2–3 large palmate tubercles bearing 1–2 long setae; urogomphi similar in form to the lateral processes, multiply tuberculate and bearing 2–3 long setae; spiracles biforous, bourne on short tubes. Legs well-developed, with five segments, coxae moderately separated, tarsungulus with two short adjacent setae.

This is the first member of the genus to be formally described. Peacock (1977) presents a brief description without figures. Her diagnosis agrees with the features described here for *M. producta*.

Corticaria valida Fall
(Fig. 4)

This species is quite distinctive and fits the characters presented in the key and description of Fall (1899). This identification is tentative, however, since the type localities of Fall were the Midwest and Rocky Mountain states. Last instar larva: length 2.5–3.0 mm. Body elongate, cylindrical, whitish with scattered long setae abruptly expanded and flattened at apex. Head slightly declined, with scattered modified setae, the few aciculate setae on or near anterior margin, labrum free, four stemmata to each side, three in vertical row, the fourth posterior to the lowest stemma, epicranial suture moderately long, frontal arms broadly V-shaped; antennae three-segmented, sensorium as long as third segment, second segment twice as long as first; maxillae and labium fused at base, maxiliary palps three-segmented, mala with acute hook at apex, labial palps one-segmented; mandibles lacking apical teeth, with lateral enlarged fleshy lobe bearing two long setae at apex, mola enlarged, with series of fine teeth over surface; hypopharyngeal sclerome short, distinct. Thorax and abdomen dorsally with smoothly raised circular sclerotized patches bearing 1–4 modified setae, abdominal segments 1–8 with row of six sclerotized raised areas each bearing three



4.

Figure 4. *Corticaria valida* Fall. A, dorsal view of head; B, ventral view of maxillae and labium; C, dorsal view of mandible and hypopharyngeal sclerome; D, dorsal view of abdomen apex; E, dorsal view of left antenna. Line equals 0.1 mm unless otherwise indicated.

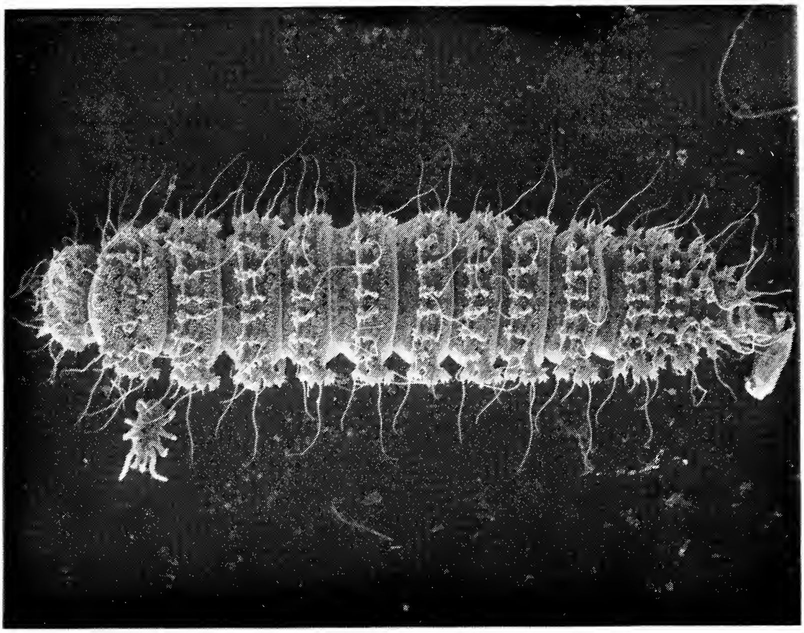


Figure 5. *Monotoma producta,* dorsal view of larva.

modified setae, outer sclerotized patches on lateral margin visible dorsally, segment 9 with two lateral aciculate setae on each side, setae on segment 10 all aciculate. Spiracles annular, not raised on tubes. Legs well-developed, with five segments, coxae widely separated, tarsungulus with one seta.

Hinton (1945) is the only author who has provided a complete set of figures describing *Corticaria.* The form of the mandibles and mala, and the four stemmata to a side seem to characterize this genus. The most obvious difference between species are the setal forms. The long apically expanded setae of *valida* are most similar to those in *C. pubescens* (Gyllenhal) (Hinton 1945). Other larvae have been poorly or briefly described, and comparison with those species is not attempted.

ACKNOWLEDGMENTS

I would like to thank Dr. Alan L. Baker, Mary Lou Turner, and David Gadoury for their efforts in the identification of the two

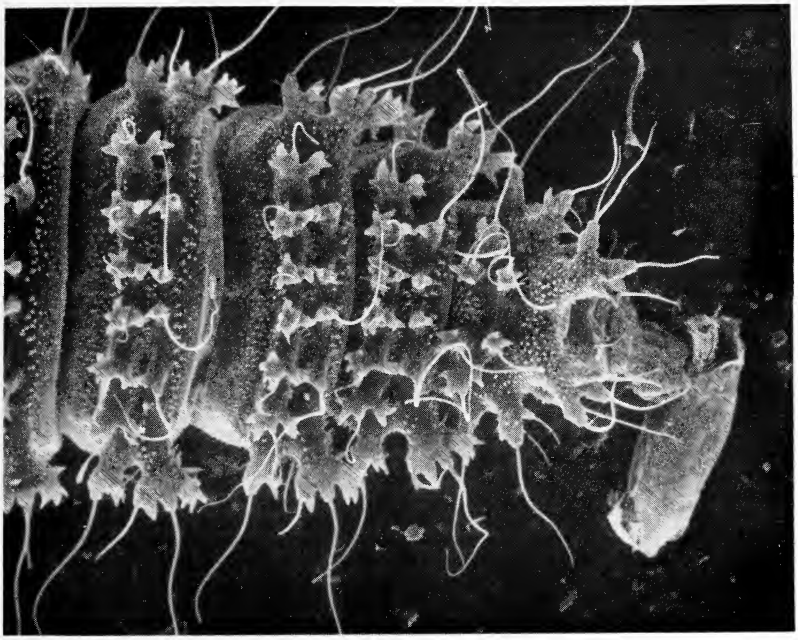


Figure 6. *Monotoma producta,* dorsal view of abdomen apex.

fungi. Dr. Ronald J. McGinley permitted the examination of the LeConte types in the Museum of Comparative Zoology, Harvard University. Dr. John F. Lawrence, C. S. I. R. O., Australia, offered comments on the manuscript and graciously sent copies of his characterizations of the three families. Drs. John F. Burger and R. Marcel Reeves, University of New Hampshire are thanked for checking the manuscript. Mrs. Marilyn Ecker, University of New Hampshire, kindly provided the photomicrographs.

SUMMARY

Wrack inhabiting larvae of three species of Coleoptera are described for the first time. *Orthoperus scutellaris* LeConte (Corylophidae) and *Monotoma producta* LeConte (Rhizophagidae) were reared, with the third larva being associated with *Corticaria valida* Fall (Lathridiidae). Spores of *Helminothosporium* sp. and *Alternaria* sp. (Fungi Imperfecti) were found in the guts of all three taxa.

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THE GUEST ANT, *SYMMYRMICA CHAMBERLINI*, REDISCOVERED NEAR SALT LAKE CITY, UTAH (HYMENOPTERA, FORMICIDAE)*

By Alfred Buschinger[1] and André Francoeur[2]

Introduction

In a series of recent papers we investigated the social structures of *Formicoxenus nitidulus, F. hirticornis,* and *Leptothorax provancheri* (Buschinger und Winter 1976, Buschinger 1979, Buschinger, Francoeur and Fischer 1980). They are all so-called guest ants, small species living in independent colonies within the larger nests of their host species. *Formicoxenus* gains its food by soliciting it from the *Formica* hosts, or by stealing food when two *Formica* workers feed each other (Stäger 1925, Buschinger 1976). *L. provancheri* are often seen licking the head and body of their *Myrmica* hosts; however, it remains uncertain how they really get their food. Our observations revealed that these guest ants had some interesting features in common, such as a functional monogyny, a queen polymorphism with dealate and intermorphic females, and a tendency to mate within or on the upper surface of the host nest. The *Formicoxenus* species recognized up to now have wingless, workerlike males, whereas the *L. provancheri* male exhibits an ordinary winged shape.

It was a challenging task, therefore, to search for *Symmyrmica chamberlini* Wheeler (1904), another guest ant with wingless males and living together with *Manica mutica*, in order to study its biology and to find out its relationship to the species mentioned above. We took the opportunity of visiting the type area of *S. chamberlini* in the vicinity of Salt Lake City, Utah, after the 9th Congress of IUSSI in Boulder, Colorado. We were able to rediscover this ant and to collect some new material which yielded additional support for an incorporation of *Symmyrmica* into *Formicoxenus.*

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FIELD OBSERVATIONS AND COLLECTING SITE

The original description of Wheeler (1904) indicates the type locality only inaccurately as "near Salt Lake City, Utah, in the flood-plains of Jordan River", where the host species, *Manica mutica*, was said to be common in some localities. *S. chamberlini*, however, was found only in one particular ten-acre field and, despite an intensive search, in no other locality. Unfortunately Wheeler's paper (1904) contains no further details on the exact site of that field.

On August 15, 16 and 17, 1982 we located about 30 flourishing *Manica mutica* populations along the Jordan River, beginning with our search near Lehi and working down the river to North Salt Lake. We followed the roads and highways crossing the river, and, always beginning at the bridges, we looked for the host species in or near the banks. *M. mutica* was found near Lehi, on the eastern bank north of the bridge of road no. 73, and in several places in West Jordan (between 5400 South Street and 7800 South Street, east bank), in Murray and South Salt Lake (between 5300 and 3300 South Street). Often the colonies seemed loosely concentrated. A search in Big Cottonwood Canyon was not successful. We have heard since then that unfortunately, late in following September, the Jordan River heavily flooded the type area, the only known nesting site for *S. chamberlini*.

The species was detected only in one locality, on the eastern bank of the river, about 200 m south of the bridge of 3300 South Street, South Salt Lake. *Manica mutica* there forms large nests in the silty soil just in the upper edge of the steep river-bank about 2 m above the waterline. The area is a horse pasture with poor, short vegetation, which was quite dry in August. Between two nests containing *chamberlini* there was a willow brush, and in the estate adjoining to the north, some rose bushes covered partly a private garbage dump. One very large *mutica* colony with a *chamberlini* nest was found there underneath a piece of concrete (50 × 18 × 15 cm).

Altogether we found *chamberlini* in three *mutica* nesting sites, with distances of about 6 m between one other. We could not decide whether the flourishing *mutica* nests belonged to separate colonies, or whether they were parts of a large supercolony. However, two samples of living workers from two similarly adjacent nest sites of another locality (3900 South Street, South Salt Lake City) were successfully mixed and became host of *chamberlini* colony no. 3.

Single *mutica* workers or groups with and without brood were found nearly everywhere in that area when we dug a few centimeters into the soil.

The first site, the southernmost one (Fig. 1), yielded just 30 *chamberlini* workers and intermorphs, but no brood (colony no. 1 in the following). In the second site, about 6 m to the north and beyond the willow brush, we found a *chamberlini* nest (no. 2) about 15 cm below the surface, in the soil and surrounded by larger tunnels with *mutica* workers and brood. The *chamberlini* nest contained larvae and prepupae, about 38 workers and intermorphs, two wingless males, and one male pupa. The prepupae from this colony were used for a karyotype study. In the third site, again about 6 m to the north, in the garbage dump, we found a *chamberlini* nest (no. 3) with about 30 workers and intermorphs, pupae, prepupae, and larvae. One dealate female was detected but escaped capture. The relative importance of intermorphs for our samples is given in table 1 in comparison with Wheeler's data.

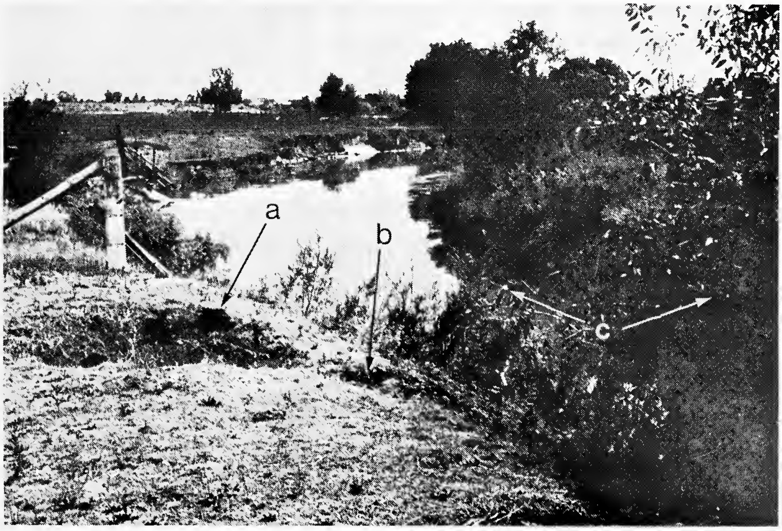

Fig. 1. The *chamberlini* site on the east bank of Jordan River, looking southward (upriver).

a) Site of *chamberlini* colony no. 1 within a *Manica* colony

b) Site of another *Manica* colony which extended along the willow brush to the right

c) willow brush between *chamberlini* colonies 1 and 2

RESULTS OF DISSECTING *SYMMYRMICA CHAMBERLINI*

The three samples were kept alive for several months. However, numerous specimens died during the first few weeks. A number of them could be dissected following the method described by Buschinger and Alloway (1978).

In a total of 15 ordinary workers without any vestiges of ocelli on their heads, the number of ovarioles was always two, except in one specimen which has three. No spermatheca could be found in any of these workers.

On the contrary, we found five slightly intermorphic specimens, with between one and three more or less perceptible ocelli, with somewhat deeper thoracic sutures, and with 6 ovarioles and a spermatheca each. Two of these specimens, both from colony no. 2 (where males had been present), contained living sperm in their receptacles. Their ovarioles, however, were short and transparent as is usual in young, not yet egg-laying females.

Additional observations were made referring to the abdominal glands of *S. chamberlini*. Thus, the poison gland reservoir was always of usual size and shape, as in other leptothoracine ants. The Dufour's gland, however, is large both in workers and intermorphic females. Its size exceeds considerably that of independent *Leptothorax* species, and it reaches that of, e.g., *Harpagoxenus sublaevis* (Buschinger and Alloway 1978).

A karyological study of 7 prepupae from colony no. 2 was made following the method of Imai et al. (1977). The results, however, were not as good as to permit the presentation of a karyotype. We could only determine the chromosome number, which is $2n = 28$.

LABORATORY OBSERVATIONS

We were not able to take large samples of the *Manica* host species with us alive. So only very few observations of interactions between *chamberlini* and their hosts were possible. However, following a method which had already worked with *Formicoxenus nitidulus* (Buschinger 1976), we tried to join *chamberlini* brood and adults with an unnatural host species. We chose a *Leptothorax* species which was nesting within dead willow stems near to our *chamberlini* site. Apparently it represents an unknown, new species belonging to the subgenus *Leptothorax* (= *Mychothorax* Ruzsky). The following experiments and observations were made:

a) After an artificial wintering, four *S. chamberlini* specimens of colony no. 3 were isolated with 5 pupae of the *Leptothorax* species. Honey and freshly killed *Drosophila* were provided. However, the *chamberlini* did not survive. Two agonizing *chamberlini*, almost without movement, were returned to the *Manica mutica* artificial nest arena. The *Manica* workers immediately brought them into the nest, and licked them all over. A few hours later, the two *chamberlini* could feebly walk. Next day, they were running normally in the nest and its arena, having completely recovered. When an apparently dead *chamberlini* was offered to *mutica* workers, they put it in the refuse heap confirming its death. Trophallactic exchange between *chamberlini* nestmates was never seen, but only one was noted between *chamberlini* and *mutica*.

b) The larvae and pupae of colonies no. 2 and 3 were put into a nest together with 20 workers of the *Leptothorax* species mentioned above. One *chamberlini* worker hatched, but died (or was killed?) after two weeks. *Chamberlini* larvae survived an artificial hibernation from 27 October to 1st December 1982. They were easily distinguished from the *Leptothorax* larvae which developed from worker-laid eggs: the *chamberlini* larvae are much hairier.

After the hibernation, the colony raised numerous alate *Leptothorax* males, but no *chamberlini*. The *chamberlini* larvae vanished one after the other.

c) About 20 workers and intermorphs of colony no. 2 were placed together with 25 white and brown worker pupae and a few larvae of the *Leptothorax* species on 1st September, 1982. After one week, the first *Leptothorax* workers had hatched, and 12 *chamberlini* were still alive. Among them an intermorph which had lost the right antenna seemed to become fertile. This specimen, later on, was observed several times to lay an egg. Together with a second intermorph it was still alive on 12 April, 1983.

The first, comparatively long-shaped eggs of *chamberlini* appeared three weeks after the beginning of the experiment. Adult *chamberlini* often fought with each other, possibly in order to eliminate supernumerary reproductives. Some of the victims of these fights were dissected, when they were not too much decomposed. In addition, not only inseminated intermorphs but also ordinary workers died rapidly. After the hibernation (cf. section b), only two *chamberlini* intermorphs were alive, among them the one with only the left antenna. Both became fertile again, and the brood still contained some hairy *chamberlini* larvae. Between 15 December and 26 January, in a temperature rhythm of 12 hours/15° C and 12 hours/25° C, several *Leptothorax* males, females and workers hatched, but no *chamberlini* larva reached the pupal instar.

After raising the temperature to 10h/17° C and 14h/28° C on 2nd February, 1983, three *chamberlini* larvae became prepupae, and on 10 and 12 March two prepupae molted into apterous male pupae. Nevertheless, it is doubtful whether breeding of *chamberlini* with that *Leptothorax* will be as successful as the experiments with *Formicoxenus nitidulus* and *Leptothorax acervorum* as host species (Buschinger 1976), since both pupae and the remaining prepupa were eaten during the following three days. In the mixed colony *chamberlini*/*Leptothorax* sp. we observed quite amicable relations between the two species. Often the *chamberlini* solicited food from *Leptothorax* workers, and sometimes they were seen licking the mouthparts of larvae. We never saw a *chamberlini* foraging outside the nest, where honey and pieces of *Tenebrio* or *Periplaneta* were offered as food. The *chamberlini* larvae, like those of the *Leptothorax* species, are fed with solid particles of the insect pieces. *Leptothorax* workers place the particles on the ventral surface of the larvae, which then chew and eat them.

DISCUSSION

Our knowledge of the biology of this rare ant still remains fragmentary. We can confirm the observation of Chamberlin, as reported by Wheeler (1904) in that we also found this ant in mixed colonies with *Manica mutica,* in the flood-plains of Jordan River near Salt Lake City. The guest ants are living within independent nests in the midst of prosperous *Manica* colonies. However, we could not observe whether they solicit food from their hosts, or what are the other relations of the two species. The observation mentioned in the previous section, experiment a, raises questions of whether the licking of *chamberlini* by the *mutica* hosts is linked to any important cuticular secretion.

The nesting habits of *S. chamberlini* resemble closely those of *Leptothorax provancheri,* the guest ant of *Myrmica incompleta* Provancher (Buschinger et al. 1980). As was already suggested by

Table 1. Ratios of workers and intermorphs in colonies of *Symmyrmica chamberlini*

Source	Workers (%)	Intermorphs (%)	Total
Wheeler (1904)	8 (38)	13 (62)	21
Colony no. 1	20 (66)	10 (33)	30
Colony no. 2	16 (42)	22 (58)	38
Colony no. 3	13 (43)	17 (57)	30
Σ	57 (48)	62 (52)	119

Wheeler (1910), *S. chamberlini* is closely allied to the genus *Formicoxenus,* guest ants of *Formica* species in Europe and North America. Since the wingless male of *chamberlini* nevertheless is not as workerlike as the *Formicoxenus* male, Wheeler may be right in suggesting that it could represent an archaic form of *Formicoxenus.*

The close relationship of *S. chamberlini* and *Formicoxenus* is further corroborated by our observations of intermorphic queens in our new material. Such queens, which often look like ordinary workers except that they have one or up to three vestigial ocelli and sometimes a little bit more developed thoracic sutures, occur quite frequently in *Formicoxenus nitidulus* (Buschinger and Winter, 1976), in *F. hirticornis* (Buschinger, 1979), and in *Leptothorax provancheri* (Buschinger *et al.* 1980). We cannot yet determine whether *S. chamberlini* also has a functional monogyny like the 3 guest ants we mentioned above. This would mean that alongside one functional queen in each nest, there exists one or several inseminated but not egg-laying potential queens. However, at least our finding of two recently inseminated intermorphic females in *S. chamberlini* colony no. 2 reveals that, as in the other guest ants, copulation takes place within or near the mother colony, and that newly mated females may remain for a while in the mother nest.

The analysis of intermorph composition presented in table 2 based on the classification of Plateaux (1970) for caste polymorphism in *Leptothorax nylanderi,* revealed only few superior intermorphs with intermediate trunk between a fully developed gynomorph and a typical ergatomorph. Moreover the inferior intermorph classes seem to be dominated by the form 4 which has 3 small or minute ocelli in any combination, a mesothorax not, or slightly enlarged, a promesonotal suture more or less prominent. The individuals with a potential or actual queen function capacity are found

Table 2. Types of *S. chamberlini* intermorphs according to Plateaux' classification of *Leptothorax nylanderi.*

Source	Form 2	Form 3	Form 4	Form 6–7	Total examined
Wheeler (1904)	0	1	5	0	6
Colony no. 1	3	1	4	2+)	10
Colony no. 2	7	0	13	2++)	22
Colony no. 3	2	2	13	0	17

+)Both with thoracic sutures and sclerites according to Plateaux' form 7, except for the lack of wings. One specimen with very short forewing rudiments.

++)Two specimens between Plateaux' form 6 and 7, without traces of wings.

mainly in that class of intermorphs. It is worthy to stress that Holliday's (1903) data for 1000 specimens of *L. provancheri* includes 37% of intermorphs without the microgynes; the intermorph composition exhibits the same trends as in *chamberlini.*

The karyotypes cannot yet confirm a closer relationship of all these guest ants. However, they also do not contradict such an assumption. *F. nitidulus* has a haploid number of $n = 15$ chromosomes, *L. provancheri* has $n = 11$, and *S. chamberlini* with $n = 14$ lies in between. For *F. hirticornis* and *diversipilosus* the chromosome numbers are not yet known.

Summing up the known features, queen polymorphism with alate and intermorphic females, males with their tendency to reduce wings and to become ergatomorphic, the presence of inseminated young (and in *Formicoxenus* also old) potential queens in the nests, and the life habits as guest ants, we believe that *Symmyrmica,* and also *L. provancheri,* should be incorporated in the genus *Formicoxenus.* A comparative morphological study has been undertaken in order to link the biological informations accumulated on the guest ants mentioned above in a taxonomic revision of the genus *Formicoxenus.*

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SUMMARY

Symmyrmica chamberlini was described by Wheeler (1904) from specimens taken by C.V. Chamberlin in 1902 in a colony of *Manica mutica* (Emery) near Salt Lake City. No further records of this species are known. In order to find out the systematic relations of *Symmyrmica* to other ants like *Leptothorax provancheri* Emery or those of the genus *Formicoxenus,* we have collected some new material in August 1982, in the Salt Lake City area. The morphology, female polymorphism, and wingless male together with biological features indicate that *S. chamberlini* is a species that should belong to the genus *Formicoxenus.*

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EMIGRATION RAIDS BY SLAVE-MAKING ANTS: A RAPID-TRANSIT SYSTEM FOR COLONY RELOCATION (HYMENOPTERA: FORMICIDAE)

By Ellen C. Kwait[1] and Howard Topoff[2]

Introduction

Polyergus lucidus Mayr is an obligate slave-making ant, found throughout north temperate regions of the world. Their slave raids are dramatic events in which columns of highly aroused workers penetrate nests of the related ant genus *Formica,* and carry the target colony's pupae back to their own nest (Marlin 1969; Talbot 1967). Although many of these pupae are consumed, varying numbers are reared through eclosion and become permanent members of the mixed-species nest. During the evolution of social parasitism, *Polyergus* workers lost the ability to participate in the ordinary chores of foraging, nest maintenance, and brood rearing, all of which are left to the *Formica* slaves.

Raiding behavior in *Polyergus* has only been reported in the context of slave raids, or of intraspecific territorial raids (Topoff et al. in preparation). Field observations of colonies in late summer, however, have revealed an entirely new function of raiding behavior: the rapid transport of colony members during emigrations to new nests at the end of the slave-raiding season. During such colony movements, the low level of mixed-species ant traffic is periodically interrupted by the abrupt emergence of *Polyergus* workers, and their formation into a well-organized swarm. The *Polyergus* workers promptly "raid" the old nest, and transport adult *Formica* individuals to the new site. For such group processes, occurring in the context of nest relocation, we propose the term "emigration raid."

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METHODS

Emigration raids were observed in three mixed colonies of *P. lucidus* and *F. schaufussi* Mayr, located in a pine-barrens habitat in North Centereach, Long Island, N.Y. The most detailed data were collected from a colony monitored continuously from July through September, 1976. The emigrations occurred on September 19 and 20, as the colony moved to a previously-constructed nest, 5.9 m southwest of the old site. Movements of individual ants shuttling between nests were monitored with hand-held tally counters. Callow age was estimated by comparing their degree of pigmentation with individuals of known age in laboratory nests (Kwait 1982).

RESULTS AND DISCUSSION

During the morning and early afternoon of each day, the population characteristics of the emigrations were similar to those described for *Polyergus* nest movements that occasionally occur in the spring (Marlin 1971). Thus, only *Formica* workers functioned as transporters, carrying adults and brood of both species to the winter nest (Fig. 1). As the afternoon progressed, however, several *P. lucidus* workers periodically joined the emigration. Although these *Polyergus* individuals made 5–23 trips between nests, the important point to note is the relatively low level of overall activity during most of the afternoon (Fig. 2A). But starting about 1600 hrs (EDT), at approximately the same time as the onset of slave raids earlier in the season (compare Fig. 2A and 2B), groups of 30–69 callow and mature- adult *Polyergus* abruptly surged out of the new nest and formed into an organized swarm. This raid swarm backtracked and penetrated the old nest, and after several minutes the *Polyergus* workers emerged carrying nestmates (Table 1). On both emigration days, the first emigration raid was promptly followed by a second raid (Fig. 2A). Activity levels for both species then dropped abruptly, as they typically do during slave raids on freeliving colonies of *Formica*.

Aside from our field observations on emigration raids, the only other reference to *Polyergus* carrying adult *Formica* individuals is Huber's (1810) study in Switzerland, of an emigration into an abandoned *Formica* nest. A more recent observation of comparable behavior stems from studies of *P. breviceps-Formica gnava* mixed colonies in a desert habitat in southeastern Arizona (Topoff et al. in

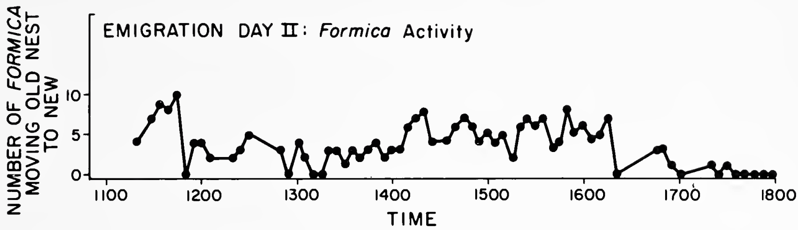

Figure 1. Activity of *Formica schaufussi* during colony emigration. Most of the workers are carrying adults and brood of *Polyergus* and *Formica* to the winter nest.

preparation). On August 14, 1981, colony #1 raided another mixed nest (#2), 30 m to the east. Fighting between resident and intruding *Polyergus* workers was minimal, and only about 11 pupae were captured. Early in the afternoon on August 15, *Polyergus* workers emerged from colony #2 and backtracked over the previous day's trail towards mixed colony #1. At 1715 hrs (MST), traffic again reversed direction, as hundreds of *Polyergus* workers penetrated nest #2. This time, however, the *Polyergus* emerged carrying hundreds of *Formica* brood, callows, and mature-adult individuals. All of the adult *Formica* being transported had their appendages closely appressed to the body, in the "pupa-like" position that is typical during social carrying behavior (Möglich and Hölldobler 1974). The adult *Formica* were carried into mixed nest #1, and none had re-emerged by the end of the observation period at sunset.

The description by Huber (1810) of adult *Formica* transport by *Polyergus* clearly took place within the context of a colony emigration. Our observation of similar behavior by *P. breviceps* is more difficult to interpret, but we suggest that it occurred in the context

Table 1. Quantitative Description of Emigration Raids

Date	Raid #	Time	*Polyergus* on raid	Adult *Formica* retrieved	*Formica* pupae retrieved
9/19/76	1	1525	56	37	3
	2	1625	45	35	0
9/20/76	1	1620	69	30	0
	2	1703	30	15	0

of colony reunification shortly after division by budding. The important point in both cases, however, is that adult transport of *Formica* by *Polyergus* took place in a staggered, prolonged, emigration-type column, without the intervention of an abrupt, short-lived, and full-scale raid.

That the *P. lucidus* emigration raids reported in the present study are fundamentally similar behavioral processes to their slave raids is evidenced by the congruence of several parameters, including: (1) the immediate organization of the emerging workers into an organized swarm; (2) the time of raid onset; (3) the occurrence of multiple raids; and (4) the participation of recently-eclosed *Polyergus* callows. The number of *Polyergus* workers in the emigration raids was lower than that characteristic of most slave raids. This difference is probably not significant, because it is known that even slave-raid participants decrease to as few as 13–50 individuals towards the end of the raiding season (Talbot 1967). Nevertheless, the social context of an emigration does produce at least one major difference in the behavior of the *Polyergus* workers. During emigration raids, it is principally *Formica* adults that are carried by the *Polyergus*. Because these adult slaves were reared from the pupal stage in the chemical and tactile environment of the mixed nest, the communicatory basis for social carrying behavior is well established. During slave raids, by contrast, *Formica* adults respond to the intruding *Polyergus* by exhibiting various forms of withdrawal behavior (Wilson 1971). As a result, it is principally *Formica* pupae and callows that are retrieved during slave raids.

Emigration behavior with adult transport is common in many ant species (Smallwood 1982), including free-living colonies of *Formica schaufussi*. Because *F. schaufussi* is considered related to *Polyergus*, emigrations probably pre-date the evolution of slave-raiding behavior. The secondary use of raiding behavior for *Polyergus* colony relocation represents an adaptive evolutionary transition, consistent with Simpson's (1958) principle of "transformation." Accordingly, when changes at any level of organization take place during a species' evolution, previously existing adaptations are often remodeled and eventually serve new functions. Because group raiding in *Polyergus* involves a complex recruitment process specialized for the efficient retrieval of other ants, it is clearly advantageous for the colony to utilize the process in all appropriate behavioral contexts.

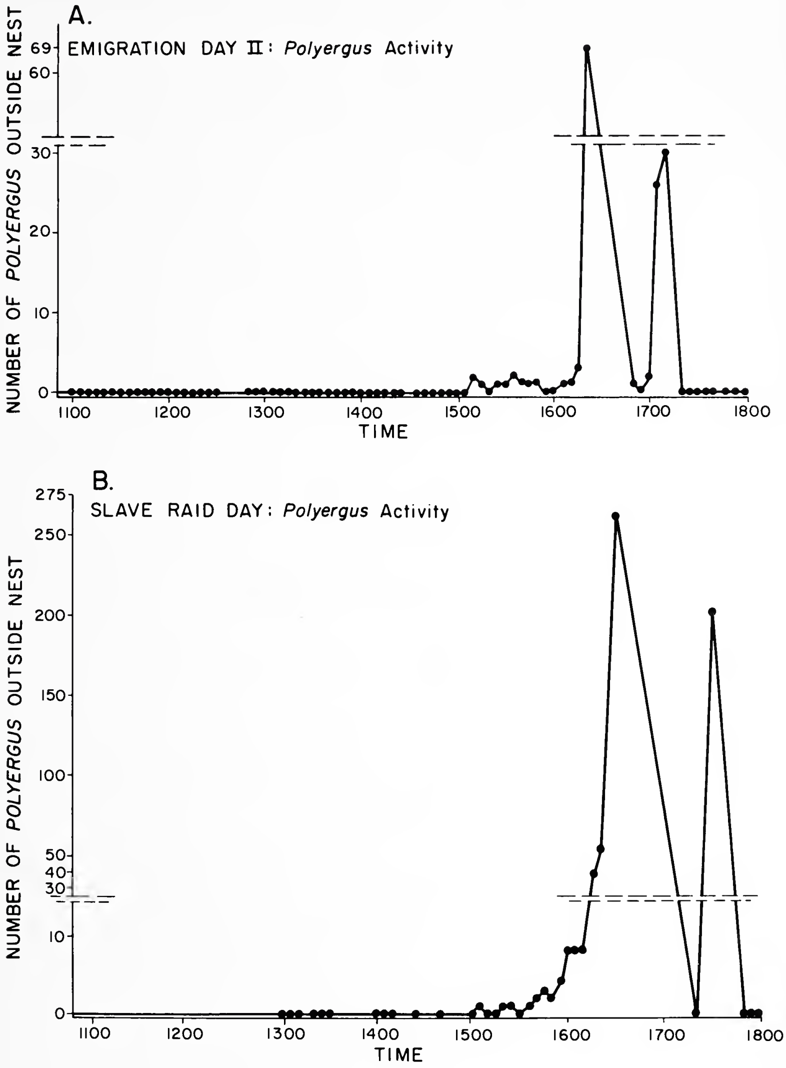

Figure 2. (A) Activity of *Polyergus lucidus* during colony emigration. The two consecutive peaks in afternoon activity represent emigration raids conducted on the old nest by *Polyergus* workers that were transported to the new nest by *Formica* individuals. (B) Activity of *P. lucidus* during typical slave-raid day. Note the similarity in timing of slave raids and emigration raids.

The rapid transport by *Polyergus* of adult *Formica* slaves to an overwintering site shortens the emigration time during a season characterized by increasingly unfavorable weather, and quickly relocates the *Formica* slaves to the new nest where they are needed for overall colony maintenance.

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DEFENSE OF BRACKEN FERN BY ARTHROPODS ATTRACTED TO AXILLARY NECTARIES

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Introduction:

The phenotypically variable bracken fern, *Pteridium aquilinum* (L.) Kuhn, is an economically important plant that establishes dense monocultural stands by spore dispersal and by spreading subterranean rhizomes throughout the world, except for hot and cold desert regions (Page, 1976). Bracken produces a number of so-called "secondary plant compounds" that have been shown to protect it from some nonadapted insects (Cooper-Driver et. al., 1977). These compounds include the cyanogenic glucoside, prunasin (Cooper-Driver and Swain, 1976; Cooper-Driver et. al., 1977), lignins and silica (Lawton, 1976), sesquiterpene pterosins (Jones and Firn, 1979a), phytoecdysteroids (Jones and Firn, 1978), and the protein thiaminase (Evans, 1976). Tannins, flavonoids, and phenolics have also been implicated as possible defensive compounds in bracken fern (Cooper-Driver et. al., 1977; Jones and Firn, 1979b).

Despite bracken's well-developed biochemical arsenal, adapted and nonadapted herbivorous insects in experimental plots located in Michigan and Massachusetts often destroy up to 30 percent of a frond's biomass after the pinnae are completely expanded. In addition to these herbivores, stands of Michigan bracken also support a diverse community of ectoparasites, parasitoids, and predators of bracken herbivores, including nearly 20 species of ants and spiders that form temporary symbiotic relationships with the bracken croziers.

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METHODS AND STUDY SITES

During 1980–1982, Gordon VanWoerkom (Hope College) and I observed the relationships between bracken fern and its associated arthropod community in Michigan. Our original intent was to determine to what extent seasonal patterns of insect species diversity are a reflection of quantitative or qualitative changes in the chemical composition of their host plant. We uncovered an arthropod community associated with bracken that is much more complex than expected. These arthropods were identified to species whenever possible, and their behavior was recorded by 16mm and 35mm cameras.

The bracken-arthropod study was conducted on four 100-m^2 plots of bracken occupying different environments within the confines of the Hope College Field Station. This 80 acre field station is located in Allegan County, 2 miles south of Holland, Michigan. The mild climate of the preserve is due to the thermal moderating effect of Lake Michigan. Primary vegetation consists of virgin forest, mature (second generation) deciduous forest, as well as open fields punctuated with sand "blow-outs" in various stages of ecological succession.

In upland areas, where the bracken plots are located, the soil consists of a relatively thin layer of sandy-loam topsoil overlying what was formerly extensive sand dunes from Lake Nipissing. Bracken fern has established extensive stands in discrete patches throughout the preserve, some under forest canopy and others under open field conditions.

RESULTS

Although predaceous ants and spiders are abundant during the spring, the diversity of herbivorous species is low, supporting Lawton's (1976) observation that, "The evidence strongly suggests that bracken in May and June may not be an easy resource for herbivores to exploit." However, protein levels are highest in the spring (about 25 percent of the dry weight) and 40 percent lower by August-September (about 10 percent of the dry weight). Furthermore, concentrations of lignins, tannins, and silicate are lowest in the early spring and tend to increase throughout most of the season, all of which might be expected to make the plants tougher and therefore less palatable. As Lawton (1976) further points out,

"...bracken-feeding herbivores face progressive deterioration in "food quality" as the growing season progresses." Yet, we have found that herbivorous species diversity and abundance, particularly of adapted herbivores, increase dramatically after the second week of June, and peak during late July and August.

Bracken's palatability early in the spring may also be affected by the production of thiaminase and the cyanogenic glucoside, prunasin (Jones and Firn, 1978). But bracken in England is polymorphic for the production of HCN: some bracken clones contain the B-glucosidase enzyme and not prunasin, while others contain neither enzyme nor the glucoside (Cooper-Driver and Swain, 1976; Cooper-Driver et al., 1977). Likewise, Zavitkovsky (1979) found uniformly negative results for cyanogenesis in Massachusetts bracken fern.

Thiaminase may be the only known chemical deterrent in bracken with any potential for disrupting normal insect development, since thiamine is essential to insect development (Dadd, 1973). However, bracken does contain thiamine (Berti and Bottari, 1968), and thiaminase activity in English bracken drops from a high of nearly 30 ug to 7 ug thiamine destroyed per min/g dry weight between the last week of April and the second week of May (Evans, 1976). Even so, populations of adapted bracken herbivores increase only after the second week of June in Michigan, perhaps weeks after cyanogenic glucosides (if functional) and thiaminase activity have fallen to low levels. By contrast, most other diapausing and temperature sensitive insects such as butterflies have eclosed from the pupae by early May in Michigan, and their larvae can be found by the second and third weeks of May.

Our study in Michigan suggests that bracken has evolved another line of defense that complements its biochemical defense system, and protects it from serious herbivorous damage during the rapidly-developing crozier stage. This second line of defense consists of predaceous arthropods, particularly ants and spiders attracted to a sweet, viscous fluid secreted by a number of axillary nectaries. The nectaries are dark oval enlargements that appear in the axils where the pinnae and major pinnules branch off from the rachis. Large numbers of "nonassociated" arthropods which utilize bracken for purposes other than food are also attracted to the developing bracken canopy and their oozing nectaries early in the spring. In turn, these nonassociated arthropods are preyed upon by the predaceous ants and spiders. Biochemical analyses of nectary secretions in California bracken indicate the presence of relatively large concentrations of glucose and fructose, minute concentrations of sucrose and maltose (Irene Baker and Peter Atsatt, pers. comm.), and an undetermined number of free amino acids.

By mid-May, when the primary nectaries at the axils of the pinnae are secreting microliters of "nectar" daily, the thiaminase activity is declining rapidly and the cyanogenic glucoside may or may not be offering protection. In addition, the levels of tannins and silicate are still at low levels, while proteins are at optimal level (Lawton, 1976). Thus, the crozier stage of bracken may at once present a nutritious stage to attack as well as a "loophole" in the biochemical arsenal. The potential for attack at this time by nonadapted polyphagous herbivores is great, and we have established that several nonadapted herbivores will feed readily on bracken croziers without ill effect. These include the gypsy moth, *Porthetria dispar* (L.) (Lepidoptera: Liparidae), the large milkweed bug, *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae), the common rose chafer, *Macrodactylus subspinosus* (Fabricius) (Coleoptera: Scarabaeidae), and a large tropical cockroach, *Blaberus giganteus* (L.) (Orthoptera: Blaberidae).

Many croziers are not attacked because their actively secreting nectaries are quickly located by at least five species of ants in Michigan: *Formica subsericea* Say, *Formica obscuriventris* Mayr, *Formica pallidefulva nitidiventris* Emery, *Camponotus pennsylvanicus* (De Geer), and *Camponotus nearcticus* Emery. *Camponotus pennsylvanicus, Formica obscuriventris,* and *Formica subsericea* in particular defend the nectaries and the developing crozier by patrolling the plant in a very systematic manner. An ant patrol typically begins after both primary nectaries at the base of the pinnae are antennated and sampled with the mouthparts for 1–3 minutes. The ant then proceeds up and down each pinna, investigating the pinnules and attenating the smaller nectaries even though these rarely secrete visible quantities of nectar. A single patrol, covering the entire frond, may last from 2 to 15 minutes, depending upon the size of the crozier and the length of the time spent at each nectary.

One ant, or several ants from the same colony may patrol a given crozier, but all other "intruding" arthropods are bitten and stung until they are driven off or killed by the patrolling ant(s). Corpses are removed and taken down to the nest. Patrolling predaceous ants thus obtain both a nutrient-rich secretion in addition to arthropod prey attracted directly to the plant tissues or to the nectaries. The result is that the croziers are protected (to an unknown extent) from adapted and nonadapted herbivores during this most susceptible stage of growth).

Species of smaller ants such as *Tapinoma sessile* (Say), *Leptothorax curvispinosus* Mayr, *Leptothorax muscorum* (Nylander) and *Lasius alienus* (Foerster) engorge at the nectaries as well, but often in non-aggressive interspecific groups. However, none of these species appears to defend the bracken croziers from other arthropods, and thus they may be "parasitic" in the broad sense of the concept since the ants obviously benefit by gathering nectar, but the bracken potentially suffers because it loses its attraction to more aggressively-defensive ants. Although we have not documented any defensive role by these small ants in Michigan, it is possible that they remove the eggs of herbivores (Susan Koptur, pers. comm.).

The immatures of at least 10 species of spiders also imbibe at or are attracted to the axillary nectaries, while several others are intimately associated with the unfurling pinnae. For example, when the immatures of *Enoplognatha ovata* (Clerck) bind the 3 pinnae together, the nectaries become effective "baits" within the pyramidal web, ensnaring many smaller nonassociated dipterans and parasitic ants. Other spiders such as the thomisid *Tibellus* sp. extend their body against the rachis, cepthalothorax pointing towards the nectary, and ambush other arthropods as they arrive to extract nectar. Finally, several species of salticid spiders (e.g. *Metaphiddipus protervus* Walckenaer), prowl the developing bracken canopy, leaping from pinna to pinna in search of prey. Encounters between spiders and patrolling ants are not uncommon, but it is not certain which factors predispose one or the other to dominate a given frond. However, the small parasitic ants are common prey items of the patrolling spiders in Michigan.

By the second week of June, the pinnae have completely opened, and the nectaries darken and desiccate. Even so, patrolling ants continue to defend the mature plants for a few more days, perhaps attracted to the lingering odor of the nectaries. But the ant patrols are erratic and the ants stay on the plants for far shorter periods, usually less than 30 seconds. At the end of June, defending ants and spiders cease patrolling the fronds entirely, although mature *Metaphiddipus protervus* spiders and *Formica subsericea* ants can occasionally be found on new croziers which emerge periodically throughout the growing season. As with spring croziers, these summer fiddleheads are also patrolled systematically by ants, even though their nectaries appear to dry quickly under the hot sun.

Concurrently with the declines in the ant patrols and the spider populations associated with bracken, there is a significant increase in herbivore damage, largely from adapted insects. Damage increases as adapted insect populations peak in mid to late summer, despite the "toughening" of the bracken with increasing concentrations of tannins and silicate, and despite the fact that available protein has declined by over 40 percent (Lawton, 1976). Any herbivore damage done at maturity, however, will affect proportionately less of the plant biomass than if the plant had incurred the damage during the crozier stage. Even minor chewing or sucking damage on the newly-emergent croziers can destroy part or all of the apical bud, or cause lodging of the plant at maturity if the rachis is weakened. Lodging or individual pinna or the entire frond is especially common in bracken plants attacked by minute gall-forming/mining microlepidopterans, as yet unidentified. These mining insects can stunt 50 to 90 percent of the potential growth of a given pinna, possibly because they feed on internal vascular tissues and cannot be reached by patrolling ants or predaceous spiders.

SUMMARY

Darwin (1877) was among the first to point out that the secretion of the bracken nectaries is very attractive to ants and that the ants may thus serve in some capacity to defend the ferns (Lawton, 1976). The arthropod defense system found in Michigan may help to explain why herbivorous damage from both adapted and non-adapted insects is minimal in the crozier stage. Bracken fern has a well-developed "arsenal" of potentially toxic secondary plant compounds that may also serve to deter or inhibit insects from attack. Yet, despite a relatively herbivorous-free period during its early growth stage, a diverse community of adapted herbivorous insects inflicts moderate to heavy damage later in the summer months.

Bracken may (in part) be protected by compounds such as thiaminase and cyanogenic glucosides, but our research of the past three years shows that bracken at the very least supplements its passive chemical defenses with a mobile, predaceous arthropod defense community. This community includes at least 5 species of ants and 10 species of spiders that are initially attracted to "axillary nectaries" (AN) secreting a nutrient-rich sap of sugars and amino acids. Our research shows that bracken "turns on" these nectaries during the rapidly-growing crozier stage, and turns them "off" after the pinnae are fully expanded. During the secretory stage, ants patrol and defend the pinnae from all intruders, including potential herbivores, other species of ants, and other predaceous arthropods such as spiders. However, the immature spiders also utilize the AN secretions, stalk arthropods within the developing canopy, or construct webs over the opening pinnae, turning them into effective traps with the AN enclosed as "baits."

Bracken's apparent immunity to insect attack during the crozier stage may be due not so much to the toxicity of its secondary compounds, but to the continuing coevolution of the AN and their attendant, predaceous arthropods that patrol the pinnae or otherwise rid them of herbivores during bracken's crozier stage. The bracken-arthropod system may be one of the most unique and complex hierarchies of symbiotic relationships to be found in a primitive plant-arthropod system.

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NATURAL HISTORY OF THE WORKERLESS INQUILINE ANT *POGONOMYRMEX COLEI* (HYMENOPTERA: FORMICIDAE)*

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At least 10 workerless inquiline ant species are known from North America (Francoeur 1968, 1981; Wilson 1971, 1976; Talbot 1976; Buschinger 1979; DuBois 1981; Snelling 1981), most only from original collections. In this paper I present field and laboratory observations of *Pogonomyrmex colei* Snelling a new, apparently workerless, inquiline ant inhabiting a colony of *Pogonomyrmex rugosus.*

P. colei appears to be a very rare species: extensive searching of the type locality for 4 yr has resulted in discovery of only a single colony. Nonetheless, observations on this colony provide insight into several important aspects of inquiline ant biology. *P. colei* is also of interest since it is the second apparently workerless congeneric inquiline inhabiting colonies of *P. rugosus*. Cole discovered the first inquiline species, *Pogonomyrmex anergismus,* near Silver City, New Mexico apparently prior to any major flight since he exposed "more than one hundred" inquiline reproductives upon opening the host nest (Cole 1954, 1968). Since host species mating flights occur soon after rain during mid to late summer (Hölldobler 1976; Rissing personal observation), it seemed reasonable to suspect *P. anergismus* responds to the same environmental cues for mating as does its host. Accordingly, in an effort to rediscover *P. anergismus*, I routinely checked most *P. rugosus* nests on a 25 ha study area in Boulder City, Nevada for flight activities and possible presence of inquilines during late summer 1978 and 1979 (study area described in Rissing 1981). *P. colei* was discovered during this effort.

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OBSERVATIONS

Mating Activities and Season. Five *P. colei* males were collected at a single *P. rugosus* nest during the morning of 13 August 1978; a series of thunderstorms and rain had occurred 12 hr earlier. Frenzied host worker activity suggested a mating flight or similar activity occurred immediately prior to my arrival. No flights of either species occurred at any nearby *P. rugosus* nests observed simultaneously.

I observed a complete inquiline and host flight at this same nest on 15 September 1978 following an extensive rain storm the preceding day. Flights were occurring at 2 of 23 nearby *P. rugosus* nests; *P. colei* was not found at any other nest. Mating activities began with accumulation of several hundred host workers in and around the nest crater. These workers pugnaciously defended the area throughout both flights as is typical during *P. rugosus* flights (Rissing, personal observation). As ground and air temperatures increased male *P. colei* climbed to the crater and were soon joined by much larger females. While both sexes of *P. colei* are winged, mating occurred at the nest entrance followed by females flying from the area and males re-entering the nest. Such *in situ* mating is common in rare ant species apparently due to very low probability of reproductives finding individuals from other nests with which to mate (Wilson 1963). Following copulation and departure of *P. colei* females, male and female *P. rugosus* flew from the crater as the temperature continued to climb. Reproductive forms of *P. rugosus* fly to a site away from the nest and copulate there (Hölldobler 1976). Mating activities of host and inquiline were separated by at least 30 min and, perhaps more importantly, 3° C ground temperature (Table 1). Reproductive forms of each species were seen occasionally in the nest entrance during the mating activity of the other. On at least one occasion, *P. colei* males tried unsuccessfully to mount a *P. rugosus* female. During this flight I observed no differences in behavior of host workers to host or inquiline reproductives. *P. rugosus* workers frequently encircled copulating pairs of *P. colei* and frantically ran around them, although they never interfered.

During 1979 routine observations were begun at the study area on 18 September. A complete *P. colei* flight was observed at the host nest during the afternoon of 30 September immediately following a trace of rain. No flights of either species were observed at 35 nearby *P. rugosus* nests during this time. On 8 October 1979 I poured approximately 7.5 l of water directly onto the host nest crater resulting in an immediate flight of *P. colei.* This procedure was repeated unsuccessfully on 17 and 18 September 1982. Viability of the host nest (as determined by worker activity, size of crater and refuse pile, and absence of plants growing in the crater) has remained constant and similar to that of nearby *P. rugosus* colonies from 1978 to 1982. I have never observed any forms that might be considered *P. colei* workers.

Colony foundation. Ten newly mated *P. colei* females from the 15 September 1978 flight were placed into a 7.5 m high flight enclosure made of plastic sheeting and permitted to fly. Subsequent to this all females removed their wings but did not dig burrows when placed into laboratory nest boxes containing moist sand. Five of these dealate inquilines were transferred to 5 laboratory nests containing only newly mated *P. rugosus* queens. These *P. rugosus* queens had been collected one week earlier at a mating site 3.2 km from the host nest making it unlikely that they were related to the host colony. Four of these laboratory nests contained a single, mated dealate *P. rogusus* queen; the fifth contained two *P. rugosus* queens. The *P. colei* queen added to the nest with two *P. rugosus* queens was immediately attacked and removed from the glass tube occupied by the *P. rugosus* queens. Of the *P. colei* queens added to the single queen *P. rugosus* colonies, one was found dead within several hours (decapitated), and the other was found dead (entire) 5 d later. The other two *P. colei* queens lived peacefully along side the *P. rugosus* queens for at least a month. During this time I frequently observed the *P. colei* queens grooming the *P. rugosus* queens; *P. rugosus* queens did not reciprocate. These last two colonies ultimately failed during (or possibly in response to) transportation from Boulder City to Seattle.

Five other newly mated, dealate *P. colei* queens were released in the field at the entrance of large, active *P. rugosus* colonies near the host nest. Inquilines were always removed immediately from the nest by one or more workers and dropped several meters from the crater. The *P. colei* queens made no attempt to re-enter these nests following removal.

DISCUSSION

Repeated (and continuing) attempts to find *P. colei* or *P. anergismus* around Boulder City, NV, or Globe, AZ, where a single *P. colei* male has been collected (Snelling 1981) have yet to be successful. Nonetheless, observations of *P. colei* from the type nest in Boulder City provide insight into several questions of general inquiline biology including possible method of inquiline entry into host colonies and fate of host queen.

Inquiline entry into host colonies. Newly mated *P. colei* queens are accepted into 1 week old workerless host nests in the laboratory, while they appear incapable of entering established host nests in the field (see above). Similar observations have been made in laboratory experiments with the inquiline *Plagiolepis xene* and its host, *Plagiolepis pygmaea* (Passera 1964). This suggests that at least some inquiline species enter a host colony at the founding stage prior to production of any workers. That this may occur in the field is supported by discovery of a workerless inquiline queen (*Strumigenys xenos*) in an incipient host colony containing one queen, brood and a single worker of *Strumigenys perplexa* (Brown 1955).

If entry into host colony commonly occurs at host colony foundation in some species of inquilines, overlap with host species flight season would be advantageous. Since all nests of a given species in a locality tend to have a longer "flight season" than any single nest (e.g. for *P. rugosus* see Hölldobler 1976), the inquiline might further be expected to lengthen its flight season relative to that of its host colony to take advantage of the entire flight season and availability of founding nests in its locality. The extended flight season of *P. colei* relative to that of *P. rugosus* may occur for these reasons. Similarly, occurrence of *P. anergismus* reproductives during mid September in the type nest reported by Cole (1954, 1968) may also indicate inquiline-host reproductive overlap.

Fate of host queens. Simultaneous production of host and inquiline reproductives during the 1978 flight (Table 1) strongly suggests coexistence of host and inquiline queen(s) at that time. Continuing existence of the host colony until at least September 1982 further substantiates this. Estimates of maximum longevity of worker ants is 1-2 yr (Rosengren 1971, Brian 1972, Nielsen 1972). Further, there has never been a reported case of queen adoption in any *Pogonomyrmex* species. For the host colony to have a normal foraging

Table 1. Summary of mating activities of *P. colei* and *P. rugosus* in Boulder City, Nevada, 15 September 1978.

Time	Ground Temp. °C[1]	Air Temp. °C[2]	Activity
08:55			Reproductives of both species in nest entrance
09:10	20.5	20.5	*P. colei* reproductives on crater
09:37	21.0	21.5	Number of *P. colei* increases
10:03			First *P. colei* copulation
10:45	26.0	23.8	First *P. colei* female flies
12:15	29.2	25.5	Last *P. colei* female flies
12:47	32.6	26.4	First *P. rugosus* male and female fly
13:15	33.4	30.8	Last *P. rugosus* flies

[1] Temperature as determined by holding tip of a Yellow Springs Instruments direct read thermistor (YSI #405) on ground surface; temperature read on a Yellow Springs Instruments telethermometer (YSI #43TA).

[2] Temperature determined as above with thermistor 30 cm above ground and shaded.

group size in 1982, the host queen must have been alive during the 1978 and 1979 inquiline flights. Although inquiline-host coexistence has been regarded as a "primitive" inquiline trait (Wheeler 1933, Haskins and Haskins 1964), it offers the obviously adaptive advantage of a continuously renewed host worker force for the inquiline. Coexistence occurred in the type nest of *P. colei* and appears common in other workerless inquiline species where information regarding fate of host queen(s) is available (Table 2).

Host queen elimination does occur in at least two well documented cases (Table 2). Wilson (1971) suggests such behavior may develop in short-lived inquiline species; inquiline longevity, however, may be more of an effect than a cause of this behavior. Host queen elimination may be adaptive only when inquiline entry is gained by a queen after development of a host worker force. Host workers appear to be the primary defense against inquiline entry in many colonies. In order to be accepted by host workers, it may be necessary for the prospective inquiline queen to first render the prospective host colony queenless. In those cases where host queens are known or highly suspected of being eliminated (Table 2), the inquiline queen enters an established colony containing workers. In at least one of these cases, *Epimyrma vandeli*, the inquiline must fight with host workers until she is able to kill the host queen. Recent discovery that *E. vandeli* is a degenerate slave-maker

Table 2. Fate of host queen(s) for workerless inquilines. Only those species whose host queen(s) fate is known are listed.

Inquiline species	Host species	Fate of host queen(s)	Reference
MYRMECIINAE			
Myrmecia inquilina	*Myrmecia vindex*	survives	Douglas and Brown 1959 Haskins and Haskins 1964
MYRMICINAE			
Myrmica hirsuta	*Myrmica sabuleti*	survives	Elmes 1974a, 1978
Sifolinia laurae	*Myrmica sabuleti*	survive	Brian 1972
Pogonomyrmex colei	*Pogonomyrmex rugosus*	survive*	this study
Anergates atratulus	*Tetramorium caespitum*	apparently killed by host workers	Wheeler 1910, Crawley 1912, Donisthorpe 1915, Creighton 1950
Teleutomyrmex schneideri	*Tetramorium caespitum*	survives	Stumper 1950+, Kutter 1969
Leptothorax kutteri	*Leptothorax acervorum*	survive	Buschinger 1965
Leptothorax minutissimus	*Leptothorax curvispinosus*	survive	Smith 1942, Buschinger 1981
Epimyrma vandeli	*Leptothorax nigriceps*	killed by inquiline	Vandel 1927 Stumper and Kutter 1951
Doronomyrmex pacis	*Leptothorax acervorum*	survive	Kutter 1945+, 1969+
Monomorium pergandei	*Monomorium minimum*	survive*	Creighton 1950
Doronomyrmex pocahontas	*Leptothorax muscorum*	survive*	Buschinger 1979
Monomorium adulatrix	*Monomorium salomonis*	killed by host workers	Wheeler 1910 Forel 1930

Table 2. Continued.

Inquiline species	Host species	Fate of host queen(s)	Reference
Monomorium talbotae	*Monomorium minimum*	survives	Talbot 1979
Strumigenys xenos	*Strumigenys perplexa*	survive	Brown 1955, Taylor 1967
FORMICINAE			
Plagiolepsis xene	*Plagiolepsis pygmaea*	survive	Le Masne 1956; Passera 1964, 1966, 1972
Aporomyrmex ampeloni	*Plagiolepis vindobonensis*	survives	Faber 1969+

*Presence of host queen(s) determined by presence of host reproductives
+Cited in Wilson (1971)

(Buschinger 1981, Buschinger and Winter 1982) may explain this behavior which is rather unusual among most other inquilines (Table 2). Only the extreme inquiline *Teleutomyrmex schneideri* is known to enter established host nests without having to eliminate host queens; these inquilines may produce a substance highly attractive to host workers (reviewed in Wilson 1971).

Comparison with P. anergismus and other workerless inquilines. P. colei may represent an intermediate form between its host *P. rugosus* and the closely related workerless inquiline *P. anergismus* (for a complete discussion of morphological differences see Snelling 1981). Discovery of *P. colei* adds the genus *Pogonomyrmex* to a growing list of ant genera with more than one workerless inquiline species (Table 2). Such "concentration" of inquilines into a few genera may occur either due to non-random search by myrmecologists (*P. colei* was discovered during an intentional search for *Pogonomyrmex* inquilines) or because certain genera are more likely to give rise to inquilines. The basic biology of the inquiline-rich genera, however, is quite variable suggesting several evolutionary routes may lead to workerless inquilinism. The genus *Leptothorax*, for example, has small, ephemeral colonies subject to slave raids from numerous species and has given rise to several closely related *Epimyrma* inquiline species, themselves degenerate slavemakers (Buschinger 1981, Buschinger and Winter 1982). *Myrmica*, on the other hand, has larger colonies and many species that are highly polygynous (Brian 1972; Elmes 1974a,b); this genus has given rise to at least 7 workerless inquiline species: *Myrmica faniensis* (van Boven 1970), *Myrmica hirsuta* (Elmes 1974a, 1978), *Myrmica lampra* (Francoeur 1968, 1981), *Myrmica myrmecophila* (Bernard 1968), *Myrmica quebecensis* (Francoeur 1981), *Sifolinia karavajevi* (Kutter 1969) and *Sifolinia laurae* (Brian 1972), the *Sifolinia* species likely being congeneric with the other *Myrmica* species (Elmes 1978). *Monomorium* is similar with polygynous species (Dennis 1938, Cole 1940, Gregg 1945) and a number of congeneric inquilines (reviewed in Wilson 1971, see also Talbot 1979 and DuBois 1981). These inquiline species may have evolved through a process of some polygynous host queens acquiring the trait of laying only reproductive eggs (Buschinger 1970, Elmes 1978). To this list must be added the genus *Pogonomyrmex* whose basic biology is unlike any of the above three host genera. Colonies are substantially larger than *Leptothorax, Myrmica* or *Monomorium* (Lavigne 1969, Rogers et al. 1972, Whitford et al. 1976, MacKay 1981), strictly monogynous (Lavigne 1969, Hölldobler and Wilson 1977, MacKay 1981), with no slave-making or similar behavior in any species. Evolutionary processes giving rise to *P. colei* and *P. anergismus* are likely different from those that have given rise to the *Leptothorax, Myrmica* or *Monomorium* inquilines. Certainly, the idea of multiple evolutionary pathways leading to workerless inquilinism is not new (see Wheeler 1919, Buschinger 1970, Wilson 1971). Continued study and search for workerless inquilines can only serve to clarify this challenging evolutionary process.

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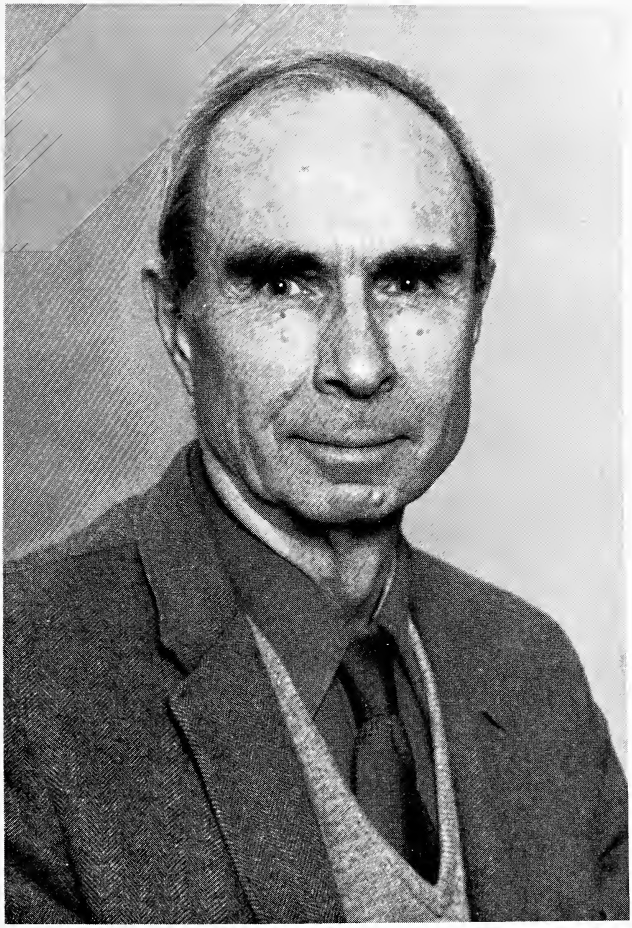

PHILIP JACKSON DARLINGTON, JR.
PHOTOGRAPH TAKEN IN 1971

This issue of Psyche is dedicated to the memory of Philip J. Darlington, Jr., who died in his 80th year in Cambridge, Massachusetts, on December 16, 1983.

I first met Philip Darlington at a meeting of the Cambridge Entomological Club on January 8, 1924, held at the Bussey Institution. The event was a significant one for us. We were both undergraduates in the same class at Harvard College and for the next sixty years we remained close friends, as well as colleagues in the Museum of Comparative Zoology.

Philip was very active in the Club. He was secretary in 1931, vice-president in 1933 and 1940, and president in 1934, 1941, and 1946, and a member of the editorial board of Psyche for thirty years. His first talk at a Club meeting, in March, 1927, was an account of insect collecting at the Harvard Tropical Laboratory in Soledad, Cuba. At many other meetings over the years we enjoyed hearing about his research and his field trips in Australia, New Guinea, and Colombia, as well as on various Caribbean islands.

He was born in Philadelphia in 1904. After attending Exeter Academy in New Hampshire, he entered Harvard University, from which he received his A.B. degree in 1926 and his Ph.D. in 1931. The following year he was appointed Assistant Curator of Insects in the Museum of Comparative Zoology. In 1939 he became the H.C. Fall Curator of Coleoptera, and in 1952 he assumed the position of Curator of Insects, which he held until his appointment as Alexander Agassiz Professor of Zoology. He retired in 1971.

Although Philip was primarily an entomologist and chiefly concerned with Coleoptera, he had very broad interests in all aspects of natural history. His knowledge of plants and of all vertebrate groups was extraordinary. With such interests he was inevitably led into studies on evolutionary theory and especially zoogeography, on which he published several outstanding books and numerous technical papers.

Frank M. Carpenter, editor

PSYCHE

Vol. 90 1983 No. 4

THE BIOLOGY OF *MYRMOXENUS GORDIAGINI* RUZSKY, A SLAVE-MAKING ANT (HYMENOPTERA, FORMICIDAE)

By

Alfred Buschinger,[1] Ursula Winter,[1] and Walther Faber[2]

Introduction

Myrmoxenus gordiagini was described by Ruzsky (1902) from material which he had collected in the Akmolinsk area in Soviet Russia, near the town of Koktschetaw. The ant was always found living together with a newly described host species, *Leptothorax serviculus* Ruzsky. The colonies inhabited narrow galleries between and underneath small stones in the rocky slopes of a hilly region, with some birch and spruce trees. Finzi (1924) described a subspecies, *Myrmoxenus gordiagini menozzii*, from the Yugoslavian peninsula of Istria. Only one male and one female were found within moss and soil at the foot of an oak tree, together with numerous females and workers of *Leptothorax unifasciatus* (Latreille). Finzi therefore believed that his new subspecies was living with that host species. Finally, in 1925, Soudek established a new genus, *Myrmetaerus*, for a new species, *microcellatus*, that he had collected near Kotor in Dalmatia, Yugoslavia. Although he explicitly discussed the close relationship of *M. microcellatus* with *Myrmoxenus*, he described this ant as representing a new species and genus "as a provisional arrangement" (Soudek, 1925). *M. microcellatus* was found under a stone in a deciduous forest, in a mixed colony with *Lepto-*

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[2] Dr. Walther Faber, Vienna, died in June, 1979. Among his papers we found a description of the colony foundation behavior of *M. gordiagini*, and also some important information on localities where he had collected this species.

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thorax nylanderi (Förster). All our material also was collected in Istria, and in the Dalmatian island Krk[3]. Since the descriptions of all the three forms mentioned above are nearly identical, we assume that *Myrmetaerus microcellatus* and *Myrmoxenus gordiagini menozzii* are junior synonyms of *Myrmoxenus gordiagini*. We have been unable, however, to check the type material.

Nothing has been known of the biology of *Myrmoxenus*/*Myrmetaerus* except the fact that they were always found living together with a host species belonging to the genus *Leptothorax* Mayr, subgenus *Myrafant* Smith (1950), and thus apparently represent socially parasitic ants. W. Faber in 1972 recorded some observations on their colony foundation behavior. Recently we found out that *M. gordiagini* is a slave-making ant. The results of our experiments are presented in the following sections.

MATERIAL AND METHODS

W. Faber collected a total of three *Myrmoxenus* colonies on 25 May 1972, on the slopes of a small valley NW of Baška, Krk. In the very same locality we found nine additional colonies between September 23 and 26, 1981. Another locality, where we gathered two colonies on 4 August 1976, and one colony on 22 September 1981, is near the ruined town Dva grada, a few kilometers east of Rovinj in Istria, and just 35 km south of the type locality of *M. gordiagini menozzii*. Ten of these 15 colonies contained a *Myrmoxenus* queen; presumably the queens of the other five colonies were either lost during collecting or were missing prior to our collecting. *Myrmoxenus* workers were present in varying numbers up to about 40 (exact numbers cannot be given since all colonies were kept alive for several breeding seasons, and thus produced additional workers). Two colonies contained only a queen and no workers; supposedly they were newly founded.

Male and female as well as worker pupae were present in the colonies collected on August 4, 1976, and a few adult sexuals were found in field colonies on September 22 and 23, 1981.

[3] Recently we found an additional population on the island Rab, south of Krk. Four colonies were collected on October 2, 1983, in an oak forest south of Suha Punta. They contained one queen each, and in one colony we found two additional females that were dealate but not inseminated.

The host species in all 15 colonies was *Leptothorax lichtensteini* Bondroit 1918. Up to about 200 host workers were found in the *Myrmoxenus* colonies. Nest sites were underneath small, flat stones in the soil, or in crevices between such stones. A common, and, in our opinion, quite important character of the *Myrmoxenus* habitats is the fact that they all were situated in rather shady places in a deciduous forest or in the underbrush. We cannot reconstruct the exact experimental device by which W. Faber studied the colony founding behavior. From his records we conclude that the colonies, which he had collected in May, produced sexuals until September. On September 9 and 22, 1972, he noted "strong flight activities," and numerous *Myrmoxenus* females were dealate in the nests and arenas. Several times he put five dealate *Myrmoxenus* females together into the feeding arenas of *L. lichtensteini* colonies. Others were placed into formicaries with different *Leptothorax* species.

Our newly collected colonies from 1976 and 1981 were kept in formicaries and under artificial daily and annual temperature cycles as described by Buschinger (1973, 1974, 1982) and Winter (1979a). For initiating slave raids, we used arenas as depicted by Winter (1979a) and Buschinger et al. (1980). During the raids the room temperature was about 27°C. Contrary to our experiences with *Harpagoxenus* or *Epimyrma*, which need bright sunshine or at least blue sky for raiding, the *Myrmoxenus* seem to prefer a clouded sky. Thus, the first raid which we observed in our labroatory took place on a cloudy day; for the second one, on a sunny day, we closed the window shades.

Colony Founding by *MYRMOXENUS GORDIAGINI*

As indicated above, we rely on the quite brief notes of W. Faber, who observed colony founding by *M. gordiagini* females in 1972. According to these notes, the young *Myrmoxenus* queen enters a host species colony (*L. lichtensteini*), apparently soon after mating and dealation, in late summer. Most *Myrmoxenus* females were attacked and often killed by workers of the host species. In a few experiments, however, a parasitic queen survived the attacks and at last was accepted by the host species workers. She then assaulted the host species queen in a very characteristic manner (Fig. 1). She grasped the *Leptothorax* queen's "throat" with her mandibles, and

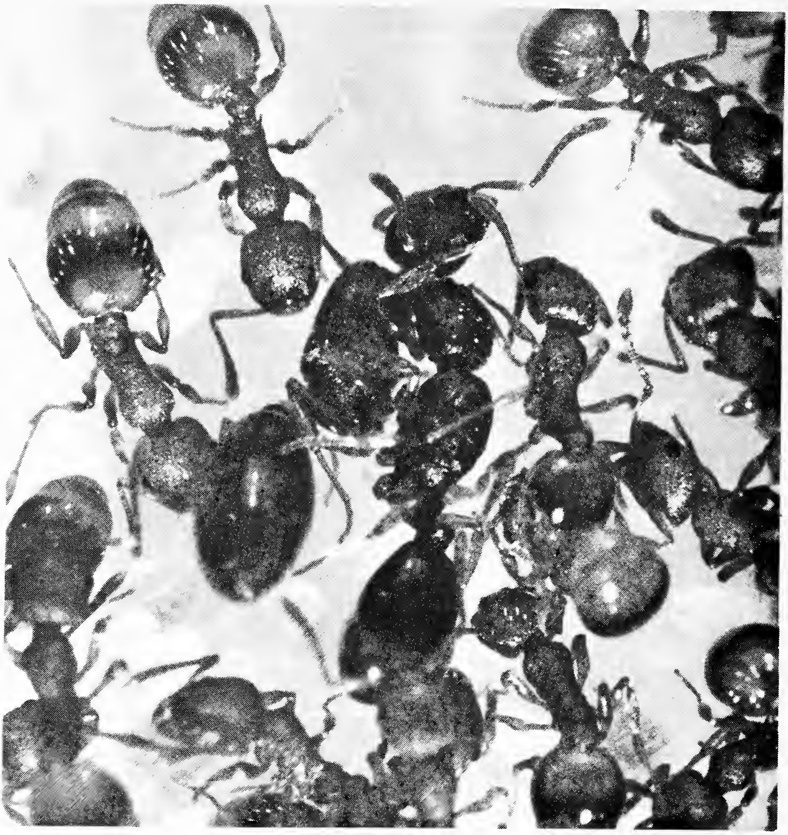

Fig. 1. A queen of *Myrmoxenus gordiagini* (right) is throttling the host species queen during colony foundation (photograph: Faber).

throttled her repeatedly, and often for several hours, as was described for *Epimyrma ravouxi* females (Gösswald 1930). Other *Myrmoxenus* queens were seen to throttle the *Leptothorax* queens by seizing their necks from the back. Like *Epimyrma stumperi* females (Kutter 1951) the *Myrmoxenus* queens also scent themselves by first rubbing their legs over the surface of the victims, and then over their own backs. Sometimes the *Myrmoxenus* queens throttled some host species workers, too, or stung them to death. Furthermore, they attacked the alate *Leptothorax* females which were present in the nests, and killed some of them. In one *L. lichtensteini* colony, where five *Myrmoxenus* females had been put on September 12, the *lichtensteini* queen was dead on September 17, and one surviving *Myrmoxenus* female was observed to bite the large queen larvae of the host species.

Experiments with *L. parvulus* (Schenck 1852) as host species did not succeed; the *Myrmoxenus* queens were all killed.

SLAVE RAIDS OF *MYRMOXENUS GORDIAGINI*

We observed two slave raids of one *Myrmoxenus* colony, on June 24 and July 7, 1982. The colony was collected in September, 1981. After an artificial hibernation from 12 December 1981, in a constant 6° C until 22 April 1982, the colony began to bring up its larvae. The first prepupae appeared on 4 June, six weeks after the end of hibernation, the first worker and sexual pupae were recorded on 11 June. Sexuals hatched towards mid-July, after the raids, and sexual activity was observed in the beginning of September. A second colony, which was kept under identical conditions, exhibited some scouting activity between June 4 and 25, but did not conduct a raid.

The first colony was put into an arena on 4 June. Simultaneously a colony of the host species, *L. lichtensteini*, was placed into another part of the arena, which was subdivided by a plastic wall.

No *Myrmoxenus* workers were seen outside the nest until 22 June.

On June 23 and 24, between one and three *Myrmoxenus* workers appeared in the arena. Scouting occurred between 1000 and 1500 on June 23. On June 24, a hole in the separating wall of the arena was opened, and a *Myrmoxenus* scout found the way through to the host species territory at 1740. At 1754 this scout ran across the *lichtensteini* nest. It returned to the *Myrmoxenus* nest, entered there at 1804, and suddenly a mass of ants was whirling around inside the nest entrance.

At 1808, a file of about 20 *Myrmoxenus* came out of the nest (Fig. 2) and walked across the arena towards the hole. Sometimes the procession stopped, milling around, apparently until the leading scout had found its way again.

At 1905 the group had reached the entrance of the target nest, and entered it one after the other. Almost no fighting could be observed. After 6 minutes, the *lichtensteini* queen and most of the workers had left their nest, carrying a few small larvae and eggs. Only two *Leptothorax* were stung. Some *Myrmoxenus* workers

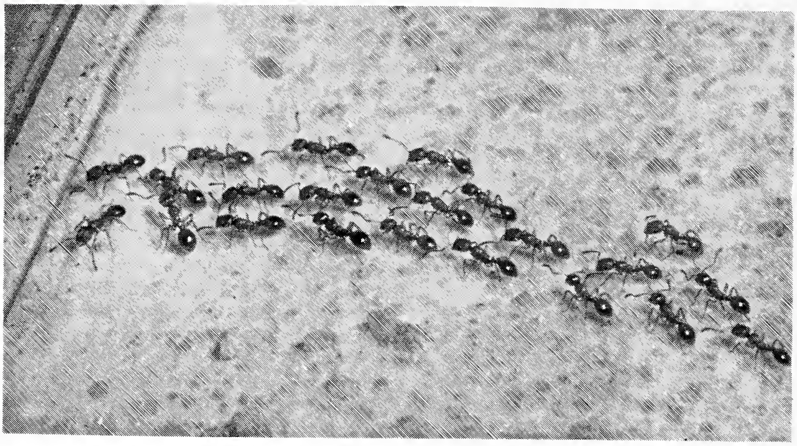

Fig. 2. A raiding party of *Myrmoxenus gordiagini* has just arrived at the nest of the host species (photograph: Buschinger).

returned to their own nest, and at 2030 another file of 5 *Myrmoxenus* arrived at the *Leptothorax* nest. By the next morning, the *Myrmoxenus* colony had moved into the former *Leptothorax* nest.

The arena was then subdivided again, and a new *Leptothorax* nest was placed in the position of the former *Myrmoxenus* nest.

The second raid, in the same arena, was observed two weeks later, on 10 July. Scouting began at 0830 and a successful scout returned to the *Myrmoxenus* nest at 0912. However, in this case, a file did not form before 0933. At 1009 a total of 14 *Myrmoxenus* arrived at the target nest, entered it at 1012, and a few minutes later they had overwhelmed the colony and were in possession of its brood. Eight *Leptothorax* were immediately stung to death. Contrary to the first raid, this time the *Myrmoxenus* soon began to carry pupae and large larvae back into their own nest. One returning *Myrmoxenus*, at 1150, led a further file of 15 conspecifics to the raided nest. At 1320 the *Leptothorax* nest was empty except for a few eggs and one *Leptothorax* male. A total of 26 dead *Leptothorax* workers were counted in the arena, indicating that during this raid more fighting had occurred than during the first one.

DISCUSSION

Our results, despite the low number of raids observed, reveal that *Myrmoxenus gordiagini* is a slave-making ant. The organization of the raids is essentially the same as in *Epimyrma ravouxi* (André) (Winter 1979b, Buschinger et al. 1980), and in the North American *Leptothorax duloticus* (Wesson 1940), with group recruitment and sting fighting.

The colony foundation behavior of *Myrmoxenus* also corresponds to that observed in several species of the genus *Epimyrma* (Kutter 1951, Gösswald, 1930, Buschinger and Winter, in press), where the queens throttle the host species queens.

The only major difference between *Myrmoxenus* and *Epimyrma*, therefore, pertains to antennal segmentation. *Myrmoxenus* females and workers have 12-segmented antennae (males 13), like their host species group, whereas *Epimyrma* has 11-segmented antennae (males 12). We have not yet decided whether this difference can really justify the maintenance of the two genera; however, we are convinced that the very particular raiding and colony foundation behaviors have a monophyletic origin.

We are not entirely certain that *Myrmoxenus gordiagini* is the correct name of our ants. That they are identical with Finzi's *M. g. menozzii* (1924) seems assured, since they were collected in the same area. We are also sure about the identity of this *M. g. menozzii* with Soudek's (1925) *Myrmetaerus microcellatus*. However, if a later revision reveals that *M. gordiagini* Ruzsky and *M. g. menozzii* Finzi were two different species, then our material should be named *M. menozzii*.

The different host species recorded for the three "forms" represent a minor problem. Slave-making ants often have more than one host species. Thus, *Epimyrma ravouxi* (André) enslaves *Leptothorax unifasciatus* (Latr.), *L. nigriceps* Mayr, and *L. affinis* Mayr, sometimes having two slave species together within one colony (Gösswald 1930). It is also quite conceivable that both Finzi and Soudek found their ants, as we did, with *L. lichtensteini* as host species; *L. lichtensteini* has a superficial resemblance to *L. unifasciatus*, and it is quite often confused with *L. nylanderi*.

SUMMARY

Myrmoxenus gordiagini Ruzsky from Dalmatia, Yugoslavia, conducts slave raids with group recruitment and sting fighting.

Young queens enter the host species colonies (*Leptothorax lichtensteini* Bondroit) and kill the *Leptothorax* queens by throttling them. These biological features correspond well with those observed in the genus *Epimyrma*.

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TEMPERATURE-INDUCED CHANGES IN THE CALLS OF THE GREEN LACEWING, *CHRYSOPERLA PLORABUNDA* (NEUROPTERA: CHRYSOPIDAE)*

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Animals communicate acoustically in many different ways and for many different purposes; in fact, a vast literature exists on the subject, and comprehensive efforts to summarize current knowledge have not been attempted since the early 1960's (e.g., Lanyon and Tavolga 1960, Busnel 1963). Insects are especially rich in singing or noise-making species, and it seems likely that every insect order will eventually prove to include acoustically active taxa. Neuroptera has long been regarded as a "silent" order of primitive, behaviorally simple insects. However, recent work suggests that many, if not most, species of the large neuropteran family Chrysopidae are characterized by complex courtship displays accompanied by a specialized form of acoustical signalling (Smith 1922, Toschi 1965, Ickert 1968, Henry 1979 and 1983b). Such lacewing calls or songs are not acoustical in the traditional sense, but instead consist of species-specific substrate-borne vibrations produced by vigorous, stereotyped jerking motions of the insects' abdomens: a phenomenon known as tremulation in other insects (Morris 1980; Henry 1980a, c), and found also in the ancestral neuropteroid taxon Megaloptera (Rupprecht 1975). Calling behavior is most elaborate in *Chrysoperla* Steinmann; conspecific males and females of species within that genus cannot mate without first reciprocally exchanging similar or identical vibrational signals in a prolonged courtship duet (Henry 1980b, 1983b). The best studied species in this regard is *Chrysoperla plorabunda* (Fitch), a common North American form that for some years was considered synonymous with the morphologically identical Eurasian species *Ch. carnea* (Stephens) (Tjeder 1960, Henry 1983a). Both sexes of this species, when sexually

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receptive, produce brief, repetitive volleys of low-frequency abdominal vibration at (approximately) one-second intervals for up to several minutes at a time (Henry 1979, 1980c); in heterosexual duets, the two partners alternately and repeatedly exchange single volleys until copulation is achieved. Each volley in *Ch. plorabunda* is characterized by a smoothly increasing and then decreasing amplitude envelope and by pronounced frequency modulation (see Fig. 1): the rate of abdominal vibration gradually declines to less than half its initial value during the course of the volley (Henry 1980c).

Green lacewings of the genus *Chrysoperla* are unusual among acoustical animals in that females are just as likely to sing as males (Henry 1983b). In contrast, males alone (or principally) sing and call conspecific females to them in most species of the best studied animal taxa like birds (Catchpole 1982), lizards (Frankenberg 1982), frogs (Littlejohn 1977), katydids (Dumortier 1963), homopterans (Ossiannilsson 1949, Young 1980), and crickets (Walker 1962, Dumortier 1963). Such unilateral male signalling has been interpreted in most acoustical animals as indicative of sexual selection operating on the higher variance in reproductive success of males (Halliday 1978, Otte 1974, Alexander 1975). On the other hand, the unusual presence of calling behavior in both sexes of *Chrysoperla* species may stem from the proven importance of their vibrational signals in the reproductive isolation of closely related species. For example, neither of the sibling, interfertile species *Ch. plorabunda* and *Ch. downesi* (Banks) will respond to the song of the other, thus precluding courtship duets and preventing interspecific mating under natural conditions (Henry 1983b). If such signals are to be effective as reproductive isolating mechanisms, however, they must remain unambiguous to recipients over the wide range of temperature typically experienced by lacewings in the field. Abundant documentation exists of gross alteration in chirp rate, wing-stroke frequency, pulse or chirp duration, or call notes by temperature changes in many taxonomically disparate insect groups (Brooks 1882, Hayward 1901, Alexander 1956, Walker 1962, Dumortier 1963, Shaw 1968, Booij 1982), and similar temperature-related changes should be characteristic of lacewing songs (see Henry 1982b for preliminary work on *Chrysopa oculata* Say). One would also predict that the calls of the two sexes of a given species of *Chrysoperla* should vary in a closely parallel fashion over a wide range of temperatures, since mutual recognition of highly specific call features is so important to the reproductive success of both members of each courting pair. Here, I report on the effects of temperature change on the principal parameters of the calls of individual male and female *Chrysoperla plorabunda* from North America. This paper also contains the first complete description of the frequency structure of the abdominal volleys of that species, together with an experimental analysis of the effects of abdominal mass on frequency characteristics. Regressions of call parameters against temperature in *Ch. plorabunda* are compared with those described for other singing insects, in an attempt to identify any unifying principles.

MATERIALS AND METHODS

A breeding colony of *Chrysoperla plorabunda* was started in the fall of 1982 from seven males and ten females collected in a field of senescent goldenrod (*Solidago* spp.) at Storrs, Connecticut. Subsequently, adults were maintained on a Wheast™/sucrose diet while larvae were fed ether-killed *Drosophila* spp. (see Henry 1979, 1983a for details). Males for experimentation were drawn from second-generation laboratory stock, while females were third-generation insects; five unmated individuals of each sex were acoustically monitored at various temperatures between 19.5° C and 29.8° C. For each of five call characteristics of interest, I analyzed an average of 40 volleys of abdominal vibration per individual, delivered at three to six different temperatures between the extremes mentioned above; in no case was a regression line for an individual based upon fewer than 18 volleys. Temperature was monitored within 25 cm of the calling insects, and was controlled by heating and cooling an entire 120 cubic meter room.

Lacewings were induced to call either by playing back to them cassette tape recordings of conspecific signals or by simulating such signals by means of a sweeping audio frequency generator (Tektronix™ FG 507) gated by a physiological stimulator (Harvard ™ 340). Patterns of abdominal vibration were detected and analyzed with techniques and equipment described in other papers (Henry 1980a, 1982b). Details of call parameters were obtained from Polaroid ™ photographs of oscilloscope tracings, using conventional overlay methods.

Several individuals of *Ch. plorabunda* from a breeding colony of different geographical origin were selected for use in experiments testing the effect of abdominal weight on vibrational frequency. This stock was bred from five males and five females collected in the sagebrush country of southwestern Idaho on 24 May, 1983 by Dr. James Johnson (University of Idaho). I tested one field-caught male, two first-generation laboratory males, and one first-generation laboratory female for the frequency characteristics of their calls at two different temperatures; after ascertaining that all were essentially identical to one another and to Connecticut *plorabunda* in those characteristics, I weighed each individual to the nearest tenth of a milligram on a Mettler™ H6T or Sartorius™ 1212 MP balance and added weight to the middle of their abdomens, using water-based Liquid Paper™. Mass-loaded specimens were then reweighed and tested again for the vibrational frequencies of their calls at temperatures in the 25-30°C range. All such frequency values were also adjusted to 27°C using linear regression C in Fig. 3.

Curve-fitting of paired variables to linear, exponential, or logarithmic functions employed a program designed for a Hewlett-Packard™ HP-25 pocket calculator. Any reference in the Results or

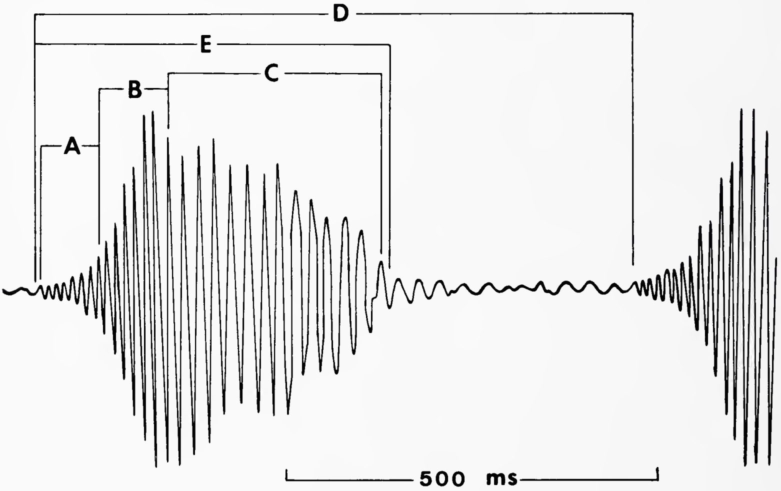

Figure 1. Detailed fragment of the call of *Ch. plorabunda*, re-drawn from an oscilloscope tracing, showing principal parameters A–E defined in text. A = initial volley frequency, B = median volley frequency, C = terminal volley frequency, D = volley repetition rate, E = volley duration.

Discussion sections to "significant differences" indicates that the means of two normally distributed samples were demonstrated to differ from one another by a 2-tailed t-test using confidence limits of 95% or better. Values following a +/− sign are one standard deviation of the mean.

RESULTS

I measured five different characteristics of the calls of *Chrysoperla plorabunda* males and females. These are listed and defined below and illustrated in Fig. 1

A. *Initial volley frequency:* The cycling rate per second of the first eight strokes of the abdomen, at the start of a volley of abdominal vibration.

B. *Median volley frequency:* The cycling rate per second of the eight abdominal strokes following the initial period defined above.

C. *Terminal volley frequency:* The cycling rate per second of the abdominal strokes that remain in a volley after A and B have been deleted.

D. *Volley repetition rate:* The rate per minute at which a calling lacewing produces volleys of abdominal vibration.

E. *Volley duration:* The length of time in seconds required for completion of a volley of abdominal vibration.

Frequency of abdominal vibration versus temperature is tabulated for all males and females in Table 1 and expressed as linear regressions for each sex in Figure 2. Since vibration frequency decreases during the course of a *plorabunda* volley, it is necessary to subdivide each volley into the three portions A, B, and C, defined above; frequencies measured for those portions are plotted separately on the graph. Other call parameters like volley repetition rate and volley duration are similarly plotted separately for each sex on the same figure, using different units on the y-axis. All data are combined for both sexes in Figure 3, which also displays the range of variation in the calculated regression lines for all 10 individuals.

Several obvious features emerge from these tables and plots. First of all, it appears (Table 1) that males and females differ from each

TABLE I

Temperature	Sex	Vibration Frequency, strokes/sec Initial (A)	Median (B)	Terminal (C)	Volley Repetition Rate, volleys/min (D)	Volley Duration, msec (E)	Number of Abdominal Strokes/Volley
19.5–20°C	Male	71.55 ± 3.41 (44)	59.35 ± 4.20 (51)	39.86 ± 6.57 (59)	33.30 ± 4.10 (37)	848 ±121 (39)	40.05 ± 4.80 (37)
19.5–20°C	Female	69.23 ± 2.49 (63)	54.69 ± 4.26 (68)	35.56 ± 2.53 (69)	36.95 ± 4.73 (44)	868 ± 97 (50)	38.69 ± 4.90 (52)
23.5°C	Male	86.19 ± 3.60 (37)	68.81 ± 3.64 (52)	42.81 ± 2.82 (50)	48.39 ± 3.79 (62)	682 ± 93 (41)	36.25 ± 4.63 (40)
24.5-25°C	Female	84.40 ± 2.91 (56)	65.79 ± 4.52 (66)	39.39 ± 3.87 (71)	47.77 ± 6.01 (40)	626 ± 70 (58)	34.94 ± 3.92 (54)
27°C	Male	98.75 ± 5.86 (47)	76.17 ± 5.34 (54)	45.71 ± 3.45 (57)	49.88 ± 7.13 (77)	553 ±107 (47)	32.53 ± 5.43 (40)
29.5°C	Male	±112.35 ± 5.52 (57)	84.32 ± 5.88 (66)	46.53 ± 3.57 (77)	66.15 ± 8.02 (80)	465 ± 54 (61)	28.64 ± 3.51 (61)
29.5°C	Female	113.25 ± 4.16 (71)	82.43 ± 4.77 (84)	45.79 ± 3.98 (100)	69.52 ± 8.30 (53)	505 ± 79 (81)	32.61 ± 5.49 (74)

Table 1. Principal characteristics of the calls of males and females of *Chrysoperla plorabunda*, as measured at several different temperatures. Mean values and their standard deviations are tabulated. Sample sizes are entered parenthetically; in each row, the same five males or five females produced the given number of measured volleys. Parameters A–E are depicted in Fig. 1 and defined in the text.

other very little, at any temperature, in any major characteristics of their calls. Particularly coincident between males and females are the initial volley frequencies and the volley durations (Table 1 and Fig. 2A and E) of *Ch. plorabunda* calls. There is a consistent tendency for females to vibrate their abdomens in later portions of their volleys at somewhat lower frequencies than do males (35 cycles/sec. vs. nearly 40 cps at 20° C; see Fig. 2C) and for volleys to be produced rather more slowly by males than by females (about 66 volleys/min vs. nearly 70/min at 29.5° C; same figure, D), but neither of these differences is statistically significant.

Secondly, it can be seen from Figures 2 and 3 that the slopes for the linear regressions of frequency versus temperature differ radically from one portion of a volley to another, gradually becoming less steep as the volley progresses. Thus, initial portions of volleys change frequency rapidly with temperature (slope = 4.27x; Fig. 3A), while terminal portions remain within a much narrower range of values over equivalent temperature extremes (slope = 0.960x). X-intercepts also differ significantly for each of the three regressions calculated from pooled frequency data on all ten individuals: intercepts of 3.60, −1.27, and −19.09° C respectively characterize initial, median, and terminal portions of volleys. Regression of another call parameter, volley repetition rate, against temperature produces a line with a slope of 3.25x and an X-intercept of 9.14° C (Fig. 3D).

Thirdly, Figure 3E demonstrates that volley duration decreases markedly with increasing ambient temperature, and that the mathematical relationship between the two can equally well be interpreted as linear or exponential. In theory, the total number of abdominal strokes per volley could remain constant as temperature varies, since the increased frequency of abdominal vibration at higher temperatures would automatically shorten volley duration. However, data in Table 1 suggest that higher temperatures induce a slight but significant reduction in the total number of abdominal strokes produced during each volley, and that this phenomenon facilitates the volley-shortening process.

Finally, the table and figures all support the view that deviation is relatively slight between the temperature data for each of the various call parameters and the linear regressions calculated from those data. The closest fit to a mathematical relationship is found in the initial frequency of abdominal vibration during a volley: for data

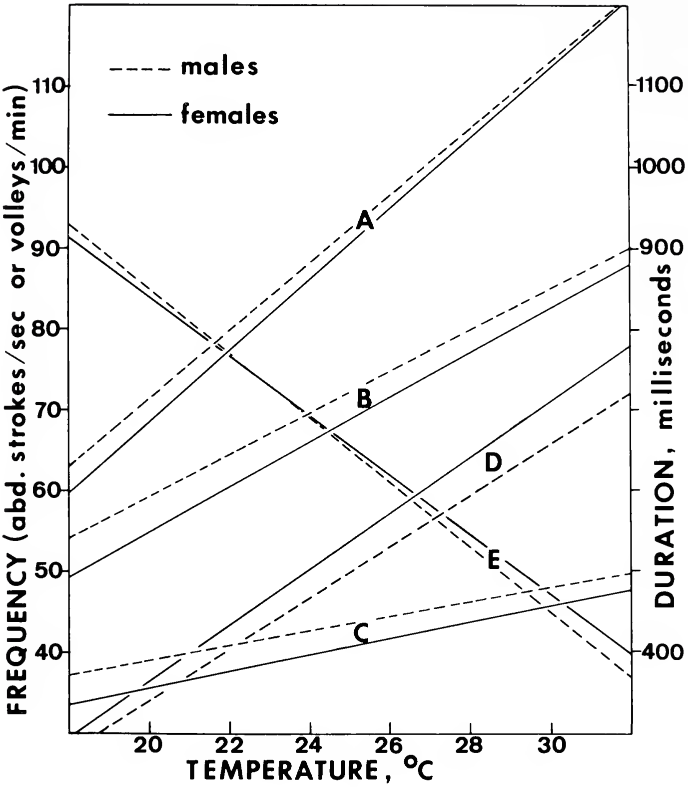

Figure 2. Regression lines, calculated from data in Table 1, showing the effect of temperature on the five principal characteristics A–E of the calls of five males (dashed lines) and five females (solid line) of *Ch. plorabunda.* The left-hand "frequency" axis applies to parameters A–C (strokes/sec) and to D (volleys/min), while the right-hand axis for "duration" applies only to E.

A,	males:	$y = 4.16x - 11.74$, $r^2 = 0.96$
	females:	$y = 4.37x - 18.79$, $r^2 = 0.95$
B,	males:	$y = 2.57x + 7.89$, $r^2 = 0.88$
	females:	$y = 2.77x - 0.55$, $r^2 = 0.92$
C,	males:	$y = 0.87x + 21.66$, $r^2 = 0.69$
	females:	$y = 1.01x + 15.40$, $r^2 = 0.74$
D,	males:	$y = 3.12x - 27.85$, $r^2 = 0.81$
	females:	$y = 3.44x - 32.32$, $r^2 = 0.88$
E,	males:	$y = -40x + 1650$, $r^2 = 0.80$
	females:	$y = -37x + 1580$, $r^2 = 0.89$

pooled from all ten individuals, over 95 percent of variance is explained by regression line A shown in Figure 3. Even for the worst case—terminal volley frequency—nearly two-thirds of raw data variance is compatible with the calculated linear regression ($r^2 = 0.65$). And data for individuals are neither more nor less variable, on average, than pooled samples: for the five principal call features graphed in Figure 3, individual r^2 values average 0.93, 0.84, 0.59, 0.79 and 0.76 and never fall below 0.40 for any single insect. Also shown in that figure is the close congruence of all individual lines for each of the same five call features but particularly for initial volley frequency, suggesting that such temperature relationships are consistent, repeatable, and predictable on an individual basis.

Results of experiments manipulating abdominal mass in individual lacewings are shown in Figure 4 and Table 2. Table 2 presents the raw temperature-frequency data taken from four insects, while Figure 4 shows how those data relate to the linear regressions generated from the terminal volley frequencies of the ten unmodified individuals tested earlier. Converting the frequency measurements to their equivalent values at 27°C (Table 2) dramatically reveals how little those data are affected by mass-loading of the abdomen: in none of the four experimental animals was the terminal volley frequency altered significantly by the treatment. Weight increments (from painting) amounted to 10-27% of total body mass; however, abdominal weights were only 2.8 mg for the female and approximately 2 mg for the three males, so increments to the mass of the vibrating structure itself in each insect actually ranged from 36 to 50%.

DISCUSSION

The results described above amply document the striking similarity of male and female calls of *Chrysoperla plorabunda*, consistent with the proven importance of such signalling behavior to the reproductive isolation of this species from several of its morphologically identical siblings in the genus (Henry 1980b, 1983b). Females closely resemble males in every detail of volley structure and spacing, and those few differences that do exist in pooled samples tend to break down when the characteristics of individual insects are compared (Figs. 3 and 4). Also as predicted, males and females

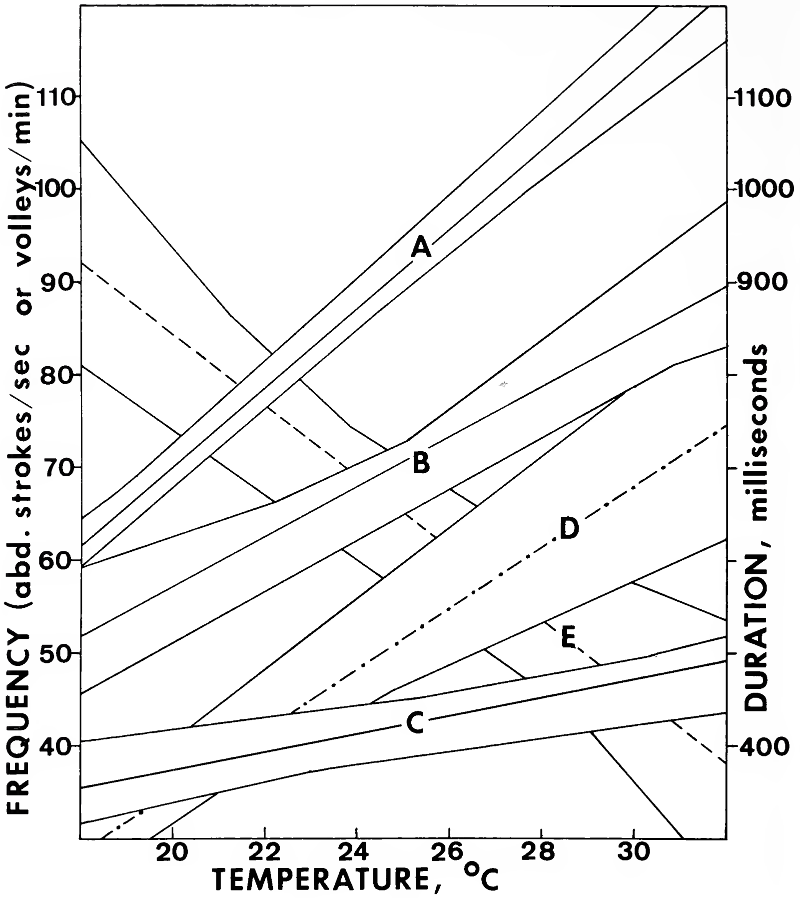

Figure 3. Total range of individual variation of temperature regression lines for the five major call characteristics A–E of *Ch. plorabunda*. The area above and below each straight line includes within it the linear regresssions for all 10 individuals tested, while the line itself summarizes temperature data for those 10 insects in a single regression equation. Axes and labels as in Fig. 2.

A: $y = 4.27x - 15.37$, $r^2 = 0.95$
B: $y = 2.69x + 3.41$, $r^2 = 0.88$
C: $y = 0.96x + 18.33$, $r^2 = 0.65$
D: $y = 3.25x - 29.72$, $r^2 = 0.83$
E: $y = -39x + 1620$, $r^2 = 0.83$

change their various call characteristics in precisely parallel ways as temperature is altered, so that the sexes' calls remain indistinguishable over the range of temperatures they would typically encounter. The only apparent exception to this conclusion concerns the slightly lower vibration frequencies characteristic of the terminal portions of the volleys of females at all temperatures (Fig. 2C). Such a difference is expected if the terminal volley frequency of a lacewing's abdomen is determined by its inherent capacity to oscillate like a weight on a spring, since the demonstrably heavier abdomen of a female would resonate at a lower frequency than that of a male. However, artificially mass-loading the abdomens of several males and females produced no obvious downward deflections of their frequency characteristics, suggesting that neuro-muscular mechanisms actively "drive" the vibrating system for the entire duration of each volley (Table 2) and that resonance effects have relatively little influence on resultant frequencies. Also, as mentioned earlier, the male-female difference in terminal volley frequencies is considerably less impressive when the responses of individual insects are dissected from the pooled data (Fig. 4), thus raising the suspicion that it is an artifact of some sort.

Studies of other acoustical insects overwhelmingly support the existence of linear functions relating temperature to most song parameters that repeat over time, as best exemplified by and documented for rates of wing-stroking, chirping, and "rolling" in crickets (Alexander 1956, Walker 1962, Dumortier 1963, Prestwich and Walker 1981) and a few katydids and homopterans (Dumortier 1963, Shaw 1968, Whitesell and Walker 1978, Booij 1982). Similarly, most of the temperature data reported here for *Ch. plorabunda* conform well to linear statistical models, although they are insufficiently detailed to discriminate linear from exponential interpretations. The least individual or pooled variance from the calculated regression is found for the abdominal vibration frequency of the first eight cycles of a volley, suggesting that this feature of the call is particularly crucial to unambiguous communication between the sexes; otherwise, it seems there would exist no need for such precision.

In his 1962 paper on cricket song, Walker drew attention to the apparent convergence of many of his linear regressions on 4°C; that is, it seemed that for many different cricket species the chirp

Table 2. Effect on terminal volley frequency (C), in abdominal strokes/sec, of artificially mass-loading the abdomen of three males and one female of *Ch. plorabunda*. Weight gains are tabulated in column 3; the last column lists n, the number of volleys measured. Equivalent frequencies (at 27° C) in column six were calculated from the slope of regression line C in Fig. 3. Superscript "x" denotes lab-reared insects.

		Weight, mg.	Temp., °C.	Vibration frequency,±SD	Equivalent at 27° C.	n
Male 1	control	7.5	26.8	39.78 ± 1.83	39.98	29
	mass-loaded	9.0	30.0	47.08 ± 1.84	44.00	20
Male 1^{x}	control	6.7	27.1	44.49 ± 2.44	44.51	20
	mass-loaded	8.5	27.0	44.59 ± 3.52	44.59	25
Male 2^{x}	control	7.2	27.3	45.98 ± 2.44	45.60	36
	mass-loaded	8.5	26.8	44.92 ± 2.80	45.15	36
Female 1^{x}	control	9.6	27.3	43.47 ± 2.31	43.20	28
	mass-loaded	10.6	27.0	43.14 ± 2.50	43.14	19

and pulse (=wing stroke) rates went to zero at about 4° C when their temperature regressions were extrapolated downward. The same phenomenon can be seen in other insects, as well, including several tettigoniids studied or reported by Dumortier (1963), Shaw (1968), and Whitesell and Walker (1978) and two delphacid homopterans studied by Booij (1982). Temperature data for initial volley frequency and volley repetition rate of lacewing calls are also reasonably consistent with the concept of regression convergence, since the x-intercepts for relevant call parameters range from 2.82° C to 9.40° C in *Ch. plorabunda* and average 8.31° C in *Chrysopa oculata* (Henry 1982b). However, the flatter slopes of the temperature-frequency regressions for middle and terminal portions of *plorabunda* volleys cause those lines to intersect the x-axis at −1.27° C and −19.09° C, respectively, which does not fit well with Walker's generalization. Moreover, other examples from the literature fail to confirm the phenomenon, even in certain crickets and katydids recently studied by Walker himself (and collaborators): for instance, *Anurogryllus arboreus* and winter races of *Neoconocephalus triops* both display rather flat regression lines of temperature versus wing stroke rate that intersect the x-axis well below −5° C (Prestwich and Walker 1981, Whitesell and Walker 1978). Thus, Walker's "four

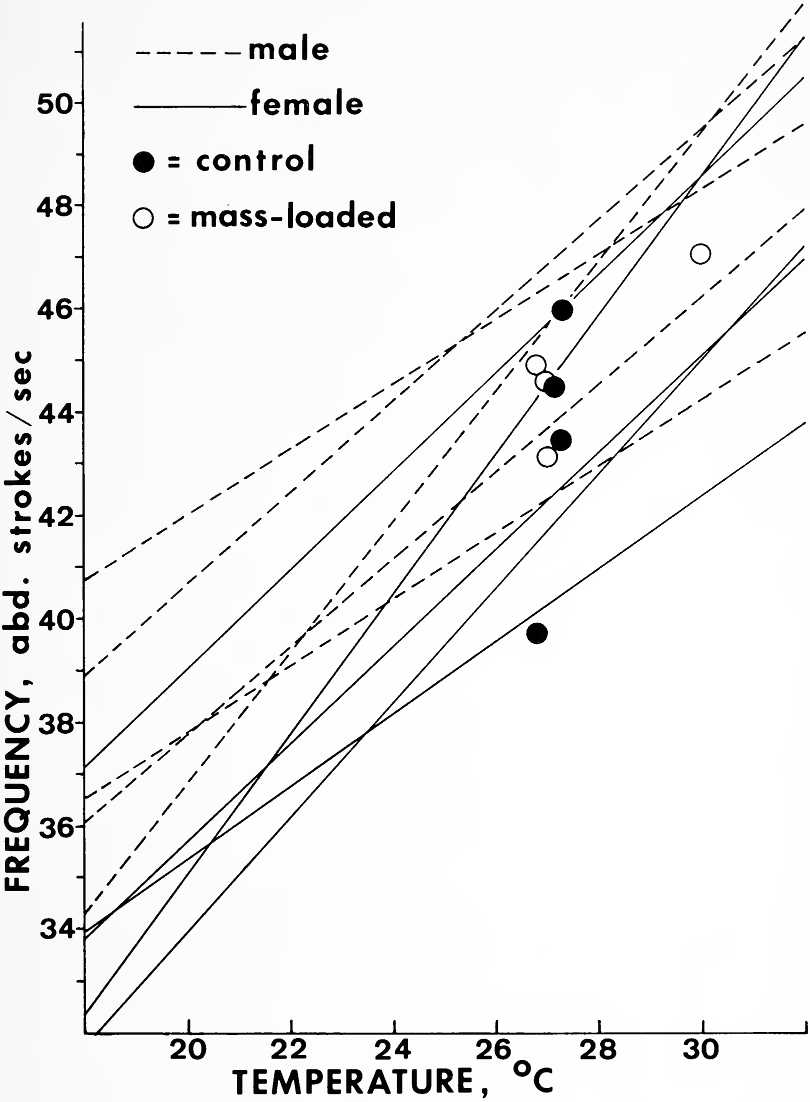

Figure 4. Effect on terminal volley frequency (C) of artificially mass-loading the abdomen of four *Ch. plorabunda* individuals, superimposed on a graph showing the calculated temperature regression lines of terminal volley frequency for 10 other insects of the same species.

degree rule" is intriguing but far from universal and applies only partially to the lacewing calls described here; why the rule should apply at all, to any insect call parameter, is still unknown.

It should not be assumed from the discussion above that linear regressions characterize the temperature relationships of all insect song parameters. In fact, it is likely that all temperature regressions are ultimately exponential in form when based upon data taken over a sufficiently wide temperature range, since the kinetics of the physiochemical processes underlying song production are non-linear with respect to temperature. One conspicuous example is the pulse (or chirp) duration of the French tettigoniid *Ephippiger provincialis* (Yers.), which varies inversely with temperature in a "hyperbolic" manner (Dumortier 1963, fig. 229). The volley duration typical of calling *Ch. plorabunda* also decreases with temperature (Fig. 3E), but the function describing that decrease seems more linear than hyperbolic or logarithmic over the chosen range of temperatures, and the slope of the relationship is twice as steep as that shown for the tettigoniid. Unless thermoregulation by the larger-bodied katydids accounts for these differences, one can conclude only that distinct physiological mechanisms determine pulse, chirp, or volley durations in different insect groups.

Recently, Michelson *et al.* (1982) published a comprehensive theoretical and empirical study treating general aspects of the physics, transmissibility, and energetics of the vibrational songs of insects. This study provides a rationale for the observed frequency modulation of *Ch. plorabunda* volleys, and by implication helps to explain why lacewing singers strictly control the frequencies of all portions of their volleys, rather than simply allowing their abdomens to oscillate at their frequencies of resonance. Viewing the plant substrates of vibrating or tremulating insects as acoustical filters, Michelson *et al.* concluded that signals consisting of multiple frequencies should propagate more uniformly (and effectively) through their substrates than narrow-bandwidth calls, since a signal of relatively pure tone tends to excite a certain pattern of standing waves in its substrate and will therefore vary tremendously in its intensity from place to place on that substrate. Broad-bandwidth or frequency-modulated signals, on the other hand, are ideally suited for penetrating such acoustical filters, so that at least a portion of the call's energy reaches the receptors of the recipient individual or partner. Although the authors reported frequency changes on the order of

30-40% in the calls of their bugs and small cicadas, lacewings of the species *Ch. plorabunda* alter their rate of abdominal vibration by 50-60% during each volley, suggesting that their calls can propagate efficiently and evenly through a variety of substrate types. However, if all this is true, it remains to be explained why other lacewing species like *Ch. downesi* and *Ch. carnea* (central Europe) produce long calls of nearly constant frequency characteristics (Henry 1980b, 1983a). Perhaps specific properties of the typical substrates utilized by those species have shaped and narrowed the frequency ranges of their calls over evolutionary time: for example, *Ch. downesi* may be responding to some inherent acoustical property of conifer needles, since its ecological niche is restricted to the evergreen forests of North America.

SUMMARY

This study assesses the effects of temperature on the major characteristics of the vibrational song of a North American green lacewing, *Chrysoperla plorabunda* (formerly *Ch. carnea*). Those parameters include the volley repetition rate, the average duration of volleys, the total number of abdominal strokes per volley, and the vibrational frequency structure of volleys. In general, temperature affects the call in a direct linear manner, so that linear regression equations (of differing slopes) can be used with confidence to describe the relationship between temperature and each measurable trait of a lacewing's song. Additionally, variation in these equations among individuals or between the sexes is negligible, so all members of the species produce calls of remarkably similar construction at all reasonable ambient temperatures—a prerequisite to unambiguous communication among conspecifics. That the weight of an individual's abdomen has no effect on the frequency characteristics of its call was demonstrated experimentally by mass-loading the abdomens of several sexually receptive insects. The relevance of these findings to the biological function of lacewing calling, as well as to the physics of substrate-borne vibrations, is discussed briefly.

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SOCIAL ORGANIZATION IN *LEPTOTHORAX* ANTS: WITHIN- AND BETWEEN-SPECIES PATTERNS*

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Recent application of quantitative techniques to behavior (cf. Colgan 1978) has resulted in new approaches to undertanding social interactions among animals. A technique particularly widely-used for study of ant colonies is development of the colony ethogram, or behavioral profile. We now have ethogram information for a wide variety of species. Most reports in the literature focus on a single colony (Table 1); variation within a species is rarely discussed. In addition, the colony time budget, an important second class of information, is generally not reported (Table 1). The appropriateness of behavioral comparisons across species is thereby severely limited by availability of only one type of behavior frequency catalog, for only one colony per species.

Caste complexity and division of labor related to morphological or age variation comprise another type of information contributing to an understanding of social organization. As a rule, queens have smaller repertoires than do workers; majors have different ethograms than minors; and older workers display different behavior frequencies than do younger workers. Studies of morphology affecting behavior have concentrated on polymorphic species for which descrete worker castes can be distinquished; recent work has shown that, even for monomorphic species, worker size can bias behavior (Wilson 1978, Herbers and Cunningham 1983).

A reasonably complete description of social organization for an ant species should treat ethograms, time budgets, and behavioral caste specialization, both within and between different colonies. Here I report such details for three colonies of *Leptothorax ambiguus*. This information is then compared to data from the closely-related *L. longispinosus* to arrive at an understanding of between- and within- species variation in social behavior.

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Table 1. Ethograms for many ant species have been published, but variation between colonies is rarely reported.

Species	# of Colonies Observed	# of Colony Ethograms Reported	Time Budget Reported?	Reference
Amblyopone pallipes	5	1	no	Traniello 1982
Atta sexdens	1	1	no	Wilson 1980
Campanotus (Colobopsis) sp.	1	1	no	Cole 1980
Cephalotes atratus	1	1	yes	Corn 1980
Formica perpilosa	1	1	no	Brandao 1978
Leptothorax curvispinosus	2	1 (pooled data)	no	Wilson & Fagen 1974
Leptothorax longispinosus	4	4	no	Herbers 1982
Leptothorax longispinosus	4	1 (pooled data)	yes (pooled data)	Herbers & Cunningham 1983
Orectognathus versicolor	1	1	no	Carlin 1982
Pheidole dentata	1	1	no	Wilson 1976a
Solenopsis geminata	1	1	no	Wilson 1978
Solenopsis invicta	1	1	no	Wilson 1978
Zacryptocerus varians	2	1	no	Wilson 1976b
Zacryptocerus varians	1	1	no	Cole 1980

METHODS

Colonies of *L. ambiguus* were collected in May 1982 from the E. N. Huyck Preserve (Albany County, NY). These colonies were settled in artificial nest boxes and maintained according to standard methods (Herbers and Cunningham 1983); in addition, frozen fruitflies were provided as a food source.

For detailed observations, three colonies were chosen on the basis of queen and worker number to match earlier studies of *L. longispinosus* (Herbers 1982). All *Leptothorax* colonies studied were of approximately equal worker number, all had eggs and larvae, and all produced alates by summers' end; only queen number varied significantly (Table 2).

Behavioral observations were conducted June 9—August 24, 1982 through a Wild M5-A stereomicroscope as follows: a worker was chosen at random and all her actions were recorded over a 30-minute period. In addition, activities of individuals around her in the field of view were recorded. Head widths of the randomly-chosen ants were measured at a standard depth of field, by use of an ocular micrometer.

Data analysis followed methods outlined by Fagen and Goldman (1977) for behavior catalogs; Herbers and Cunningham (1983) for statistical evidence of polyethism and morphological bias; and Cole (1980) for producing dendrograms.

Table 2. Colony sizes of *Leptothorax* used in this comparative study. Data on *L. longispinosus* were reported by Herbers (1982).

	Original # of Queens	Original # of Workers	Eggs Laid?	Larvae Present?	Alates Reared?
Leptothorax ambiguus					
La-A	3	27	yes	yes	yes
La-B	1	28	yes	yes	yes
La-C	0	20	yes	yes	yes
Leptothorax longispinosus					
Ll-A	1	30	yes	yes	yes
Ll-B	1	31	yes	yes	yes
Ll-C	5	28	yes	yes	yes
Ll-D	4	36	yes	yes	yes

RESULTS AND DISCUSSION

Social Organization of L. ambiguus *colonies*

A total of 60 hours were recorded over the three colonies for a grand total of 3145 observations. Ethograms for the three colonies of *L. ambiguus* are reported in Table 3. A total of 46 behaviors were recorded for workers and 13 for queens. Despite the large catalog size, no behavior was unique to *L. ambiguus*; all in Table 3 are relatively common to many species included in Table 1.

As expected, queens were much less active than workers (Table 3). Their behavior was almost exclusively directed towards the brood; the exceptional occasion for colony La-B occurred when a queen was observed walking outside the nest and taking a drink; she later returned inside. Because of the paucity of data on queen behavior, analyses below concern only worker behavior.

Frequencies of observations for behaviors over three colonies are given in Figure 1. Sample coverages were uniformly greater than 99% (Figure 1). Consequently inferences about the true colony repertoire can safely be made. There was considerable variation among colonies (Figure 1), yet the distributions were not significantly different from each other ($\chi^2 = 13{,}80$, 14 df, $P > .05$). Thus distributions of observations over all behavior categories were roughly equivalent.

Comparisons of absolute frequencies among colonies showed that many worker behaviors were observed in all colonies (Table 3). For some, ethogram frequencies were nearly equal (IL, CP, ATW, RW) whereas for others the correspondences were not good (RE, IE, ALW). A third class of behaviors included those observed for only one or two nests (CE, FLD, AAE, CR). Thus considerable internest variation existed. For a given colony, some behaviors known to occur in the species were missing from the ethogram, some were common or rare relative to other colonies, and some were equally frequent to others. Despite apparent discrepancies in absolute frequencies, the rankings of behaviors by frequency were similar over the three colonies (Kendall's coefficient of concordance; $W = .864$, 27 df, $P < .001$). That is, behaviors commonly observed in one colony were also common in others whereas those rare in one tended to be rare in all. In particular, behaviors missing from one colony's ethogram were generally rare in others. Therefore, although absolute frequency varied from nest to nest, relative frequencies were similar.

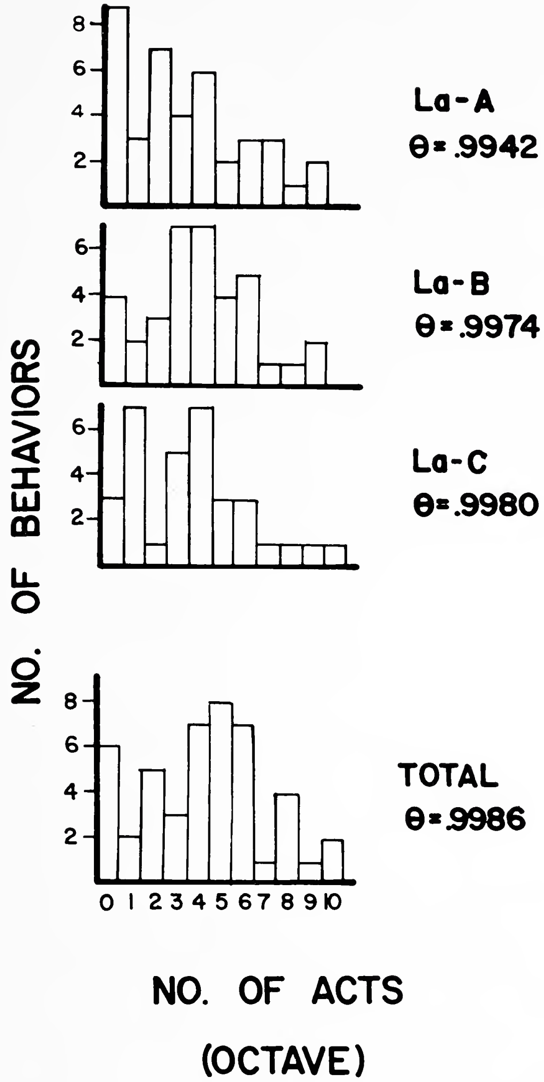

Figure 1. Abundance histograms for three colonies of *L. ambiguus* and for pooled data. The abscissa gives the number of observations per behavior, to the base 2; thus octave 0 indicates behaviors observed once, octave 1 refers to exactly 2 observations, octave 2: 3 or 4 observations, octave 3: 5 through 8, and so on. The largest octave, 10 refers to behaviors observed 513–1024 times. The value of θ given for each data set indicates the sample coverage, as described by Fagen and Goldman (1977).

Table 3. Ethograms for three colonies of *L. ambiguus*. Since Colony La-C was queenless, no data on queen behavior are reported.

Code	Behavior	Workers La-A (N=1145)	Workers La-B (N=1169)	Workers La-C (N=831)	Queens La-A (N=18)	Queens La-B (N=14)
Personal Behavior						
RE	Rest	.1519	.1104	.2078	—	—
SG	Self-Groom	.2155	.2211	.1378	.17	.21
MO	Move inside Nest	.2892	.3298	.3584	—	—
Brood Care						
IE	Inspect Egg	.0026	.0123	.0088	.22	.07
GE	Groom Egg	.0006	.0058	.0061	.06	—
CE	Carry Egg	—	.0032	.0061	.11	.07
LE	Lay Egg	—	—	—	.11	.14
AL	Assist Egg-Laying	—	—	—	—	.07
IL	Inspect Larva	.0415	.0336	.0292	.17	—
GL	Groom Larva	.0461	.0336	.0428	.06	—
CL	Carry Larva	.0058	.0071	.0149	—	—
RL	Regurgitate w/Larva	.0084	.0052	.0061	—	—
FLD	Feed Larva Solid	—	—	.0014	—	—
ALE	Assist Larval Ecdysis	.0026	.0006	—	—	—
IP	Inspect Pupa	.0019	.0052	.0102	—	—
GP	Groom Pupa	.0039	.0039	.0061	.05	.21
CP	Carry Pupa	.0006	.0006	.0014	—	.14
AAE	Assist Adult Eclosion	—	.0019	—	—	—
Social Interactions						
BC	Be Carried	—	—	.0007	—	—
ATW	Antennate Worker	.0454	.0472	.0570	—	—
ATB	Antennate Body	.0058	.0084	.0061	—	—

RW	Regurgitate w/Worker	.0441	.0271	.0380	—	—
ALW	Allogroom Worker	.0195	.0310	.0156	—	—
BG	Be Groomed	.0019	.0142	.0048	—	—
ATQ	Antennate Queen	.0006	.0026	—	—	—
ALQ	Allogroom Queen	—	.0006	—	—	—
RQ	Regurgitate w/Queen	.0013	.0013	—	—	—
FQ	Fight Queen	—	—	—	.06	—
Social Interactions (continued)						
ATM	Antennate male	.0006	—	—	—	—
ALM	Allogroom Male	.0026	—	—	—	—
CM	Carry Male	.0013	—	—	—	—
RM	Regurgitate w/Male	.0006	—	—	—	—
ALF	Allogroom Alate Female	—	—	.0007	—	—
Physical Nest Maintenance						
LN	Lick Nest Wall	.0039	.0065	.0129	—	—
LOT	Look Outside Nest	.0091	.0271	.0027	—	—
LEx	Inspect Exuvium	.0006	.0013	—	—	—
CEx	Carry Exuvium	.0006	.0045	.0034	—	—
EEx	Eat Exuvium	.0006	.0058	.0041	—	—
HM	Handle Nest Material	.0019	.0110	.0041	—	—
CR	Carry Refuse	.0006	—	—	—	—
Provisioning						
FF	Forage	.0221	.0058	.0014	—	—
MOT	Move Outside	.0195	—	.0014	—	.07
IDr	Inspect Prey	.0052	.0039	.0007	—	—
CDr	Carry Prey	.0019	.0026	.0014	—	—
EDr	Eat Prey	.0071	—	—	—	—
FdN	Feed Inside Nest	.0013	.0065	.0054	—	—
FDO	Feed Outsde Nest	.0058	.0006	.0014	—	—
IFd	Inspect Food	.0032	—	—	—	—
DR	Drink	.0214	.0045	.0014	—	.07

Table 3 Ethograms for three colonies of *L. ambiguus*. Since Colony La-C was queenless, no data on queen behavior are reported

Code	Behavior	Workers La-A (N=1145)	Workers La-B (N=1169)	Workers La-C (N=831)	Queens La-A (N=18)	Queens La-B (N=14)
Personal Behavior						
RE	Rest	1519	.1104	2078	—	—
SG	Self-Groom	.2155	.2211	1378	.17	21
MO	Move inside Nest	2892	.3298	.3584	—	—
Brood Care						
IE	Inspect Egg	.0026	.0123	0088	.22	07
GE	Groom Egg	0006	.0058	0061	.06	—
CE	Carry Egg	—	0032	.0061	11	07
LE	Lay Egg	—	—	—	11	.14
AL	Assist Egg-Laying	—	—		—	.07
IL	Inspect Larva	0415	0336	0292	17	—
GL	Groom Larva	0461	0336	.0428	06	—
CL	Carry Larva	.0058	.0071	.0149		—
RL	Regurgitate w/Larva	.0084	0052	.0061	—	—
ELD	Feed Larva Solid	—	—	.0014		—
ALE	Assist Larval Ecdysis	.0026	0006	—	—	—
IP	Inspect Pupa	.0019	0052	.0102	—	—
GP	Groom Pupa	0039	0039	0061	.05	21
CP	Carry Pupa	.0006	0006	0014	—	14
AAE	Assist Adult Eclosion	—	0019	—	—	
Social Interactions						
BC	Be Carried	—	—	0007	—	—
ATW	Antennate Worker	.0454	0472	0570	—	—
ATB	Antennate Body	0058	.0084	.0061	—	—
RW	Regurgitate w/Worker	0441	0271	0380	—	
ALW	Allogroom Worker	.0195	0310	0156	—	—
BG	Be Groomed	0019	0142	0048	—	
ATQ	Antennate Queen	0006	0026	—	—	
ALQ	Allogroom Queen	—	0006	—	—	—
RQ	Regurgitate w/Queen	.0013	.0013	—	—	—
FQ	Fight Queen	—	—	—	.06	—
Social Interactions (continued)						
ATM	Antennate male	0006	—	—	—	—
ALM	Allogroom Male	.0026	—	—	—	—
CM	Carry Male	.0013	—	—	—	—
RM	Regurgitate w/Male	0006	—	—	—	—
ALE	Allogroom Alate Female	—	—	.0007	—	—
Physical Nest Maintenance						
LN	Lick Nest Wall	0039	0065	.0129	—	—
LOT	Look Outside Nest	.0091	.0271	.0027	—	—
LEx	Inspect Exuvium	0006	.0013	—	—	—
CEx	Carry Exuvium	.0006	.0045	.0034	—	—
EEx	Eat Exuvium	.0006	.0058	.0041	—	—
HM	Handle Nest Material	.0019	.0110	.0041	—	—
CR	Carry Refuse	.0006	—	—	—	—
Provisioning						
FF	Forage	.0221	0058	.0014	—	—
MOT	Move Outside	0195	—	.0014	—	07
IDr	Inspect Prey	.0052	0039	0007	—	—
CDr	Carry Prey	0019	.0026	.0014	—	—
EDr	Eat Prey	.0071	—	—	—	—
FdN	Feed Inside Nest	0013	0065	0054	—	—
FDO	Feed Outsde Nest	0058	.0006	.0014	—	—
IEd	Inspect Food	.0032	—	—	—	—
DR	Drink	.0214	.0045	.0014	—	07

Table 4. Time budgets for *L. ambiguus* workers.

Behavior	Proportion of Time (p_t)			
	La-A	La-B	La-C	Total
RE	.6362	.5985	.8157	.68064
SG	.0565	.0922	.0153	.05520
MO	.1453	.1384	.1281	.13753
IE	.0016	.0056	—	.00242
GE	.0003	.0018	—	.00072
CE	—	.0013	—	.00044
IL	.0144	.0117	.0051	.01052
GL	.0282	.0115	.0034	.01478
CL	.0022	—	—	.00078
RL	.0077	.0018	—	.00331
FLD	—	—	—	—
ALE	—	.0012	—	.00040
IP	.0007	.0018	.0024	.00158
GP	.0017	.0030	.0012	.00196
CP	—	—	—	—
AAE	.0008	.0009	—	.00029
ATW	.0048	.0070	.0066	.00611
ATB	.0011	.0013	.0015	.00129
RW	.0235	.0167	.0103	.01704
ALW	.0039	.0153	.0005	.00658
BG	.0055	.0449	.0058	.01864
ATQ	—	.0001	—	.00002
ALQ	—	—	—	—
RQ	—	—	—	—
ATM	—	—	—	—
ALM	—	—	—	—
CM	—	—	—	—
RM	—	—	—	—
ALF	—	—	—	—
BC	—	—	—	—
LN	.0028	.0024	.0002	.00184
LOT	.0013	.0100	.0001	.00378
IEx	.0001	.0008	—	.00032
CEx	—	.0024	.0012	.00119
EEx	—	.0020	.0014	.00111
HM	—	.0020	.0007	.00089
CR	—	—	—	—
FF	.0010	—	—	.00036
MOT	.0293	.0120	—	.01424
IDr	.0001	.0030	.0001	.00107

Table 4. Time budgets for *L. ambiguus* workers. (Continued)

Behavior	Proportion of Time (p_t)			
	La-A	La-B	La-C	Total
CDr	—	.0042	—	.00139
EDr	.0291	—	—	.01021
FdN	—	.0065	.0004	.00229
FdO	.0005	—	—	.00016
IFd	.0005	—	—	.00017
DR	.0008	—	—	.00027

Time budgets for workers of the three colonies are given in Table 4. The largest elements in Table 4 correspond to resting; overall, workers spent 68% of the time motionless. It is interesting to note that the most sedentary colony was La-C, which had no queen; perhaps the high rate of inactivity was related to a lower rate of egg production or overall lack of queen stimulation. Even so, resting was predominant for all nests. The second dominant behavior was moving inside the nest, on average accounting for 13.8% of the worker time budget. In addition, self grooming was a large contributor in all colonies observed, consuming on average 5% of worker's time. Thus personal behavior accounted for the vast majority of the time budget; activities which can be called "social" consumed less than 15% of the workers' time.

Among social behaviors, time budget variation among colonies was minimal for some types (GP, ATW, ATB). Proportions of time spent in other behaviors were quite different among colonies; the most extreme case was LOT, which varied by two orders of magnitude ($p_t = .0100$ for La-B and .0001 for La-C). Kendall's test for concordance showed that, despite differences in absolute proportion of time, rankings of behaviors by relative proportions were similar over all colonies ($W = 0.763$, 13 df, $P < .005$). That is, behaviors consuming a large portion of the time budget in one colony tended to be important for other colonies, and behaviors rare in one colony were usually rare in all. Despite quantitative differences in specific types of activity, overall qualitative agreement in time budgets was strong.

To sum, no significant differences in relative importance of behaviors were observed over the three colonies. Histograms of behavior frequency (Fig. 1), rankings of ethogram frequency (Table 3) and relative time budget frequencies (Table 4) were not significantly different. Therefore, in subsequent analyses of within-species social organization below, data were pooled over three colonies. I will return to consideration of between-colony variation below.

Division of labor among workers was investigated by considering the matrix of transition frequencies among behaviors listed in the ethogram. Within this 46 x 46 matrix, elements indicate how often each behavior followed and preceded every other behavior. To simplify presentation of the results, transitions among behaviors listed in the ethogram are synopsized in Table 5. Diagonal elements represent the frequencies by which behaviors in the same categories followed each other whereas off-diagonal elements represent transition frequencies between behaviors in different groups (Herbers and Cunningham 1983). Division of labor is implicated if nonzero transition frequencies are clustered in diagonal blocks of the matrix and zeroes occur in off-diagonal blocks.

Examination of Table 5 shows that transitions from (column 1) and into (row 1) Personal Behavior commonly occurred. This is no surprise, since virtually all workers displayed a form of personal behavior. However, among social behaviors, the overall distribution of nonzero transitions deviated strongly from random expectation ($G = 55.24$, 16 df, $P < .001$), in a pattern consistent with organization of behaviors into roles: behaviors within the group Brood Care were positively correlated in time, as were those within the groups Social Interactions, Physical Maintenance, and Colony Provisioning. Between these groups, there were significantly fewer transitions than random expectation (Table 5). The pattern of overabundance of nonzero transitions in diagonal blocks, and under-representation in off-diagonal blocks was absolutely consistent with expectation. Overall, nonzero transitions clustered in diagonal blocks, thereby providing statistical evidence of polyethism.

Worker behavior can be provisionally categorized into four roles: brood care, social interactions, physical nest maintenance, and provisioning, since transitions among behaviors within a role occurred more often than random expectation whereas links between roles occurred less often than by chance. Information from the single-step

Table 5. Synopsis of one-step transition probabilities among worker behaviors. Entries indicate the number of nonzero transitions from Behavior i to Behavior j observed over three colonies.

		Behavior j				
	Category	Personal Behavior	Brood Care	Social Interactions	Physical Maintenance	Provisioning
Behavior i	Personal Behavior	9	20	15	8	9
	Brood Care	16	33^+	6^-	2^-	0^-
	Social Interactions	14	8	17^+	0^-	2^-
	Physical Maintenance	7	2^-	1^-	7^+	1^-
	Provisioning	8	0^-	2^-	3^-	21^+

$^+$ more than expected by chance
$^-$ fewer than expected by chance
$G = 55.24$, 16 df, $P < .001$

transition matrix therefore gave important insights to the nature of polyethism in *L. ambiguus*. However, Table 5 must be interpreted with caution, since it does not report linkage over several acts. Analysis of per-second transition probabilities cannot detect transitions between behaviors intervened by other acts. That is, over a relatively long period, workers may switch roles, which would not be disclosed by single-step transition analysis (Herbers and Cunningham 1983). While single-step transitions suggest patterns of polyethism, inferences must be corroborated by long-term observations of behavior.

Information on worker behavior over 30-minute periods is given in Table 6. There is indicated the number of ants (out of a total of 57) that executed two behaviors within a 30-minute period. It is clear from Table 6 that behaviors provisionally assigned to different roles were often displayed by one worker over 30-minutes' time. Results of statistical testing of Table 6 are summarized by Venn diagrams in Figure 2. Behaviors intersecting in this figure co-occurred more often than expected by chance (χ^2 tests) whereas sets not intersecting were observed for the same individuals at a rate no different from chance expectation. Thus behaviors involved in egg care were related, as were those concerning care of larvae and those related to care of pupae. However, no greater proportion of egg-workers also tended for larvae and pupae than chance expectation. That is, individuals specializing on eggs were not necessarily those specializing on pupae or larvae. The final set of behaviors is a large but loosely-connected cluster. Regurgitation, grooming, and antennation were closely interconnected (Figure 2); these were also peripherally connected with inspecting the nest exterior and moving outside, since individuals returning from an outside foray elicited interest and grooming from nestmates. Similarly, LN and HM do not directly intersect, since they co-occurred no more often than chance expectation; these two behaviors were indirectly linked through ATW and RW (Figure 2). Behaviors in the roles of social interactions, physical maintenance, and provisioning were therefore not strongly separated.

Thus analysis of sets of behaviors displayed over 30-minute periods illustrated the expectation that individual workers tended to specialize, particularly within the brood care role. An ant grooming larvae was more likely to also carry or regurgitate to larvae than chance expectation. By a similar token, a worker guarding the nest

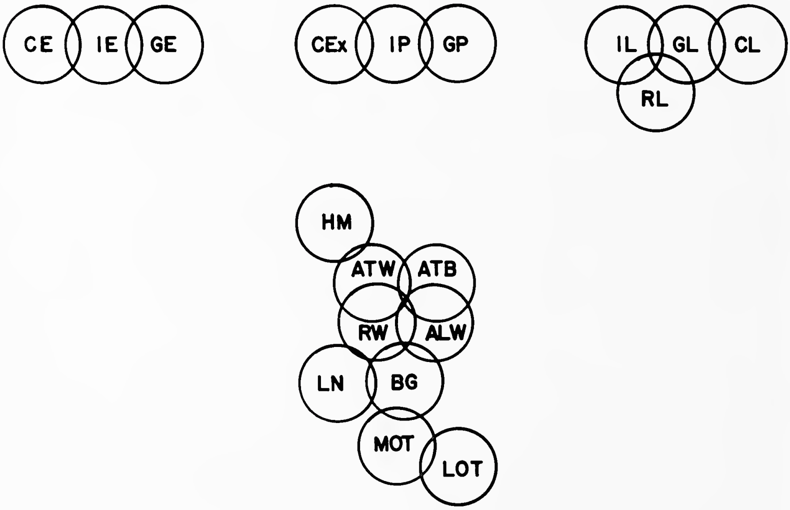

Figure 2. Sets of behaviors that co-occurred within 30-minutes. Two intersecting behaviors were observed more often than expected by chance (χ^2 tests; for all intersections $P < .05$). Behaviors not intersecting occurred as often or less than random expectation.

entrance (LOT) was likely to move outside the nest, then to be groomed by nestmates upon reentry. Thus some components of polyethism were statistically verified by examination of long-term individual worker behavior. However, the division of labor inferred from Table 6 was considerably weaker than the instantaneous transition matrix (Table 5) suggested. Individuals involved in brood care acts also displayed behaviors in other roles over a 30-min. period. Likewise, co-occurrences of behaviors in other roles were very common. The pattern emerging from consideration of all data is that workers strongly specialized in the short-term but over 30-minutes the specialization was weakened.

A final component of social organization is morphological bias in polyethism. Worker size is known to be correlated with behavior in many species, including the monomorphic *L. longispinosus* (Herbers and Cunningham 1983). The range of worker sizes in *L. ambiguus* is indicated in Figure 3. Pooled data are drawn there, since

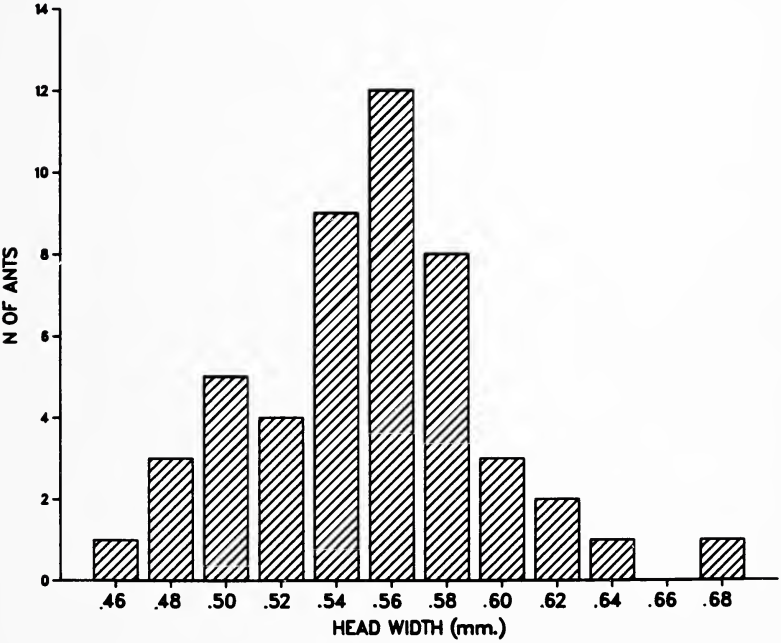

Figure 3. Morphological variation in *L. ambiguus* workers. Head width distribution was normal, and the largest worker was less than 1.5 times that of the smallest.

distributions were not significantly different among colonies (ANOVA, F = .09, 2 df, $P < .05$). Head widths were relatively invariant in this species ($\bar{x} = .552$ mm, s = .043 mm) such that the largest individual was less than 1.5× the smallest (Figure 3). Thus the potential for size-biased polyethism was quite restricted.

Head widths of workers displaying different ethogram behaviors were considered. Data were again pooled over three colonies since mean head widths did not differ significantly for any behavior (ANOVA with variable df; in all cases $P < .05$). Figure 4 illustrates statistics of head width for workers displaying each behavior. No obvious differentiation of head width according to roles can be discerned. Analysis of data in Figure 4 is summarized in Table 7, which is based on ANOVA's for differences between mean head widths (LSD tests). Most of the significant differences separate workers regurgitating with larvae from other behaviors (row and column headed RL in Table 7). That workers displaying RL were on average larger than others is evident from Figure 4. Starred entries of Table 7 are sporadic; certainly patterns of differences in mean head width showed no clear segregation by roles. Workers exhibiting a brood care behavior were not more similar in size to those displaying other brood care behaviors than they were to workers involved in social interactions or provisioning. Thus there was no apparent morphological bias underlying polyethism for *L. ambiguus*.

The overall picture that emerges of *L. ambiguus* social organization is short-term specialization of individual on task according to four roles: brood care, social interactions, physical nest maintenance, and provisioning (Table 3). However, the division of labor was rather loose, since switching between roles was often observed over 30-minute periods (Table 4). The nonrandom co-occurrence of sets of behaviors (Figure 2) statistically reinforced inferences about polyethism from the transition matrix. Finally, no strong morphological bias was demonstrated for ants specializing on specific tasks.

Comparison with L. longispinosus

Results of this study were compared with data from its closely-related congener *L. longispinosus*; such comparisons were valid since all observations were conducted in the same laboratory using standard husbandry techniques. The major difference in culture conditions between species was the addition of fruitflies to *L. ambiguus* diets. The earlier study had not incorporated feeding insect prey

Table 6. Number of workers observed to exhibit two behaviors over a 30-minute period. Numbers in the left column refer to total number of ants observed to display each behavior.

		RG	SG	MO	IE	GE	CE	IL	GL	CL	RL	ALE
56	RG	—										
45	SG	44	—									
51	MO	50	43	—								
6	IE	6	5	6	—							
4	GE	4	3	4	4	—						
1	CE	1	1	1	1	1	—					
21	IL	21	18	20	3	2	0					
16	GL	5	13	16	3	2	0	14	—			
2	CL	2	2	2	1	0	0	2	2	—		
4	RL	4	4	4	0	0	0	4	4	1	—	
1	ALE	1	1	1	0	0	0	0	1	0	0	—
10	IP	10	8	9	1	1	0	7	5	0	1	1
5	GP	5	4	4	0	0	0	3	3	0	0	1
1	AAE	1	1	1	1	1	0	1	0	0	0	0
36	ATW	36	30	36	3	2	0	14	9	2	3	1
14	ATB	14	13	14	1	0	0	7	5	2	2	1
25	RW	24	25	25	2	1	0	12	8	2	3	1
7	ALW	7	6	7	1	0	0	3	3	1	0	1
15	BG	15	14	15	1	1	0	9	6	0	1	1
1	ATQ	1	1	1	0	0	0	0	0	0	0	0
9	LN	9	9	9	1	1	1	5	4	1	2	1
8	LOT	8	8	8	1	1	0	0	1	0	0	0
2	IEx	2	2	2	1	1	0	1	0	0	0	0
3	CEx	3	3	3	1	1	0	2	1	0	0	0
4	EEx	4	4	4	1	1	0	2	1	0	0	0
6	HM	6	2	6	0	0	0	1	1	0	0	0
1	FF	1	1	1	0	0	0	0	0	0	0	0
6	MOT	6	6	6	0	0	0	1	1	0	0	1
3	IDr	3	3	3	0	0	0	1	0	0	0	0
1	CDr	1	1	1	0	0	0	0	0	0	0	0
1	EDr	1	1	1	0	0	0	0	0	0	0	0
2	FdN	2	2	2	0	0	0	1	0	0	0	0
1	FdO	1	1	1	0	0	0	0	0	0	0	0
1	IFd	1	1	1	0	0	0	0	0	0	0	0
1	DR	1	1	1	0	0	0	0	0	0	0	0

Table 6 (continued).

		IP	GP	AAE	ATW	ATB	RW	ALW	BG	ATQ	LN	LOT
56	RG											
45	SG											
51	MO											
6	IE											
4	GE											
1	CE											
21	IL											
16	GL											
2	CL											
4	RL											
1	ALE											
10	IP	—										
5	GP	5	—									
1	AAE	1	0	—								
36	ATW	7	2	1	—							
14	ATB	2	1	0	13	—						
25	RW	4	1	1	21	11	—					
7	ALW	1	1	0	7	5	6	—				
15	BG	2	1	0	13	5	10	5	—			
1	ATQ	0	1	0	1	0	0	0	0	—		
9	LN	0	0	0	8	3	7	2	6	0	—	
8	LOT	0	0	0	7	2	5	2	4	0	2	—
2	IEx	1	0	1	2	0	2	0	0	0	0	0
3	CEx	2	0	1	3	1	2	0	1	0	0	0
4	EEx	2	0	1	4	1	2	0	2	0	0	0
6	HM	2	1	0	6	1	3	0	3	1	1	0
1	FF	0	0	0	0	0	0	0	0	0	0	1
6	MOT	0	0	0	5	3	4	3	5	0	2	5
3	IDr	0	0	0	2	1	0	0	1	0	0	1
1	CDr	0	0	0	1	1	0	0	0	0	0	0
1	EDr	0	0	0	0	0	0	0	0	0	0	1
2	FdN	0	0	0	2	1	0	0	1	0	0	0
1	FdO	0	0	0	0	0	0	0	0	0	0	1
1	IFd	0	0	0	0	0	0	0	0	0	0	1
1	DR	0	0	0	1	0	0	1	0	0	0	0

Table 6 (continued).

		IEx	CEx	EEx	HM	FF	MOT	IDr	CDr	EDr	FdN	FdO	IFd
56	RG												
45	SG												
51	MO												
6	IE												
4	GE												
1	CE												
21	IL												
16	GL												
2	CL												
4	RL												
1	ALE												
10	IP												
5	GP												
1	AAE												
36	ATW												
14	ATB												
25	RW												
7	ALW												
15	BG												
1	ATQ												
9	LN												
8	LOT												
2	IEx	—											
3	CEx	1	—										
4	EEx	1	2	—									
6	HM	0	1	2	—								
1	FF	0	0	0	0	—							
6	MOT	0	0	0	0	1	—						
3	IDr	0	0	0	1	1	1	—					
1	CDr	0	0	0	1	0	0	1	—				
1	EDr	0	0	0	0	1	1	0	0	—			
2	FdN	0	0	0	1	0	0	2	1	1	—		
1	FdO	0	0	0	0	1	1	1	0	1	1	—	
1	IFd	0	0	0	0	1	1	1	0	1	1	1	—
1	DR	1	0	0	0	0	0	0	0	0	0	0	0

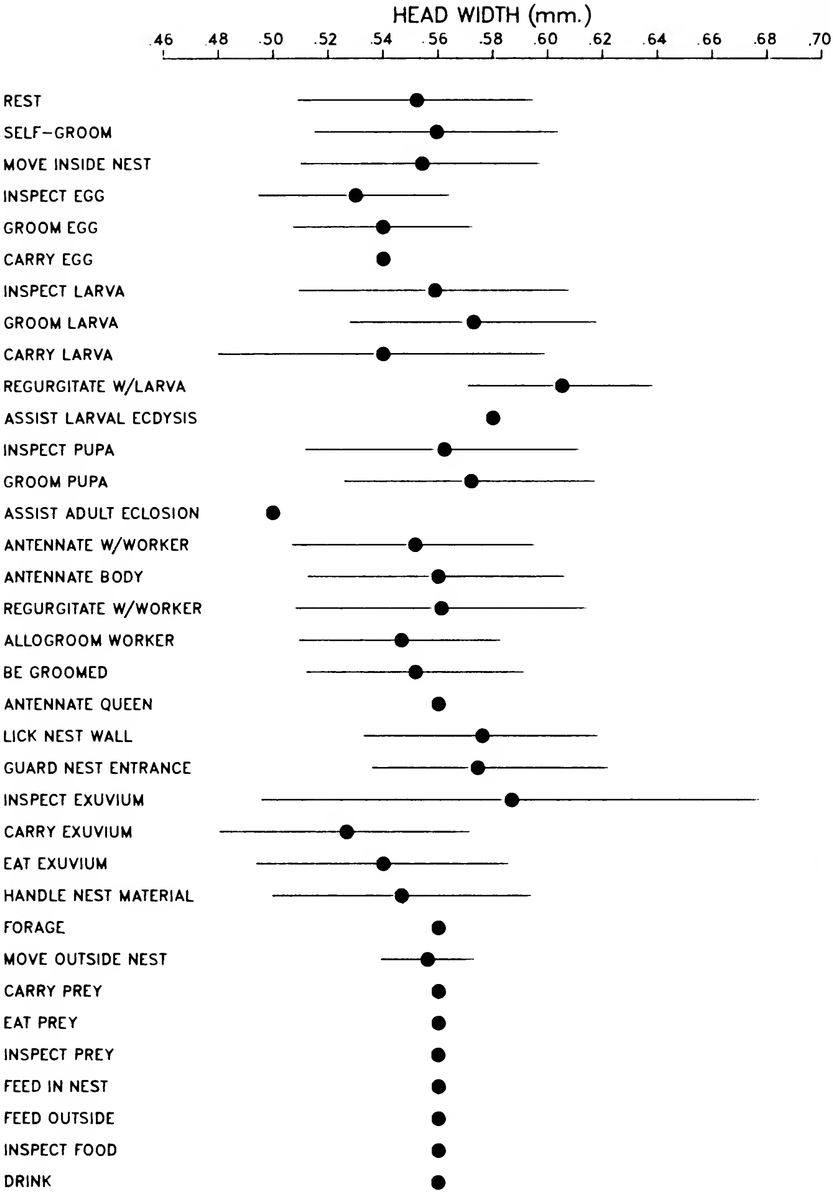

Figure 4. Head width distributions for workers exhibiting behaviors in the ethogram. Means and standard deviations are plotted.

Table 7. Results of ANOVA tests of mean head widths for workers exhibiting different behaviors. Starred entries indicate average head widths were significantly different (LSD tests; *P < .05).

	RE	SG	MO	IE	GE	CE	IL	GL	CL	RL
RE										
SG										
MO										
IE		*	*							
GE	*									
CE										
IL	*	*	*		*					
GL		*	*		*					
CL										
RL	*	*	*	*	*		*	*	*	
ALE										
IP					*					*
GP										
AAE										
ATW				*			*			*
ATB				*						*
RW				*			*	*		*
ALW				*						*
BG				*						*
ATQ										
LN					*					*
IEx										
LOT					*					*
CEx							*	*		*
EEx							*	*		*
HM										*
FF										
MOT				*			*			*
IDr										*
CDr										*
EDr										*
FdN										*
FdO										
IFd										
DR										*

to *L. longispinosus* (Herbers and Cunningham 1983); to correct for this different rearing condition comparisons below deleted the prey-handling behaviors reported for *L. ambiguus* (Table 3: IDR, EDR, CDR). In addition, colonies had been matched with respect to worker number in order to eliminate variation correlated with colony size (Table 2). Therefore, comparisons between these studies were not confounded by variation between observers, husbandry techniques, or colony size.

The two species are ecologically similar. Both inhabit temperate forests throughout eastern North America, nest in small plant cavities such as acorns, twigs, and hollow roots, and scavenge for arthropod parts. On the Huyck Preserve, *L. longispinosus* is more common, preferring deep woods, while *L. ambiguus* appears restricted to relatively open habitats; despite some microhabitat segregation, the two do co-occur in many places.

A subjective analysis of their overall demeanor suggests that *L. ambiguus* is the higher-tempo species (*sensu* Oster and Wilson 1978). That is, they are more excitable and appear to move faster than *L. longispinosus*. While this study was not designed to detect tempo differences, one set of behaviors clearly illustrated it: for the *L. ambiguus* colonies, certain workers were often stationed at the nest entrance. While there, they periodically roused to inspect the entrance, moving a few cm outside the opening before returning to their position. This combination (LOT, MOT) was observed for all 3 colonies (Table 3). By constrast, *L. longispinosus* workers only occasionally positioned themselves near the nest entrance, and the apparent guarding behavior was observed for only one of four colonies watched (Herbers 1982). Thus the more excitable nature of the presumed higher tempo species was evident in the colony ethograms.

Both species displayed a division of labor, with similar patterns of polyethism. Roles of brood care, social organization, and nest maintenance were identified in each. For *L. longispinosus*, though, foragers comprised a unique caste whereas in *L. ambiguus* foragers displayed other provisioning behaviors as well. Moreover, in *L. longispinosus* the division of labor was much tighter: very few instantaneous transitions between roles were observed, most of them between brood care and nest maintenance (Herbers and Cunningham 1983). For *L. ambiguus*, transitions among roles were more frequent (Table 5), although less common than chance expectation. Over 30-min. periods, workers of both species switched roles, but again, role-switching was far more common for *L. ambiguus* than for *L. longispinosus*. Therefore, although specialization occurred in both species, division of labor was considerably tighter for one.

A startling difference between species was the strong morphological bias underlying polyethism in *L. longispinosus* but lacking in *L. ambiguus*. Size differentiation according to task was clear in *L. longispinosus*; the pattern strongly corroborated influences of role and caste delineation from the transition matrix (Herbers and Cunningham 1983). For *L. ambiguus*, however, there were relatively few differences in average worker size among behaviors, and those few significant differences were not correlated with roles inferred from behavior transitions. Perhaps the absence of morphological correlation was due to the fact that the range of worker size was narrower for *L. ambiguus* (Figure 3) than *L. longispinosus* (Herbers and Cunningham 1983); a small size range of workers may have precluded task specialization by size for *L. ambiguus*.

Both species displayed considerable among-colony variation with respect to behavior frequency and time budgets. To ascertain the relative importance of within- and between-species variation, cluster analyses were performed. These techniques involve calculating similarity indices for all possible pairwise comparisons. Then each unit (i.e. colony) is placed in a dendrogram based on its similarity to every other unit. If behavior data reflect phylogeny, then the three *L. ambiguus* colonies should form one cluster while the four *L. longispinosus* form a second. Moreover, one might expect colonies with similar numbers of queens to cluster more closely to each other than colonies with different queen numbers.

The simplest comparisons used the matching coefficient, or number of behaviors shared by two colonies relative to the total number observed over all (Cole 1980). This similarity index utilizes information only on presence or absence of behavior types in the ethogram, thereby ignoring relative frequency. Analysis of matching coefficients yielded the dendrogram of Figure 5. This simplest clustering technique produced the satisfying results that *L. ambiguus* colonies were more closely related to each other than to *L. longispinosus* nests: the three formed a distinct cluster. Moveover, queenright *L. ambiguus* colonies were more similar to each other than to the queenless nest; this result, however, was simply an artifact of the presence of behaviors directed towards queens (ATQ, RQ, ALQ) in queenright but not queenless ethograms. Even so, *L. ambiguus* colonies did cluster as expected. However, the *L. longispinosus* nests did not. Two (L1-A and L1-B) clustered closer to *L. ambiguus* nests

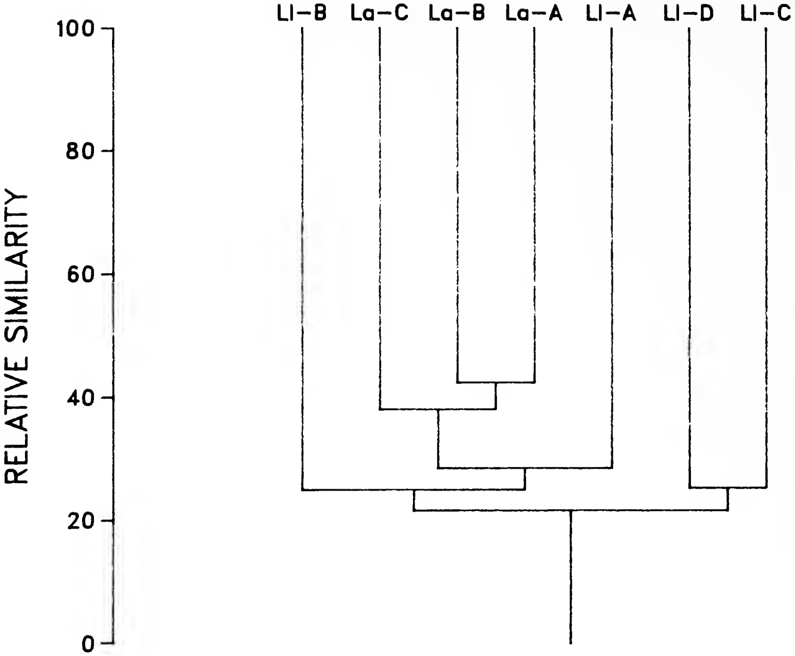

Figure 5. Dendrogram of similarity among *Leptothorax* colonies based on the simple matching coefficient.

than to conspecific nests (Figure 5). The simple matching coefficient which weighs all behaviors equally, therefore produced a dendrogram that gave satisfactory results for one species but far from pleasing results for the second. That is, differences among *L. longispinosus* nests were stronger than differences between species, based on simple matching coefficients.

A second type of cluster analysis used geometric distance between ethogram frequencies of the colonies. This technique incorporated information on frequencies of different behavior types, yielding results more biologically meaningful than the matching coefficient (Cole 1980). For this analysis, rest was excluded. A dendrogram of the seven colonies produced from ethogram frequencies is shown in Figure 6. All colonies were quite similar to each other (minimum similarity was 97.72 on a scale of 100) because proportion data were used. Use of frequencies changes the scale but not relative positions of colonies within the dendrogram. Just as with the simple matching coefficient, geometric distance between colonies failed to produce separate species clusters (Figure 6). Interestingly, queenright colonies of *L. ambiguus* clustered, as did monogynous colonies of *L. longispinosus*. However, an anomalous cluster was comprised of La-C and Ll-D, thereby reducing the significance of other clusters in the dendrogram. In sum, consideration of ethogram frequencies produced a dendrogram for which within-species variation swamped between-species variation.

A final dendrogram was produced from comparison of time budgets over all colonies (Figure 7), based again on geometric distance. This analysis was more discriminating than that based on ethograms (minimum similarity = 83.17). The dendrogram shows three *longispinosus* colonies clustered closely and three *ambiguus* clustered closely. The single aberrant entry was Ll-D, a polygynous

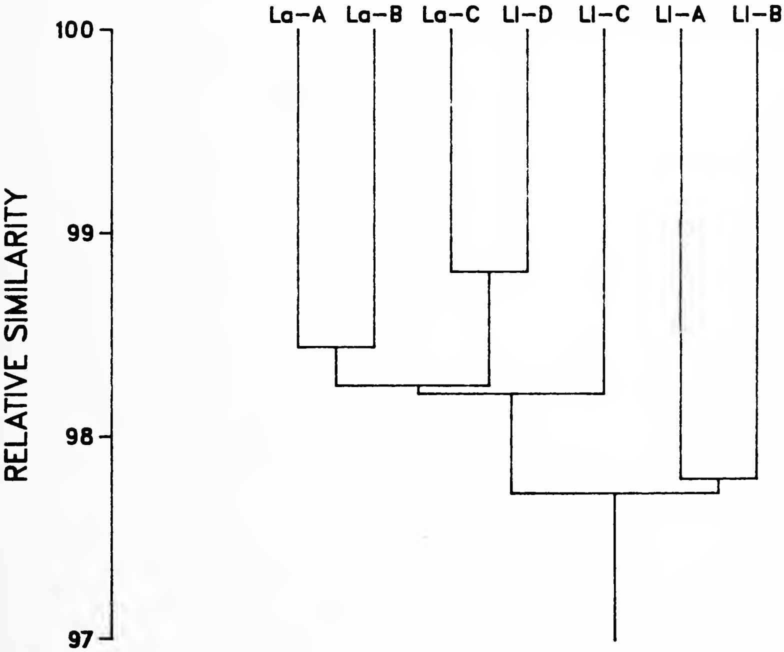

Figure 6. Dendrogram of similarity derived from geometric distance based on ethogram frequencies.

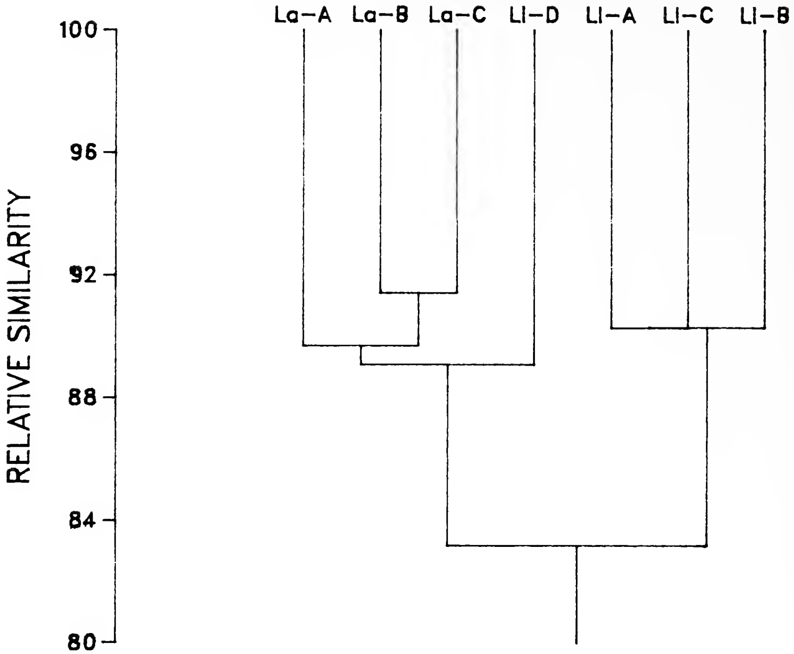

Figure 7. Dendrogram of similarity derived from geometric distance based on time budget frequencies.

longispinosus clustering with the three *L. ambiguus* colonies. Consideration of time budget data gave a reasonable but not perfect fit to expectation.

Of the three dendrograms produced, the best fit to expectation derived from time budget data. Even this best-fit tree, though, contained an anomaly. By no statistical means could I produce a cluster diagram that accorded perfectly to species identity. In no case did the two species separate into discrete clusters. Variation among colonies within a species therefore makes separation between species tenuous. Because most studies report data from a single colony, the utility of cross-species comparisons of behavior is severely limited. Moreover, ethograms themselves appear less discriminating than time budgets for separating out variation between species. It appears, then, that standard methods of reporting social organization (i.e. ethogram frequencies from a single colony) neglect critical information on between-colony variability and on time budgets.

Only with more extensive studies of within-species variability with respect to ethogram and time budget frequencies can valid between-species comparisons be drawn.

ACKNOWLEDGMENTS

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'PROTEST' SOUNDS OF A GRASSHOPPER: PREDATOR-DETERRENT SIGNAL?*

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INTRODUCTION

Some animals emit sounds when grasped or handled. Referred to as alarm, protest, distress or disturbance signals—the sounds themselves, the behavior accompanying their emission and the mechanisms responsible for their production have been described, analyzed and discussed (Haskell 1974). But only recently have experimental data become available in support of the oft-stated hypothesis that these sounds may startle a predator into releasing a noisy morsel (Bauer 1976; Smith and Langley 1978; Masters 1979; Buckler et al 1981).

The grasshopper *Pareuprepocnemis syriaca* Giglio Tos (Acrididae) when grasped, immediately begins to chirp (the biology and acoustic behavior of this grasshopper will be described separately). Though there are individual differences in intensity and quality of the sounds, males have a greater tendency to squeak while females tend to click. Emission of the sounds is easily observed to correspond to movements of the mouthparts; if the labrum is lifted, the mandibles can be seen rubbing against one another to the rhythm of the chirps. Immobilization of the mouthparts prevents sound emission.

It had been observed in our laboratory that on casual feeding of this grasshopper to representatives of several lizard families (Lacertidae, Scincidae, Gekkonidae) the grasshopper was captured, then promptly released. A male grasshopper introduced into the cage of the lizard *Lacerta danfordi* was caught head-first and held in the mouth of the lizard for several seconds, after which the lizard slowly opened its mouth and the grasshopper fell free. Several additional grasshoppers of this species were offered to two *Eublepharis macularius*, a gecko from Pakistan present in the vivarium at the

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time. They grabbed, then released the insects. Additional observations were then made with a microphone in the cage transmitting sounds to earphones worn by the investigator. A skink, *Mabuya vittata* caught and then released a sound-producing *P. syriaca* male; three geckos, *P. h. guttatus* each caught and promptly released sound-producing males of *P. syriaca.* These rejected grasshoppers were removed and immediately replaced by mute grasshopper nymphs of *L. m. migratorioides,* equivalent in size to the rejected *P. syriaca* males; the nymphs were caught and immediately consumed, one by each gecko. These preliminary observations raised the question: were the sounds emitted by the grasshoppers a factor in their release? The following experiments were designed to answer this question.

MATERIALS AND METHODS

Grasshoppers: Adult males of *P. syriaca* were field caught in the hills of Jerusalem a few days prior to experiments and were maintained in 60 l laboratory cages providing fresh plants, light and heat. As males were lifted from the cage for assignment to an experiment, the thorax was squeezed gently. Of 48 males squeezed, only three failed to produce sound. Half the sound-producing males were then silenced by releasing a drop of melted paraffin onto the closed mandibles; when it hardened, these males could no longer emit sound, though they hardly differed in appearance from untreated males.

Fourth instar nymphs of *Locusta migratoria migratorioides* R & F maintained in the gregarious state in stock cages in the laboratory, served as additional controls. Their size, dark color and small wing buds provided a phenotypically reasonable facsimile of the brachypterous adult male of *P. syriaca.* These nymphs did not produce sound when handled.

Predators: Ptyodactylus hasselquistii guttatus von Heyden was selected as the predator for the series of experiments. The candidacy of this gecko was supported by the following credentials: *P. h. guttatus,* a poikilotherm like *P. syriaca,* is at least partially sympatric with it and shares its biotope; it is an opportunistic insectivore; like *P. syriaca,* it emerges from its retreat in rock ledges and crevices in warm weather and has been known to feed during daylight (Werner 1965; Perry & Werner 1981); juveniles could handle a grasshopper the size of the *P. syriaca* male, while adults could handle even the large female; the frequency spectrum of the sounds of *P. syriaca* falls within the hearing range of *P. h. guttatus* (Werner 1976); and finally, a laboratory stock of this gecko was available. Though wild-caught, the geckos had been kept in captivity in the vivarium for months to years. Though the memory span of this gecko species is not known, it may well be that the long laboratory incarceration had dimmed recollections of possible previous encounters with this grasshopper and its ruse.

Experimental procedure: A series of three grasshoppers was introduced simultaneously into the cage of a gecko whose habitual diet of fly maggots had been removed at least a day previous: an untreated *P. syriaca* male, a silenced *P. syriaca* male and a fourth instar nymph of *L. m. migratorioides.* The insects were introduced at noon, prior to the peak activity hours of the gecko (Frankenberg 1979), and observations were made every half hour from noon to 5:00 PM and from 8:00 AM to noon. The first item eaten was assigned the number 1; the second item, 2; and the third, 3. If two grasshoppers disappeared between any two readings, both were assigned the same number. In the few instances in which all three grasshoppers were alive and apparently unharmed at the end of 24 hours, it was assumed that the gecko was not hungry; the experiment was not included in tallying the results. After an interval of several days, the gecko was used again. Silenced *P. syriaca* were checked at the end of the experiment to ascertain that they were indeed still unable to produce sound.

RESULTS AND CONCLUSIONS

In the cages of the 26 geckos tested, no untreated *P. syriaca* was ever the first to disappear and 69% were never eaten at all. The silenced *P. syriaca* was eaten first in 46% and the *L. m. migratorioides* nymphs in 78% of the experiments (Table 1 and Fig. 1). A G-test (Sokal and Rholf 1969) was carried out to test for independence between the three choices of prey and the order of predation. It was found significant ($G = 49.9$; $df = 6$, $p < 0.001$). A sign test (Siegel 1956) between each of the three combinations of paired insects for all the 26 instances in which a grasshopper was eaten showed that silenced *P. syriaca* were eaten before untreated ones in 18 experiments ($p \leqslant 0.002$), *L. m. migratorioides* were eaten before

Table 1: Order of predation* by the gecko *P. h. guttulatus*, on a choice of grasshoppers.

serial number gecko	normal *P. syriaca* male	silenced *P. syriaca* male	4th instar nymph, *L.m.m.*
1	0	1	1
2	0	1	1
3	0	1	1
4	3	1	2
5	3	2	1
6	2	0	1
7	0	1	0
8	0	1	1
9	2	3	1
10	3	1	2
11	0	2	1
12	2	3	1
13	0	0	1
14	0	1	0
15	3	1	1
16	0	2	1
17	0	0	1
18	0	1	0
19	3	1	2
20	0	0	1
21	0	2	1
22	0	1	1
23	0	2	1
24	0	0	1
25	0	2	1
26	0	0	1

*The numbers 1, 2, and 3 represent order of predation; 0 indicates that the grasshopper was alive at the end of the 24 hr test period. The same number for more than 1 grasshopper indicates that they were consumed between the same two observation periods.

the untreated *P. syriaca* in 23 experiments ($p \leq 0.001$) and before silenced ones in 14 experiments (p = n.s.). It is therefore concluded that the protest sounds produced by *P. syriaca* apparently reduce predation on it by *P. h. guttatus*.

DISCUSSION

To a hungry caged gecko offered a choice between fly maggots and grasshoppers, the latter are invariably preferred. However, it is apparent from the present results that the appetite for grasshoppers may be tempered by their behavior. In the present case, mandibular sounds emitted by *P. syriaca* appeared to interfere with predation by this gecko.

Because of its confinement in the cage of the gecko during experiments, a grasshopper which had chirped its way to freedom was prevented from escaping its predator as it might in the wild. *P. syriaca,* though it cannot fly, is an excellent jumper and under natural field conditions would probably have jumped far and hidden itself well before the predator had recovered from its encounter.

The sound itself has a wide frequency spectrum such as that characterizing alarm calls of birds (Marler 1957; Morton 1977). The utility of sounds such as these might include conspecific warning, since these grasshoppers occur in loose aggregates. However, holding a chirping male in close proximity to conspecifics, or playing the recorded sound back into a cage of *P. syriaca* failed to produce any discernible reaction.

It was observed that these grasshoppers are often seized headfirst. It is suggested that the hollow bones of birds, or the large buccal cavity of lizards may act as a resonating chamber, enhancing the intensity of the insect's sounds or vibrations.

For the few grasshopper species known to produce mandibular sounds spontaneously or in encounters with conspecifics, an intraspecific communicative function has been suggested: (*Paratylotropidia brunneri,* Alexander 1960; *Oedaleonotus fuscipes,* Varley 1939; *Calliptamus italicus,* Faber 1949) but no experiments have been reported in support of this hypothesis. Henry (1942) reports that *Mesambria dubia* emits a shrill creak when seized and investigation may reveal that this sound, like the protest sound of *P. syriaca* studied here, may play a predator-deterrent role.

Whether a remnant of an intraspecific communicative cue or a language of predator deterrence, a signal such as that presented here has quite probably been playing a part in the evolutionary history of the struggle for survival in this species.

ACKNOWLEDGMENT:

This paper is intended to answer the question of Dr. David Blondheim, who at age 10 asked his mother (SAB) why *P. syriaca* made those strange noises with its mouth when you caught it. Thanks are extended to Dr. N. Ben-Eliahu and to Profs. R. Galun,

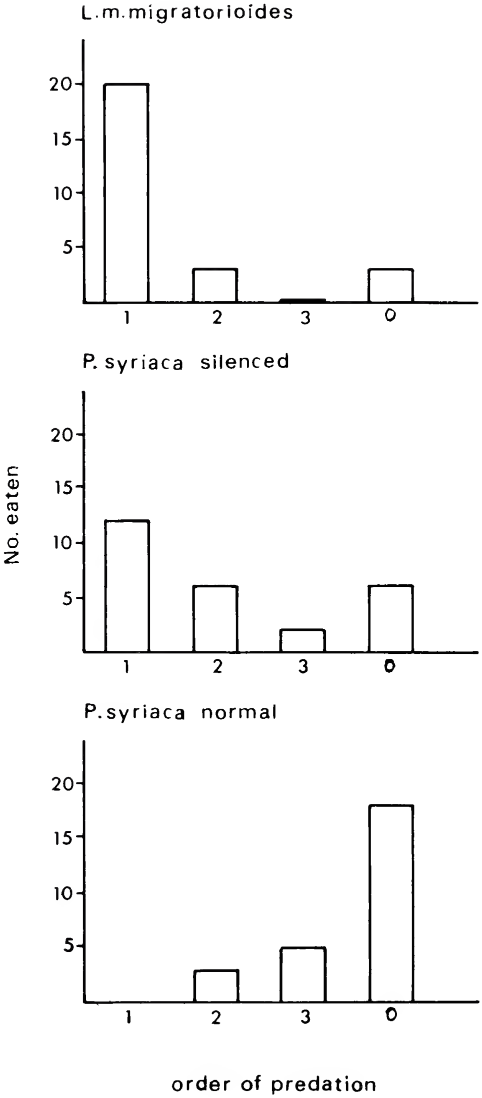

Fig. 1. Order of predation on sound producing and silenced *P. syriaca* males and mute nymphs of *L. m. migratorioides*.

Legend: The numbers 1, 2, and 3 in the abscissa represent order of predation; 0 indicates that the grasshoppers were alive at the end of the 24-hr. test period.

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SUMMARY

Mandibular sounds produced by the grasshopper *Pareuprepocnemis syriaca* Giglio Tos, when seized, appear to reduce predation on it by a probable natural predator, *Ptyodactylus hasselquistii guttatus* von Heyden, an insectivorous gecko. Sound-producing grasshoppers which had been silenced by treatment in the laboratory, untreated sound-producing grasshoppers, and silent *Locusta migratoria migratorioides* nymphs were introduced simultaneously to the geckos. Survival of normal, sound-producing *P. syriaca* far surpassed that of both controls.

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AGE POLYETHISM: ITS OCCURRENCE IN THE ANT *PHEIDOLE HORTENSIS*, AND SOME GENERAL CONSIDERATIONS.

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Introduction

A main theme of eusociality is division of labor (Wilson 1971, 1975), which can be based on physiological differences (as in the case of the reproductive queen and sterile workers), morphological (size) differences among workers, or age differences within a physical class. In social insects both age and physical classes can comprise castes, that is, groups of individuals which perform specialized labor for sustained periods of time (physical castes: Oster and Wilson, 1978; Wilson, 1980a,b; Herbers, 1980; age castes: Oster and Wilson, 1978; Porter and Jorgenson, 1981; Mirenda and Vinson, 1981; Seeley, 1982). We constructed an ethogram for the Indo-Australian ant *Pheidole hortensis*, and tested the general hypothesis of division of labor in the worker caste by seeking to answer these questions:

1. Is there division of labor between physical castes?
2. Is there division of labor among age classes within a physical caste?
3. And if there is age polyethism, is it continuous or discrete? (See Wilson 1976a.)

We will consider and discuss each question separately, and then compare our results with those from other studies on social insects. In particular we will contrast age polyethism in *Pheidole hortensis* with that of a New World *Pheidole* species, *P. dentata*.

Materials and Methods

Data Collection

Three colonies of *Pheidole hortensis* were collected in July 1979 from virgin rainforest at Gilmalé, Sri Lanka by Anula Jayasuriya.

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The ants were identified by E. O. Wilson, and voucher specimens deposited in the collection at the Harvard Museum of Comparative Zoology. Colonies thrived and produced brood in artificial nests made of glass tubing of 5 mm diameter (approximately that of twigs in which wild colonies have been found (Jayasuriya 1979), and fitted with moist cotton plugs. Colonies were maintained at 26° C while observations and experiments were carried out.

As is typical of this genus, *P. hortensis* has a completely dimorphic worker caste. And, as is true for many ant species in general, newly eclosed *P. hortensis* are quite light in color, and darken as they age. Using the method first described by Wilson (1976a), we found that based on these color differences and the degree of pigmentation of body parts each physical caste could reliably be separated into five color or age classes (see Appendix I). Using the obvious size and color differences, ethogram data on workers of different ages was compiled from 24 hours of observation on one colony over a ten week period.

The nest tube and surrounding area were watched, and every observed act was noted along with the age class and physical caste of the ant performing it. During the 24 hours of observation 3,689 acts of 25 behaviors were recorded for minor workers, and 256 acts of six behaviors for majors. At the end of the study the colony consisted of 192 minors, 32 majors, brood, and the queen.

Data Analysis

Completeness of the behavioral repertory was assessed by statistical comparison with a lognormal Poisson distribution (Bulmer 1974, Fagen and Goldman 1977).

The hypothesis of age-based division of labor was tested with a standard χ^2 comparison between observed performance frequencies by each age class for behaviors, and expected frequencies generated with the following formula (Altmann and Altmann 1977):

$$E_{ij} = \frac{(B_i)(n_j)}{N}$$

E_{ij} = Expected frequency of Behavior$_i$ by age class$_j$
B_i = Observed frequency of Behavior$_i$ by all age classes
n_j = Number of ants in age class$_j$
N = Total number of ants in all age classes combined

We excluded from analysis behaviors with frequencies $< 1\%$ of all behaviors performed by that physical caste; for *P. hortensis* that gives a possible frequency per behavior of about 25, or five occurrences per age class, under the null hypothesis.

Associations between age class and behavior were assessed by a relative performance measure (RPM). We calculated the probability that ants of a particular age class will perform a given behavior, and divided those ratios by the highest such probability for that behavior. Thus

x = frequency of behavior$_i$ performance by ants of age class$_j$,
y = frequency of all behaviors by age class$_j$,
z = highest such frequency for that behavior$_i$, and RPM = $(x \div y) \div z$.

Finally, any attempt at an ergonomic assessment requires that one distinguish between task and non-task behaviors. We use the terms as follows. "Behavior" means a logical unit like grooming, made up of one or more physical acts, such as drawing the tibial comb over the antennae. "Task" is used in the sense of Oster and Wilson (1978) to denote a set of acts which achieve some purpose of the colony. Thus there are task and non-task behaviors, and though all tasks are behaviors, not all behaviors are tasks.

RESULTS

1. Completeness of Repertory.

The repertory of each physical caste separately and of the species as a whole was judged complete, based on statistical comparison with a lognormal Poisson distribution (Bulmer 1974, Fagen and Goldman 1977). For minors, the observed repertory size is 25 behaviors, and the estimated size is 26, with a 95% confidence interval of [23, 29]. For majors, six behaviors were observed, and six estimated, with a 95% confidence interval of [5, 7]. For *P. hortensis* the observed repertory includes 31 behaviors, with 33 estimated, and a 95% confidence interval of [30, 36].

2. Division of labor by physical castes.

Comparison of the behavioral repertories of the two physical castes shows that there is, with the exception of trophallaxis, no overlap in task performance (Table 1). Of the tasks carried out, brood care, food acquisition, and allogrooming are performed by minors and defensive tasks by majors. Defense by minors was seen only when the colony was experimentally submitted to attack by other ant species, and even then the two physical castes performed different tasks: minors pinioned foreign ants, making it easier for majors to snip them up.

	MINOR	MAJOR
Selfgroom	789 (.21)	110 (.43)
Allogroom Minor	136 (.04)	0
Allogroom Major	70 (.02)	0
Allogroom Queen	9 (.002)	0
Carry Egg	307 (.08)	0
Carry Larva	1235 (.33)	0
Carry Pupa	149 (.04)	0
Groom Egg	24 (.01)	0
Groom Larva	223 (.06)	0
Groom Pupa	225 (.06)	0
Assist Larval Eclosion	114 (.03)	0
Assist Pupal Eclosion	6 (.001)	0
Trophallaxis w/Larva	25 (.01)	0
Trophallaxis w/Minor	48 (.01)	8 (.03)
Trophallaxis w/Major	5 (.001)	0
Trophallaxis w/Queen	2 (.001)	0
Retrieve Food	186 (.05)	0
Forage	22 (.01)	0
Eat Brood/Exuvia	37 (.01)	0
Eat Dead Adult	26 (.01)	0
Carry Brood/Exuvia	46 (.01)	0
Carry Dead Adult	7 (.001)	0
Carry Meconium	1 —	0
Carry Nest Material	1 —	0
Eat Solid Food in Nest	4 (.001)	0
Patrol at Food	0	52 (.20)
Patrol Arena	0	22 (.08)
Guard	0	63 (.25)
Totals	3685 (1.00)	255 (1.00)

Table 1. Ethogram of *Pheidole hortensis.* Observed frequencies are followed by values in parentheses indicating the frequency of each act relative to the total number of behaviors performed by a physical caste.

Both castes exchange food with minors, but trophallaxis is relatively more important in the majors' repertory. Though its actual frequency is low, it constitutes their only non-defense task, and it comprises 5% of the tasks they perform versus only 1% for minors. In fact, when all categories of trophallaxis by minors are combined (with majors, larvae, and the queen as well as with minors), trophallaxis still comprises only 2% of the minors' task repertory. This relative frequency of the behavior by majors led us to ask whether majors serve as a replete or "cask" caste, as in *Camponotus fraxinicola* (Wilson 1974). *Pheidole hortensis* majors with full gasters show a three-fold weight increase, but we were unable to perform the critical experiments and test for proportionate weight gain. However, in random surveys of the colony, replete majors (those with distended gasters) performed virtually none of the behaviors typcial of majors (Table 2). During experimentally induced attack (assault with sympatric *Tetramorium* spp.), replete majors engaged in defense only if the attack was severe (many ants) or extended in time. How much of this inactivity by "storage" majors is due to protecting the food supply and how much to relative inability to move is not clear.

Another potential set of caste differences relates to the granivorous habits of many *Pheidole* species in which minors harvest and majors mill seeds. In an attempt to observe such caste differences in *P. hortensis*, we offered grass, vegetable, and bird seeds of various sizes and fat contents. All were ignored by both physical castes.

3. Division of labor by age classes within a physical caste.

To answer this question, we tested the null hypothesis that each age class should perform a given behavior in proportion to the number of ants in that age class. Thus, in a colony with three age

	"Replete" Majors	Non-"Repletes"
Patrol at Food	12	66
Patrol Arena	0	8
Attack Intruder	1	18
Guard Nest Entrance	0	20

Table 2. Behavioral differences within the major worker caste of *Pheidole hortensis*. The numbers of individuals observed performing various acts during random surveys of the colony are presented.

classes comprising 30, 20, and 50% of the total colony, there is no age polyethism if those age classes perform 30, 20, and 50% respectively of any task. The data show that the age classes of both physical castes do not perform tasks in proportion to their numbers (Table 3). On the basis of χ^2 comparisons, for most tasks with adequate sample sizes the null hypothesis can be rejected because there are significant differences between the observed and expected frequencies. This indicates that there is age-based division of labor in both physical castes (Table 4). Four tasks by minors (assist ecolsion, allogroom majors, trophallaxis with minors, and carry exuviae) are performed without apparent age bias, and eight behaviors by minors and one by majors were observed too rarely to permit assessment.

Thus of behaviors with an adequate sample size, for *P. hortensis* minors 13 of 17, and for majors four or five, behaviors show age-based division of labor.

4. Continuous versus discrete age castes.

Wilson (1976a) states that division of labor is discretized if there is an exclusive association between (sets of) tasks and age class(es) and that it is continuous under all other conditions of age class/task association. The general question of age polyethism has two parts. Given that some tasks are performed more or less often by certain age classes, can adjacent age classes be combined because they show similar performance patterns? And second, are such associations between age class(es) and tasks exclusive? To test for associations, we calculated relative performance measures (RPM) for each age class by behavior. This descriptive way of treating the data controls for variation in age class size and in number of performances observed per age class, and it permits comparison between frequently and rarely occurring behaviors, as well as comparisons of age class performances within and between behaviors.

Figure 1 shows that there are no consistent similarities between the relative performance probabilities for any pairs of adjacent age classes. This implies that no pair of age classes can be combined, and that these age classes do differ behaviorally, representing real castes. It is also clear that the associations between age castes and tasks or groups of tasks are not exclusive: the age-based division of labor is continuous rather than discretized in both the minor and

MINOR WORKERS AGE CLASS	I(15)	II(27)	III(45)	IV(24)	V(81)	ROW TOTAL 192
Selfgroom	78	159	221	95	228	781
Allogroom Minor	10	5	38	22	61	136
Allogroom Major	5	7	25	11	22	70
Carry Egg	11	121	77	30	68	307
Carry Larva	20	93	470	159	493	1235
Carry Pupa	1	18	42	24	64	149
Groom Egg	5	7	6	3	3	24
Groom Larva	8	28	94	38	55	223
Groom Pupa	8	57	65	23	72	225
Assist Eclosion	10	26	23	14	41	114
Trophallaxis w/ Larva	1	1	15	2	6	25
Trophallaxis w/ Minor	1	7	19	6	15	48
Forage	0	0	0	2	20	22
Retrieve Food	0	2	24	39	121	186
Eat Brood/Exuvia	0	2	22	3	10	37
Eat Dead Adult	0	1	14	2	9	26
Carry Exuvia	0	6	13	4	23	46
COLUMN TOTAL	158	540	1168	472	1311	3654
MAJOR WORKERS AGE CLASS	I(5)	II(15)	III(5)	IV(3)	V(4)	32
Selfgroom	13	58	30	8	1	110
Guard	3	4	14	20	22	63
Patrol at Food	0	0	2	3	47	52
Patrol Arena	0	0	0	1	21	22
COLUMN TOTAL	16	62	46	32	91	247

Table 3. Observed frequencies with which each age class (I through V) performed various acts. Values in parentheses indicate the number of individuals in each age class.

MINORS	N	X^2	P
Selfgroom	781	65.9	**
Allogroom Minor	136	13.4	.01
Allogroom Major	70	7.8	NS
Carry Egg	307	178.7	**
Carry Larva	1235	212.3	**
Carry Pupa	149	13.1	.02
Groom Egg	24	14.1	.01
Groom Larva	223	58.6	**
Groom Pupa	225	34.8	**
Assist Eclosion	114	7.9	NS
Trophallaxis w/Larva	25	18.8	.001
Trophallaxis w/Minor	48	8.7	NS
Forage	186	79.3	**
Retrieve Food	22	22.5	**
Eat Brood/Exuvia	37	27.9	**
Eat Dead Adult	26	15.0	.01
Carry Exuvia	47	5.2	NS
MAJORS			
Selfgroom	110	23.7	**
Guard	63	13.3	.01
Patrol at Food	52	290.1	**
Patrol Arena	22	138.8	**

Table 4. X^2 values and significance levels for differences between observed and expected behavior frequencies for the five age classes within each physical caste. ** indicates that the P values were so small they do not appear in the X^2 table and are highly significant. NS, no significant difference. Only behaviors with frequencies $\geqslant$ 1% are included. N = total number of acts observed.

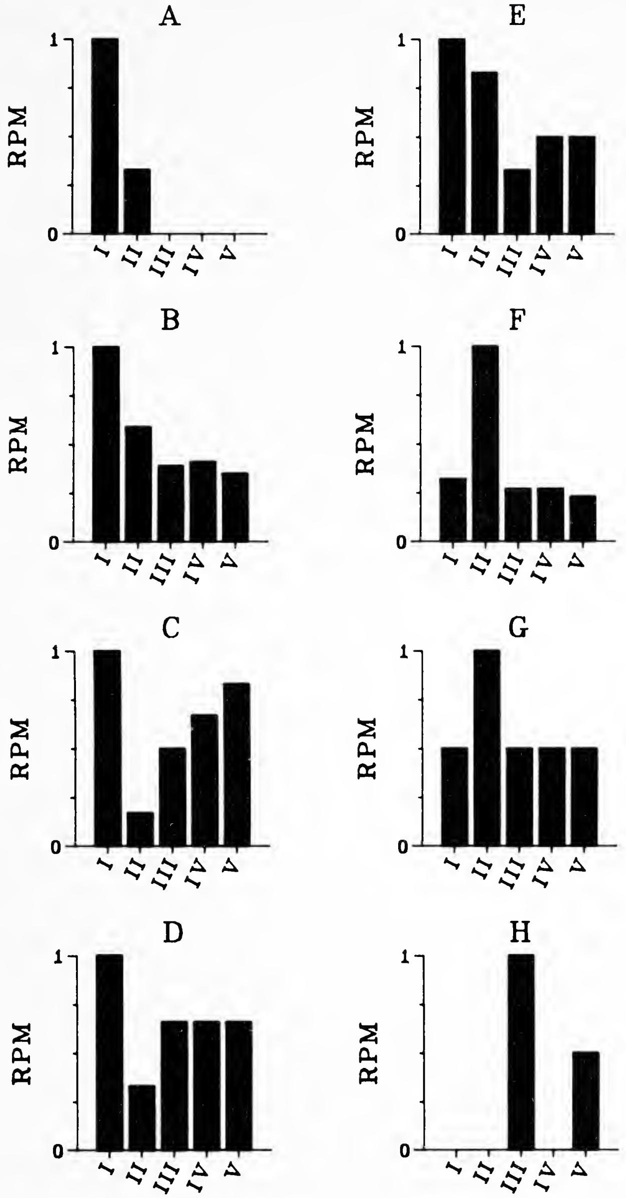


Figure 1. Relative performance measures (RPM) of various behaviors in the repertories of major (MJ1-MJ4) and minor (A-Q) workers of *Pheidole hortensis*. Roman numerals I-V correspond to worker age classes.
Additional details in Materials and Methods.

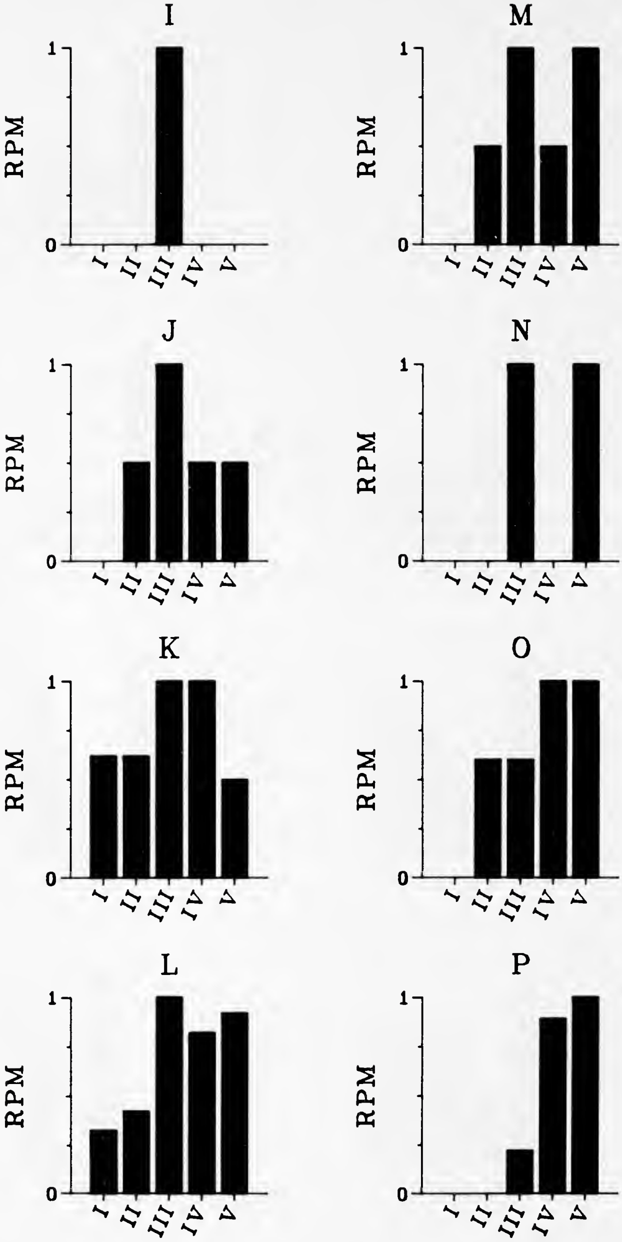
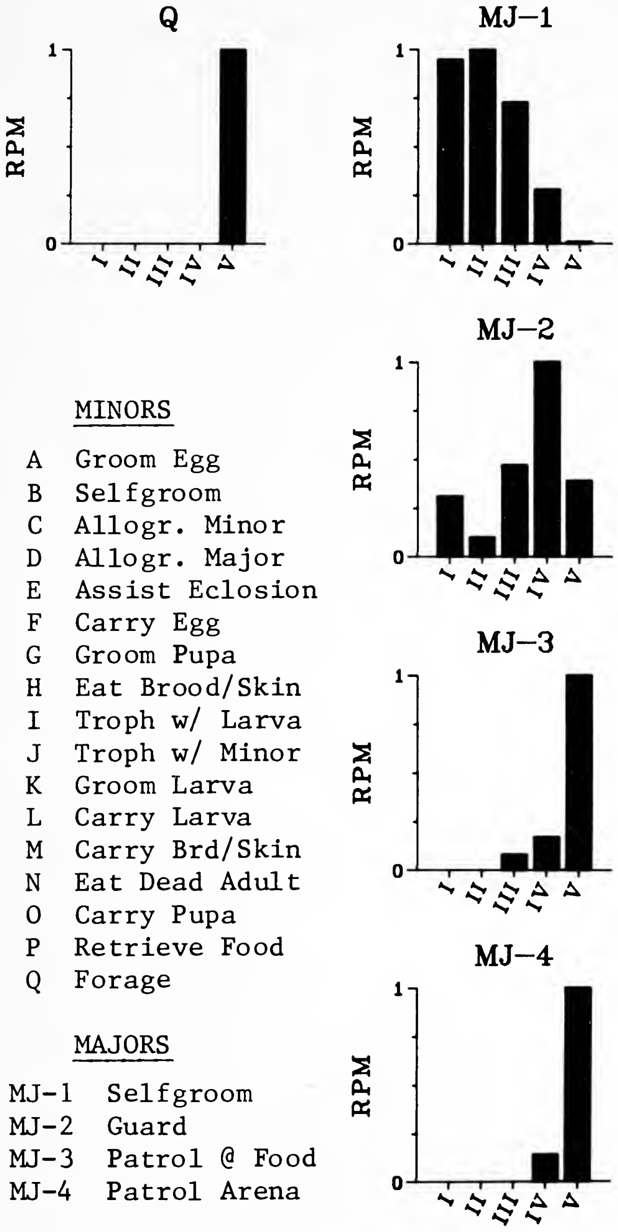


Figure 1. (Continued)



MINORS

A	Groom Egg
B	Selfgroom
C	Allogr. Minor
D	Allogr. Major
E	Assist Eclosion
F	Carry Egg
G	Groom Pupa
H	Eat Brood/Skin
I	Troph w/ Larva
J	Troph w/ Minor
K	Groom Larva
L	Carry Larva
M	Carry Brd/Skin
N	Eat Dead Adult
O	Carry Pupa
P	Retrieve Food
Q	Forage

MAJORS

MJ-1	Selfgroom
MJ-2	Guard
MJ-3	Patrol @ Food
MJ-4	Patrol Arena

Figure 1. (Continued)

major physical castes. For instance, in Figure 1 examine the minors' behaviors F, G, and E, and the series H through N. The relative performance measures for tasks F and G are highest for age class II, yet age classes II and I have similarly high RPM for task E. Or, in the second case, for all the tasks H through N, age class III shows very high RPM, but the task/age class association is not exclusive. For K, M, and N at least, other, but not necessarily adjacent age classes, show similarly high RPM.

Discussion

P. hortensis exhibits both physical and age castes, and the latter show continuous rather than discretized polyethism. We will compare these results with results from other species, and consider some of their general implications for the study of age polyethism.

1. Repertory size and numerical considerations.

Both repertory size and the proportion of rarely occurring behaviors in *P. hortensis* are in the same range as those of other species. Numbers of behaviors in repertories judged complete by Fagen and Goldman analysis are: 27 for workers of monomorphic *Leptothorax* species (Wilson and Fagen 1974) and for minor workers of *Orectognathus versicolor* (Carlin 1982), and 28 each for minor *Pheidole dentata* (Wilson 1976a), *Formica perpilosa* (Brandão 1979), and *Camponotus sericeiventris* (Busher 1982). Extremes may be represented by minor repertories of *Solenopsis geminata, S. invicta,* and *Zacryptocerus varians*: 17, 20, and 38, respectively (Wilson, 1976b, 1978). Repertories for majors range from two (*Solenopsis geminata*, Wilson 1978) to 24 (*Orectognathus versicolor*, Carlin 1982); for the dimorphic *Z. varians* and *P. dentata*, major repertories are 11 and nine (Wilson 1976a and b). Total repertories for all these species range from 20 to 40 behaviors.

Given the similarity in repertory size for minor workers of both *P. hortensis* and *P. dentata*, it may seem odd that in *P. hortensis* considerably fewer behaviors (13 vs 23) are performed with age bias. The difference results from the respective criteria used to reject rarely occurring behaviors from analysis. Because he does not make statistical comparisons, Wilson rejects only 2 of 28 behaviors on grounds of insufficient data. However, when the cut-off criterion used for *P. hortensis* is applied (rejected behaviors with frequencies $< 1\%$ of those performed by that physical caste) the number of behaviors rejected for *P. dentata* increases from two to seven of 28 ($N=1,222$; Wilson 1976a). Thus the appropriate comparison of age-biased behaviors among behaviors with frequencies $\geqslant 1\%$ shows a similar situation for the two: 13 of 17 behaviors for *P. hortensis*, and 15 of 19 for *P. dentata*. Of behaviors performed without apparent age bias, allogroom majors and trophallaxis with majors, are in common to the two species. (In general ant repertories include high proportions of infrequent behaviors: for minors 10 of 28 (*P. dentata* —Wilson 1976a), 27 of 38 (*Zacryptocerus varians*—Wilson 1976b) 7 of 28 (*Formica perpilosa*—Brandão 1979), 14 of 27 (*Orectognathus versicolor*—Carlin 1982) and 9 of 28 (*Camponotus sericeiventris*—Busher 1982). Although some castes have small repertories (majors of *P. dentata* and *Solenopsis geminata*,—Wilson 1976a, 1978), many other castes show similar proportions of infrequent to frequent behaviors (Wilson and Fagen 1974, Traniello 1978, Brandão 1979, Carlin 1982).

2. Age-based division of labor.

It is a virtual truism that among social insects older workers forage and have little or nothing to do with brood care. Yet in *P. hortensis* older workers, in addition to performing all foraging and food retrieval (P and Q, Figure 1), show high RPM for several brood-care tasks (K, L, M, and O). We suggest that these represent labor cohorts, based on ant experience or colony need. They could arise via the mechanism of task fixation, a feedback-based task stabilizing mechanism documented in wasps (Forsyth 1978) and suggested for the ant *Amblyopone pallipes* (Traniello 1978). An individual performs some task (e.g., trophallaxis with larvae), receives positive feedback (continually finds hungry larvae), and over time does not switch to other tasks because the positive feedback does not cease. The susceptibility of individuals to task fixation could vary so that even in a system with age-based task-switching, task fixation might override age-based behavioral change.

Although it remains to be demonstrated whether such fixation occurs in *P. hortensis*, we wish to point out one possible consequence of task fixation and the resultant caste "atypical" behavior. A colony labor profile by age class could be an artifact of previous colony needs and activities, specifically for the period previous to the study by just less than an average worker life span. For instance, suppose that a colony engaged in high brood production several weeks previous to observations. There would have been both need and opportunity for much brood care, and also opportunity for fixation on brood tasks. Further imagine that the food supply then dwindled and brood production decreased. Some older workers are fixated on and keep performing brood care tasks, leaving little need for younger workers to perform this task, and therefore little opportunity for task fixation. At the time of observation, RPM for brood care would show older castes performing proportionately more brood care. Yet it may be misleading and actually incorrect to draw the conclusion that older castes "typically" perform brood care. RPM are epiphenomena of past (and current) colony labor needs, and may say less about age castes as such than about behavioral flexibility and colony requirements. Therefore, appropriate conclusions must consider this, and include at least a time frame, plus consideration of colony age, size, and circumstance.

3. Continuous versus discrete castes; roles

By definition, discretization of age castes is a direct consequence of roles (a group of tasks) linked by high transition probabilities, and exclusively or principally performed by a particular age caste (Oster and Wilson 1978, Wilson 1976a). Our results for *P. hortensis* show a continuous mode and, therefore, no roles. This differs from results of other age polyethism studies. Wilson (1976a) and Seeley (1982) find behavioral discretization by age, and roles. Both also argue that spatial efficiency is its basis, with each role (suite of tasks) involving a set of physically proximate contingencies. If that is the case, differences among the species and especially between *P. hortensis* and *P. dentata*, could account for the results. Colony size in *P. hortensis* is a few hundred, in comparison with up to a thousand in *P. dentata*. The former nests in twigs or small nuts, the latter in logs often with underground galleries. Thus for *P. hortensis*, spatial efficiency may be an irrelevant consideration.

However, other more basic considerations may also be involved. Mirenda and Vinson (1981) elaborate on Wilson's (1976a) use of "caste" and "subcaste." Because the two treat their data differently, comparisons are difficult, but we suggest that the castes and subcastes of Mirenda and Vinson correspond to the discrete and continuous modes of Wilson. Mirenda and Vinson consider as subcastes "(a) groups of individuals within each caste whose behaviour is statistically but not completely differentiated from other such groups and (b) groups intermediate in behaviour between two or more castes, but not completely distinct from any caste" (1981, p. 417). Both descriptions, and especially the latter, seem to fit the criteria for a continuous caste system—overlap in frequency distribution of age classes performing various tasks—rather than the discrete system, characterized by an exclusive association between an age class and a group of tasks. If this correspondence is indeed correct, we may be that much closer to a functional understanding of labor roles, spatial efficiency, caste, and how task performance of individual ants sum to performance of whole castes. It is also noteworthy that although Mirenda and Vinson do not address the question of spatial efficiency as such, their results show a strong correspondence between ant age, location, and "career," their "role" analogue.

Clearly there is age-based division of labor in *Pheidole hortensis*. It does not seem to follow traditional role patterns, nor is it obvious which pattern it does follow. Therefore, we suggest two factors which must be considered for *P. hortensis* in particular, and in studies of age polyethism in general: "atypical" behavior due to labor cohorts, and role performance. Both have been documented for physical castes (Oster and Wilson 1978); one for age castes (Oster and Wilson 1978, Mirenda and Vinson 1981, herein). Because of these specializations, we suggest that mean behavioral performances by age classes may not be sufficiently fine-grained for detailed ergonomic analysis, and that the study of behavioral specialization and its ergonomic consequences requires bouts of continuous observation of individually marked animals throughout their lives.

SUMMARY

We present evidence for and describe age-based division of labor in the Indo-Australian ant *Pheidole hortensis*. Both the minor and major physical castes exhibit age polyethism, and in both castes age

polyethism is continuous rather than discretized. There is virtually no overlap between the sets of tasks performed by the two physical castes. These findings differ in several respects from those reported in two other studies of age polyethism (in the New World *P. dentata* and in *Apis mellifera*), and raise some interesting questions about labor roles in social insects.

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APPENDIX I

Hue and degree of pigmentation for the color (age) classes of the two physical castes of *P. hortensis*.

MINORS.

Class I—White-yellow: head and thorax, pale white/light grey; gaster, light grey; petiole and femur, pale white/light yellow; tibia, grey.

Class II—light yellow: head and thorax, light yellow with amber outlines, especially dark amber edging the mandibles; gaster, medium grey; petiole, dark yellow with amber outlines; femur, light yellow/brown; tibia, grey.

Class III—yellow-grey: head and thorax, dark yellow, head with grey in occipital region; gaster, dark grey; petiole, yellow; femur, dark yellow/brown; tibia, grey.

Class IV—amber: head and even mandibles, solid amber; thorax, amber with some brown; gaster, dark grey/black; petiole, amber with brown outlines; femur, brown; tibia, grey.

Class V—amber-grey: head, dark amber with brown streaks through occipital region; thorax, solid amber; gaster, black/dark grey; petiole, amber/brown; femur, brown; tibia, grey.

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Class I—white-yellow: head, pale white; thorax and petiole, pale white/light yellow; gaster, light grey.

Class II—yellow: head and thorax, yellow; petiole, light brown/amber.

Class III—amber: head, dark amber; thorax, dark yellow; gaster, dark grey; petiole, light brown/amber.

Class IV—medium brown: head, dark brown with lighter tinges; thorax, amber; gaster, dark grey; petiole, dark brown.

Class V—dark brown: head and gaster, dark, dark brown/black; thorax and petiole, dark brown.

DAILY RHYTHMS IN SOCIAL ACTIVITIES OF THE HARVESTER ANT, *POGONOMYRMEX BADIUS*[*]

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Daily cycles in behavior are well known throughout the animal kingdom. There is some evidence that the activities of ant colonies are temporally organized so that, at a given time of day, a certain set of tasks is done. This study explores that possibility by examining temporal patterns in the social behavior of the harvester ant, *Pogonomyrmex badius*. Such patterns should be distinguished from circadian rhythms to which conform endogenous, physiological events exhibited by individual animals (e.g. McCluskey 1958 and 1965). The present study is concerned with daily rhythms in social activities performed by groups of ants. Two questions are addressed: 1) Are certain tasks performed at characteristic times of day? 2) How do activity rhythms vary among different colonies?

There have been many studies of daily temporal patterns in the overall activity levels of ant colonies, measured as the numbers of ants entering or leaving the nest (Levieux and Diomande 1978a, Hunt 1974, Hansen 1978, Van Pelt 1966), or the numbers of ants in certain areas for specified durations (Janzen 1967, Levieux and Diomande 1978b, Levieux 1979a and 1979b, Golley and Gentry 1964). Temporal patterns of overall activity level are well documented for several *Pogonomyrmex* species (Hölldobler 1970 and 1976a, Whitford and Ettershank 1975, Whitford *et al.* 1976). Some authors have described temporal patterns of selected social activities of various ant species (Möglich and Alpert 1979, Janzen 1967, Levieux and Diomande 1978a and 1978b), including *Pogonomyrmex* (Willard and Crowell 1965, Hölldobler 1976b). But, except for Hölldobler's (1976b) study of mating activity, the cited work presents no systematic data on temporal patterns in behavior other than entering and leaving the nest. In some recent field studies of

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Pogonomyrmex behavior, I found activity rhythms of various colony tasks (Gordon 1983b and 1983c).

P. badius has received much less attention than other *Pogonomyrmex* species, perhaps because it is geographically isolated from them. Nevertheless, the scanty literature on *P. badius* behavior contains some descriptive reports that suggest the existence of activity rhythms in this species as well (Van Pelt 1966, Hangartner *et al.* 1970). The present study was made in the laboratory. In this way, activity rhythms could be investigated more systematically than would be possible in a field study.

METHODS

Four queenright colonies (colonies 1, 2, 3, and 4), each containing 300-600 workers, were observed for 30 days from March 1, 1983 through April 2, 1983. Colonies were kept in open, soil-filled terraria, and fed Bhaktar-Whitcomb (1970) diet or chopped mealworms. The study colonies had all been kept in the laboratory for about one year. They were chosen for the study because they had been consistently active and healthy since being brought into the laboratory. The laboratory temperature was maintained at 27° C (±1°).

Observations of each colony were made 5 times daily, once in each of five 100-minute time periods, as follows: Time period 1 (TP1), 9:50–11:30; TP2, 11:30–13:20; TP3, 13:20–14:50; TP4, 14:50–16:30; TP5, 16:30–18:10, and usually in the middle of the time period at the following five times; 10:40, 12:20, 14:00, 15:40 and 17:20. Overhead fluorescent lights in the laboratory were on from 7:30 to 23:00. A lamp with a 60 watt bulb was placed from 30 to 50 cm above each colony as a heat source. These lamps were illuminated daily from 11:30 until 16:30. Thus, during the first and last observations, room lights but not individual lamps were on; during the 2nd–4th time periods, individual lamps were on as well. Temperatures on the terraria surfaces, both under the individual lamps and at other points on the opposite side of the tanks, were measured with a thermistor (Yellow Springs Instrument Co. #408). Temperature measurements were made in the terraria of the four study colonies and also in those of four other colonies maintained in an identical manner. The colonies were fed every other day immediately after the 12:20 observation.

All behavior observed taking place outside the nest was classified as one of five activities: Foraging, Nest Maintenance, Patrolling, Midden Work, and Convening (Table 1). For each nest, observations noted the numbers of ants in each of the five activities. The sum of the five numbers is the total number of ants observed outside the nest. A total of 600 observations were made on the four colonies.

The data were analysed by profile analysis (Timm 1975) to determine whether the numbers of ants engaged in particular activities depend significantly on both activity and time of day. Since the times of foraging corresponded so obviously to the time the ants were fed, foraging was not considered in the analysis.

Profile analysis is a series of 3 multivariate analyses of variance (manova), described in detail below. Factors considered were colony and date as main effects. The hypothesis that the intercept was significantly greater than zero was also considered as a main effect. Date was considered to be a random effect. Each analysis was made using the data from all 4 colonies, then repeated for each colony separately. Data were log-transformed to ensure that ratios, not numbers of ants, were used in the analysis, making it possible to compare colonies of different sizes.

RESULTS

The first multivariate analysis of variance tested for significant differences in overall activity among time periods. For each day of observation of a given colony, a new variable was created for each time period by adding the (log-transformed) numbers of ants doing nest maintenance, midden work, convening and patrolling. Four differences between time periods were used as observation variables (Table 2, top).

The results (Table 2) show that colonies are significantly more active in TP2 than in TP1, in TP3 than in TP4, and in TP4 than in TP5. The overall activity level of the colony has a peak in the middle of the day.

The next manova tested for significant differences in the numbers of ants engaged in each activity, summed over all time periods. A new variable was created by adding, over all five time periods for each day of observation of a particular colony, the (log-transformed) number of ants doing each activity. Three differences

Table 1. Classification of activities of exterior workers of *P. badius* in laboratory colonies

Foraging	A.	Standing at the food dish, eating.
	B.	Taking food items into nest.
	C.	Piling sand on food.
Nest Maintenance	A.	Carrying sand out of nest, putting it down and going back into nest.
	B.	Rearranging sand on terrarium surface.
Patrolling	A.	Walking around edge of terrarium, inspecting sides with antennae.
	B.	Walking around with abdomen tucked under thorax, with frequent stops and changes of direction.
	C.	Pawing at sand with front legs and inspecting the resulting small depression with antennae.
Midden Work	A.	Repiling midden.
	B.	Standing on midden.
	C.	Carrying objects (dead ants, food bits, twigs, etc.) to midden
Convening	A.	Standing with a group, grooming each other.
	B.	Standing with a group, self-grooming.
	C.	With a group milling around slowly under the lamp, sometimes inspecting others of the group with antennae.

between activities were used as observation variables (Table 2, middle). The results (Figure 1 for foraging, and Table 2 for the other activities) show that the activities may be ranked as follows, according to the numbers of ants engaged in each one: Midden work > patrolling > convening > nest maintenance > foraging.

Figure 1 shows the activity rhythms of each of the four study colonies. The third manova tested whether some pairs of activities are performed by significantly different numbers of ants when the activities are compared at particular times (Table 2, bottom). Significant differences mean that the rate at which the colony invests workers in a particular task depends both on the task and on the time of day. The results (Table 2) may be best understood by inspecting Figure 1. For example, keeping in mind that the data are log-transformed, activity-time period difference number 4 (Table 2) can be stated as follows: The ratio of number of ants doing midden work to number convening in time period 1 is significantly greater than the same ratio in time period 3. In other words, from TP1 to TP3 convening increases faster, or has a steeper slope, than does midden work. This difference is especially clear in the graph for colony 4.

The overall results in Table 2 lead to the following conclusions about slope differences in Figure 1: Convening rises to a peak in TP2, increasing more rapidly than midden work, then declines more rapidly than either midden work or patrolling. In general, patrolling declines throughout the day while nest maintenance increases. The fact that activity-time period differences 7, 8, and 9 are not significant indicates that all 4 activities change at about the same rate from TP3 to TP4.

The colony main effect was significant ($p > 0.05$) for time period differences 1, 2, and 4, for activity differences 1, 2, and 3, and for activity-time period differences 1, 4, 5, 6, and 10. The date main effect was significant for time period difference 3, activity difference 3, and activity-time period differences 3, 7, 8, and 11.

Mean temperatures of the terraria surfaces are shown in Figure 2, as a function of the time of day.

DISCUSSION

The behavior of a colony clearly is temporally patterned. It has frequently been suggested that, in harvester ants, overall activity

Table 2. Results of profile analysis.

Results of test for differences in activity level by time period are shown at the top of the table; for test for differences in number of ants in each activity, middle of the table; for test for activity-time period differences (parallelism test), bottom of the table. Data are log-transformed. Symbols used are ** $p > 0.01$; *, $p > 0.05$; #, marginal significance. TP = time period; MW = midden work; CN = Convening; PT = patrolling; NM = nest maintenance.

	Source: Intercept as main effect (DF = 29)	Overall (All 4 colonies)	
		F	Mean Difference
	TP1 — TP2	346.4**	−1.24
	TP2 — TP3	3.9	−0.07
	TP3 — TP4	17.8**	0.19
	TP4 — TP5	411.5**	1.19
	Midden Work — Convening	206.6**	1.43
	Convening — Patrolling	175.8**	−1.37
	Patrolling — Nest Maintenance	256.9**	2.55
1.	TP1,MW — TP1,CN — TP5,MW+ TP5,CN	8.6**	−0.19
2.	TP1,CN — TP1,PT — TP5,CN + TP5,PT	9.5**	0.17
3.	TP1,PT — TP1,NM — TP5,PT + TP5,NM	48.1**	0.25
4.	TP1,MW — TP1,CN — TP3,MW+ TP3,CN	115.4**	0.59
5.	TP1,CN — TP1,PT — TP3,CN + TP3,PT	132.9**	−0.60
6.	TP1,PT — TP1,NM — TP3,PT + TP3,NM	13.5	0.11
7.	TP3,MW — TP3,CN — TP4,MW+ TP4,PT	2.9	−0.06
8.	TP3,CN — TP3,PT — TP4,CN + TP4,PT	0.5	0.03
9.	TP3,PT — TP3,NM — TP4,PT + TP4,NM	5.7*	0.06
10.	TP4,MW — TP4,CN — TP2,MW+ TP2,CN	51.9**	0.21
11.	TP4,CN — TP4,PT — TP2,CN + TP2,PT	28.6**	−0.21
12.	TP4,PT — TP4,NM — TP2,PT + TP2,NM	10.5**	−0.12
13.	TP4,MW — TP4,NM — TP2,MW+ TP2,NM	11.2**	−0.12
14.	TP3,PT — TP3,NM — TP5,PT + TP5,NM	26.9**	0.14
15.	TP2,PT — TP2,NM — TP5,PT + TP5,NM	32.9**	0.19

level (sometimes called foraging activity) is related to temperature (Rogers 1974, Whitford and Ettershank 1975, Bernstein 1979). My results support this suggestion. During TP2 through TP4, when the individual lamps were on and the soil temperatures were highest (Figure 2), colonies were significantly more active than they were during time periods 1 and 5. Temperatures in the field often become so high that ants are inactive from midday until early evening. In the

Table 2. (continued).

By Colony							
18		14		16		13	
F	Mean Difference	F	Mean Difference	F	Mean Difference	F	Mean Difference
203.8**	−1.65	106.9**	−1.1	65.2**	−0.96	113.7**	−1.22
0.3	0.04	7.9**	0.15	49.3**	−0.44	0.2	−0.04
6.1**	0.18	13.5**	0.27	8.1**	0.19	4.1#	0.16
422.9**	2.05	68.8**	0.89	42.8**	0.73	89.3**	1.13
152.9**	2.07	86.6**	1.55	25.5**	0.89	67.1**	1.22
117.9**	−1.74	17.9**	−0.69	60.5**	−1.52	101.8**	−1.51
75.1**	1.86	152.7**	2.02	717.5**	3.05	152.4**	3.28
18.1**	−0.49	1.1	−0.14	1.2	−0.09	0.04	−0.03
12.9**	0.39	1.6	0.16	0.1	0.02	0.9	0.10
22.7**	0.31	29.1**	0.36	13.3**	0.18	2.4	0.14
40.9**	0.63	11.6**	0.35	10.6**	0.27	114.1**	1.10
40.3**	−0.63	15.9**	−0.36	23.1**	−0.39	121.5**	−1.03
1.3	0.05	19.8**	0.26	3.8	0.10	0.3	0.04
1.7	0.20	1.8	−0.07	3.2	−0.07	0.3	−0.04
0.5	0.05	0.04	0.01	0.3	0.02	0.4	0.04
3.5	0.08	2.0	0.06	0.3	0.02	2.1	0.09
13.9**	0.23	51.9**	0.25	46.1**	0.29	2.2	0.09
13.4**	−0.24	20.8**	−0.18	22.3**	−0.21	10.5**	−0.21
1.6	−0.08	16.9**	−0.22	4.7*	−0.15	0.4	−0.05
2.4	−0.10	12.1**	−0.15	1.2	−0.07	3.5	−0.16
23.9**	0.26	3.3	0.10	4.1#	0.08	2.2	0.10
14.6**	0.26	17.9**	0.26	12.1**	0.21	0.7	0.05

laboratory conditions of the present study, temperatures never became that high. Time of food availability has also been suggested as a factor regulating activity rhythms of foraging ants (Hansen 1978, Hunt 1974, Levieux 1979a and 1979b, Levieux and Diomande 1978a and 1978b), and, in fact, all four study colonies foraged primarily at the time of peak food availability.

However, fluctuations of temperature and of food availability may not account completely for the activity rhythms observed here. For example, the results show that rates of change in the numbers of ants in each activity vary with the time of day. This means that ants doing different tasks respond differently to environmental cues such

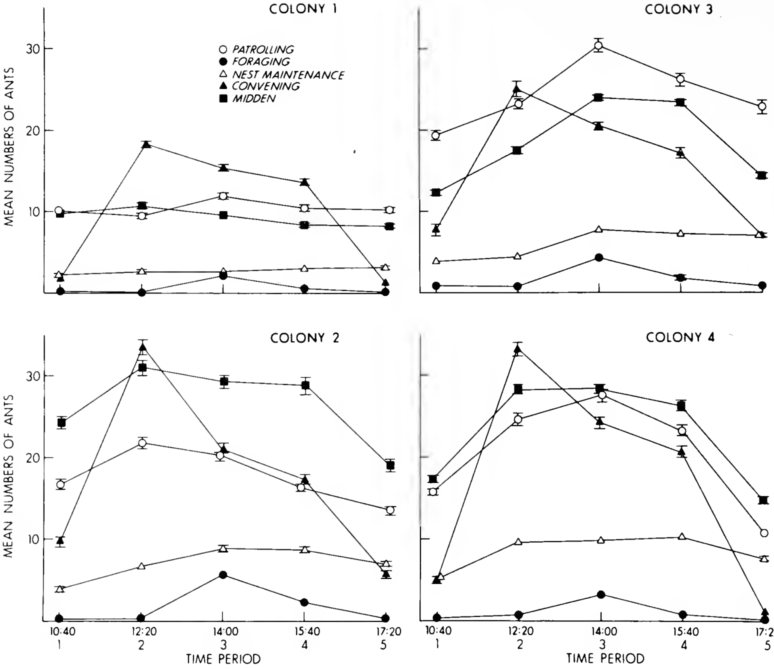

Figure 1. Daily activity rhythms.

The mean numbers of ants engaged in each activity are plotted as a function of time of day. Times shown are the usual observation times. Error bars show standard error of the mean. No error bar is present when the size of the error bar was smaller than that of the symbol for a point in the graph.

as temperature and food availability. In *P. badius*, the five activities described here are performed by four distinct groups of ants (midden work and patrolling are done by the same individuals) (Gordon 1983d). Whether there are intrinsic physiological rhythms causing these different groups to be active outside the nest in different numbers, depending on time of day, is a question still to be explored.

Temporal patterns in overall activity level are known to exist in many species of ants. Further research on such species may reveal more detailed patterns of particular activities. Cognizance of such patterns is relevant to the design of further behavioral experiments,

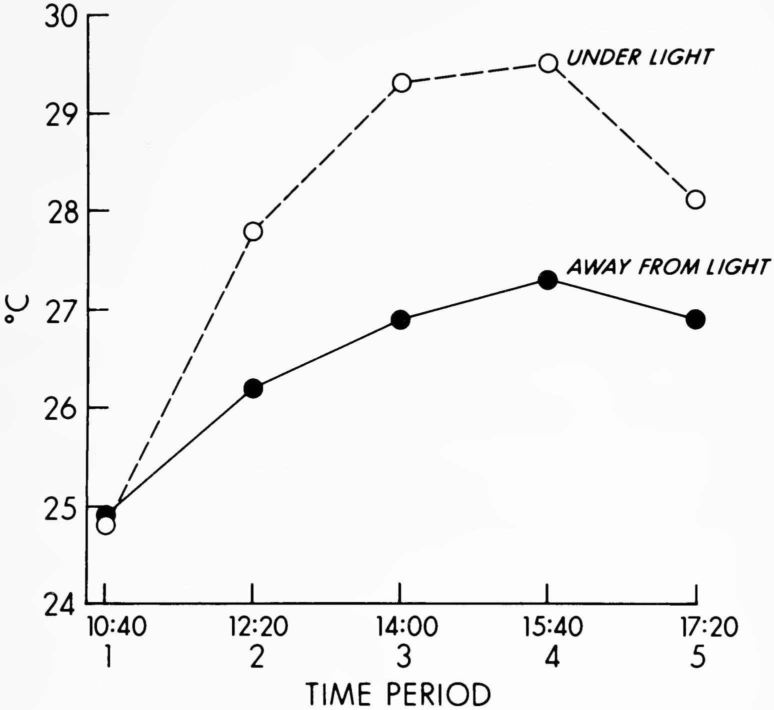

Figure 2.
Mean temperature on the soil surface, both directly under the lamp and on the opposite side of the tank, plotted as a function of the times of measurement.

because results may be affected by the times of day at which data are collected (e.g., Gordon 1983d and 1983b).

The results show that, though colonies are similar to one another, distinct colonies have distinct activity rhythms (Figure 1). Thus, intercolony variation should also be taken into account when designing experiments. The main point of this study, then, is not that the activity rhythms of *P. badius* are those shown in Figure 1, but that each colony exhibits *some* temporal pattern of activities. In every colony, certain tasks are undertaken at characteristic times. Clearly, we need to consider temporal patterns when we endeavor to understand the social organization of the ant colony.

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BEHAVIOR OF THE SLAVE-MAKING ANT, *HARPAGOXENUS AMERICANUS* (EMERY), AND ITS HOST SPECIES UNDER "SEMINATURAL" LABORATORY CONDITIONS (HYMENOPTERA: FORMICIDAE)[1]

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Introduction

Slave-making ants are social parasites that raid the nests of host-species colonies, capture brood, and transport it back to the parasite colony. There, host-species workers eclosing from captured brood become "slaves" which perform all the usual worker-ant functions in the slave-maker colony (see review by Buschinger *et al.* 1980).

Harpagoxenus americanus (Emery) is an obligatory slave-making parasite which forms mixed colonies with workers of three *Leptothorax* host species: *L. ambiguus* Emery, *L. curvispinosus* Mayr, and *L. longispinosus* Roger. Young *H. americanus* queens found colonies by entering host-species nests, killing or driving off the adults, and inducing the host-species workers which subsequently mature from worker pupae in the nest to rear a brood of slave-maker workers (Wesson 1939). These parasite workers then augment the slave worker force by raiding other host-species nests.

Wesson (1939) and Alloway (1979) observed *H. americanus* slave raids in the laboratory by placing populous *H. americanus* nests in

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experimental arenas containing an arbitrarily selected host-species target nest. Under these circumstances, *H. americanus* raids begin when one or more slave-maker workers leave the parasite nest to explore the arena. Whenever such a "scout" discovers the entrance to the target nest, it returns to its own nest and recruits a raiding party. After dispersing the adult residents of the target nest, the raiders carry the captured brood back to the slave-maker nest (Alloway 1979).

Recently, it was discovered that *H. americanus, L. ambiguus, L. longispinosus* and probably *L. curvispinosus* form facultatively polydomous colonies (Alloway *et al.* 1982; Del Rio Pesado & Alloway 1983). Colonies of the three host species are also facultatively polygynous (Alloway *et al.* 1982). However, *H. americanus* colonies apparently never contain more than one inseminated egg-laying queen (Buschinger & Alloway 1977).

In the present paper, we augment previous findings by presenting behavioral observations of *H. americanus* and its slaves interacting with ants from other *H. americanus* colonies and from unenslaved host-species colonies. These observations supplement previous findings for three reasons:

1. The interactions observed were among ants from colonies collected adjacent to one another in nature.
2. The ants were observed for several weeks.
3. Ants from small and "weak", as well as populous and "strong", *H. americanus* and host-species colonies were observed.

MATERIALS AND METHODS

Nests of *H. americanus, L. ambiguus,* and *L. longispinosus* were collected on the Erindale Campus of the University of Toronto, in Mississauga, Ontario. Since we wanted to observe the behavior of ants from parasite nests occurring close together in nature, we looked for places where there were at least two *H. americanus* nests within less than 2 m of each other. Whenever such a spot was found, we laid out a 2 m by 2 m quadrant centering on the parasite nests and then collected, numbered, and mapped the location of all *H. americanus* and host-species nests in the quadrant. Altogether, 19 quandrants were collected; but two pairs of adjacent quadrants were combined to permit observation of large groups of *H. americanus* nests. See Del Rio Pesado (1983) for a complete demographic description of the colonies studied.

In the laboratory, the ants were removed from their natural nests, established in artificial nests (Alloway 1979), and censused. Then they were transported to a naturally lighted, unairconditioned room, where the field maps were used to reconstruct among the artificial nests the same spatial relations as had existed among the natural nests. In addition to these "natural" quadrants, we also observed one control quadrant containing two *H. americanus* nests from different collection sites. In some cases, individual ants were marked. See Del Rio Pesado and Alloway (1983) for a detailed description of these procedures.

Ad libitum behavioral observations were made 8 h a day, 5 days a week during June, July, and August. Five quadrants were observed in 1980; and 14 quadrants were observed in 1981. An assistant was employed during 1981 to permit more detailed behavioral observations.

RESULTS

Raiding

The slave-makers raided or attempted to raid the nests of adjacent colonies. Most raided nests belonged to unparasitized *L. ambiguus* and *L. longispinosus* colonies. However, in the control quadrant and in the two "natural" quadrants containing more than one *H. americanus* colony, the slave-makers from one colony raided nests belonging to another parasite colony.

Alloway (1979) observed that the raiding behavior of *H. americanus* is not highly stereotyped even when ants from a single parasite nest are interacting with ants from a single target nest. In the present study in which the slave-makers were often interacting with ants from several naturally adjacent colonies, the results were so complex and variable that their complete presentation requires a separate description of the events in each quadrant. See Del Rio Pesado (1983) for such an account. Here we summarize those observations.

Much of the behavioral variability could be attributed to demographic variability. One demographic factor was the number of nests in each quadrant. The initial number of slave-maker nests in different quadrants ranged from 2 to 6, while the initial number of host-species nests ranged from 0 to 17. This variablity in nest density is probably correlated with small-scale differences in the availability and suitability of natural nest sites. In addition, the history of slavery in a particular spot might affect nest density, since *H. americanus* colonies may destroy or drive away adjacent host-species colonies.

Another kind of demographic variability involved the number of nests occupied by single colonies. Some *H. americanus* and some host-species colonies were initially polydomous. In the laboratory, some initially polydomous colonies moved into a single nest (became monodomous) before any significant interactions with members of other colonies occurred; but others remained polydomous during behavioral interactions with ants from other colonies (Del Rio Pesado & Alloway 1983). To raid host-species nests successfully, *H. americanus* colonies must deploy raiding parties containing several *H. americanus* workers. In successful polydomous *H. americanus* colonies, the slaves made this possible by carrying all or almost all the parasite workers to a single nest before raiding began. While so doing, the slaves sometimes (but not always) moved the entire *H. americanus* colony into one nest. In other polydomous slave-maker colonies where the slaves failed to assemble the parasite workers in this way, many slave-makers were killed during uncoordinated attacks on target nests.

A third kind of demographic variability involved differing degrees of maturity among slave-maker colonies. When collected, some of our *H. americanus* colonies were incipient (*i.e.* initially contained only an *H. americanus* queen, some slaves, and a brood), while others already possessed slave-maker workers. Wesson (1939), studying ants from the east-central United States, found that *H. americanus* began to raid only after the overwintered *H. americanus* brood had matured. In contrast, overwintered parasite workers in our colonies from southern Ontario began to raid before all their overwintered brood had matured. As young *H. americanus* workers eclosed, they augmented the raiding forces of mature colonies and initiated raiding in incipient colonies. Thus, mature colonies could start raiding earlier and had the potential to raid longer than incipient colonies. In both incipient and mature colonies, first-year *H. americanus* workers were involved in all phases of raiding (*i.e.* scouting, attacking target nests, and transporting captured brood).

In this last respect, *H. americanus* apparently differs from the European *H. sublaevis* (Nylander), in which slave-makers in mature colonies do not begin to scout until their second year (Buschinger *et al.* 1980). We also observed an apparent effect of experience on scouting. On their first forays in the spring or after eclosion, scouts ventured only a short distance from their nest. The distance travelled became greater as the number of forays increased.

Alloway (1979) observed that *H. americanus* workers could scout either singly or in small groups. In the present study, only individual scouting was observed. Alloway (1979) also observed that, whenever a lone scout discovered the entrance to a target nest, it would return to its own nest and recruit a raiding party. However, in the present study, lone scouts sometimes attacked target nests by themselves. Nevertheless, lone *H. americanus* workers rarely, if ever, captured any brood. Invasion of a target nest by a single slave-maker excited the target-colony workers and often caused them to attack the intruder. Some lone intruders were killed.

The success of raider recruitment was highly variable. Upon entering its nest, a scout that had discovered the entrance to a target nest was immediately surrounded by a cluster of slave-makers and slaves. Shortly thereafter, the scout would make its way back to the nest entrance and leave. That the slave-maker was now almost certainly laying down a pheromone trail was indicated by the fact that it conspicuously dragged its gaster along the substrate while being closely followed by a column of other slave-makers and/or slaves. All scouts that had located target nests excited their nestmates; and most initiated processions. The variable success of raider recruitment seemed to depend on the "steadiness" of the recruiter's movement and orientation while leading the procession. Successful recruiters moved steadily forward without making any abrupt turns. Less successful recruiters stopped for prolonged periods and changed direction abruptly. Such hesitation caused nestmates to leave the procession; and badly disoriented scouts lost all their followers. Some initially unsuccessful individuals later relocated the target nest and went back to their nest to try again.

The arrival of a raiding party containing several *H. americanus* workers and (often) a number of slaves always caused "alarm" in the target nest. Workers and queens would snatch up larvae and pupae and make frenzied efforts to leave the nest. Whenever they found a place where they could safely deposit any brood with which they had escaped, the workers returned to the invaded nest and carried off more brood. The slave-makers countered all these efforts by guarding the nest entrance (Alloway 1979) and by charging and snapping at target-nest workers.

Alloway (1979) observed that target-nest workers always fled with whatever brood they might manage to carry almost immediately after the arrival of a raiding party. In these circumstances, the slave-makers did not use their large, specialized mandibles against the residents of target nests. In the present study, a broader range of target-nest resistance and slave-maker aggression were observed. The workers in some target nests fled very shortly after the raiders arrived; and, in these cases, the slave-makers injured very few, if any, target-nest residents. However, in other target nests, the workers bit and stung the invaders. The slave-makers crushed such resistance by employing their large mandibles to dismember their adversaries. Slaves in raiding parties also attacked target-colony workers, but it was apparent that the success of the always outnumbered raiders depended mainly upon the activities of the slave-makers.

After all the adults had been killed or driven from the target nest, the raiders transported the captured brood to the slave-maker nest. Most brood was carried by slave-makers, although slaves sometimes carried one or two larvae or pupae. Brood transport generally lasted only a few hours, after which the raiding party vacated the target nest. Only one *H. americanus* colony manifested the phenomenon reported by Wesson (1939) of raiders requiring 2 or 3 days to complete brood transport. After the raiding party had abandoned the target nest, its previous inhabitants often returned.

Other Behavior

Our observations confirm that *Leptothorax* slaves do most of the work in *H. americanus* colonies. The slaves forage for food, feed and groom the parasite adults and brood, and defend the area around *H. americanus* colonies by attacking foraging workers from neighboring *Leptothorax* colonies whenever they are encountered near an *H. americanus* nest. The slave-makers do none of these things on a regular basis. Indeed, the parasites appear never to leave their nests except to scout (*i.e.* to "look for" target nests). Since scouting slave-makers invariably return to the same nest from which they departed, the parasites are even dependent on their slaves to move them from nest to nest in polydomous colonies. Nevertheless, *H. americanus* workers possess certain vestiges of non-parasitic behavior. Inside their nest, *H. americanus* workers routinely groom one another, periodically share regurgitated food with other slave-makers and slaves, and occasionally engage in what appears to be brood care. Parasite workers may even eat if they encounter food while scouting. On such occasions, one can infer that the slave-maker is scouting (and not foraging) from the fact that, after eating, it continues to "look for" a target nest, instead of returning directly to its own nest, regurgitating to nestmates, and recruiting them to the food source. *H. americanus* workers never recruit or follow nestmates except in the context of slave raids.

Although *Leptothorax* slaves generally look after the slave-makers, we observed many instances of slave aggression against slave-makers. In 9 slave-maker colonies, we saw slaves biting and dragging *H. americanus* workers out of slave-maker nests. A few *H. americanus* workers lost parts of appendages as a result of these attacks. However, we never saw a slave-maker attack a slave; and we never witnessed anything resembling a generalized "slave revolt". Individual *H. americanus* workers were attacked by individual slaves. The same slave which attacked one slave-maker would feed and groom another; and any slave-maker that was attacked by one slave was cared for by others.

A somewhat different kind of slave aggresssion was seen in one of our incipient *H. americanus* colonies. When collected, this colony possessed a single nest containing an *H. americanus* queen, 17 *L. longispinosus* workers, and a brood. Throughout the course of our observations, the slaves fed and groomed the parasite queen and tended her brood through the pupal instar. However, the slaves killed all eclosing *H. americanus* workers. Similar events have been observed in other incipient *H. americanus* colonies (R. J. Stuart, personal communication).

As we have noted, slaves ordinarily defend the area surrounding *H. americanus* nests against incursions by unenslaved *Leptothorax* workers. Similarly, unenslaved *leptothorax* workers defend areas around their nests against incursions by *Leptothorax* slaves. These phenomena, together with the fact that both enslaved and unenslaved *Leptothorax* workers fight for their respective colonies during slave raids, indicate that enslaved and unenslaved *Leptothorax* workers generally recognize one another as belonging to different colonies. However, these behavioral barriers between colonies are sometimes imperfect in the case of incipient slave-maker colonies. For example, let us consider the situation in Quadrant 3.

When collected, this quadrant contained two incipient *H. americanus* colonies, each of which was located near an apparently unparasitized *L. longispinosus* nest. In both cases, some of the slaves entered the nearest *L. longispinosus* nest without being attacked; and, reciprocally, some of the seemingly unenslaved *L. longispinosus* workers entered the *H. americanus* nest with impunity. On one occasion, a slave picked up the *H. americanus* queen in one of the parasite nests and carried her to the nearest *L. longispinosus* nest. The arrival of the parasite female caused all the adults in that nest to flee. Later the same day, a slave carried the *H. americanus* queen back to the nest from which she had come. Then, over a 12-day period, many of the workers which had originally fled moved in and began to live peacefully with the *H. americanus* queen in her nest.

Equally interesting events involved the other incipient parasite colony in the same quadrant. A slave which could peacefully enter the nearest *L. longispinosus* nest began to carry brood and workers from that nest into the *H. americanus* nest. Some of the in-coming *L. longispinosus* workers were accepted immediately by the other slaves, while others were initially attacked. However, after 15 days, all the workers from the unparasitized nest were living peacefully with the *H. americanus* queen. A few days later, several *L. longispinosus* workers killed the *L. longispinosus* queen which had been living in the unparasitized nest.

Discussion

Both Wesson (1939) and Alloway (1979) produced slave raids by selecting target nests and placing them in arenas with relatively populous, single-nest *H. americanus* colonies. The present study was the first in which a broader sample of *H. americanus* colonies has been observed and the first in which *H. americanus* colonies have been observed interacting with other colonies near which the slave-makers had been living in nature. These procedural differences probably account for the discrepencies between the behavioral events observed here and those described by Alloway (1979). Similar procedural differences, combined with possible regional differences between populations, may account for differences between the present results and those of Wesson (1939).

A number of our observations pertain to limits on the success of slave-raiding in polydomous parasite colonies. Individual *H. americanus* workers can rarely capture brood and are sometimes killed by target-colony workers. Yet, groups of 4 or 5 *H. americanus* workers can successfully raid almost any target nest. Thus, *H. americanus* colonies need to deploy their raiders in raiding parties containing several parasite workers. However, polydomy sometimes prevents such deployment. The slave-makers rely on their slaves to carry them from nest to nest in polydomous colonies; and the slaves often fail to assemble the slave-makers in a single nest from which successful raids could be mounted. As a consequence, some polydomous *H. americanus* colonies fail to organize raiding parties containing enough slave-makers to capture brood from neighboring host-species colonies.

This difficulty encountered by *H. americanus* colonies living in more than one nest has led us to question the adaptive value of polydomy in the slave-maker population studied. Both the *Leptothorax* host species enslaved by *H. americanus* in the Toronto region form facultatively polydomous colonies (Alloway *et al.* 1982). Thus, if enslaved host-species workers behave like unenslaved conspecifics, slaves should tend to provide a polydomous colony structure for the parasites. Perhaps, some *H. americanus* colonies are polydomous because of this behavioral propensity of their slaves and despite the fact that polydomy is detrimental to efficient raiding.

In addition, polydomy may account for some of the overt aggression observed in the present study. By extension, polydomy might partly explain the similar forms of slave aggression manifested by *Leptothorax* slaves living in *L. duloticus* colonies (Wilson 1975).

Let us imagine that a slave-maker colony divides, with some of the parasites and slaves remaining in the original nest, while others move to another nest. Let us further suppose that the slave-makers in the two nest raid independently. In such a situation, young slaves maturing from captured brood in each nest might learn to recognize as nestmates only those particular slave-makers with which they were living. If the ants from the two nests later reunited, then the old slaves might accept all the slave-makers, while the young slaves accepted only familiar individuals. This scenario could explain our observations of slaves biting and dragging slave-makers out of nests. The aggression observed was always an individual matter. Some slaves accepted all the slave-makers, while other slaves accepted certain slave-makers and attacked others.

A somewhat similar hypothesis might account for the imperfect behavioral boundaries between some incipient *H. americanus* colonies and nearby unparasitized nests. An *H. americanus* queen founds a new colony by entering a host-species nest, killing or driving off the adults, and capturing worker pupae that subsequently mature to become her first slaves (Wesson 1939; Sturtevant 1927). If a parasite queen founded a colony in one nest of a polydomous *Leptothorax* colony, it would not be surprising if some of the parasite's first slaves were acceptable in other nests of the same colony. Similarly, "free" workers from that colony might be acceptable in the slave-maker nest. However, this hypothesis cannot explain how, under these circumstances, a parasitized nest could unidirectionally siphon brood and workers from an unparasitized nest or how an *H. americanus* queen could become more attractive than a *Leptothorax* queen. Yet, *H. americanus* queens and the queens of many other socially parasitic species somehow usurp the place of host-species queens (Wilson 1971). How parasite queens accomplish this feat remains an important subject for future research.

Polydomy also cannot account for the case where slaves cared for an *H. americanus* queen and her brood but killed all eclosing *H. americanus* workers. Explaining this phenomenon would require understanding the mechanisms of nestmate recognition in these species; and these mechanisms are incompletely understood. However, studies in progress (R.J. Stuart, personal communication) indicate that apparent "mistakes" in nestmate recognition are possible in these host species and that*H. americanus* may exploit these possibilities. When slaves work for a parasite queen, they may be mistakenly identifying her as a nestmate. When the same slaves destroy the parasite's offspring, they may be correctly identifying them as aliens.

Gladstone (1981) discussed various theoretical reasons why slave workers should not "revolt" against slave-makers. However, our observations of *H. americanus* colonies and Wilson's (1975) observations of *Leptothorax duloticus* colonies show that individual slaves sometimes manifest what might be interpreted as "rebellious behavior". If our inferences about polydomy are correct, whole slave worker forces may even organize slave-maker colonies in a way which produces inefficient raiding. Nevertheless, we doubt that any of these behavioral phenomena are manifestations of evolved host-species defenses against slave-makers. We suppose that the behavior of host-species workers has evolved to maximize the reproductive potential of host-species queens. Slave-maker populations are so sparse that only a small proportion of host-species colonies are ever raided. Thus, slavery seems unlikely to exert significant selection pressure on host-species populations; and we believe that the facultative polydomy and polygyny found in these host-species are adaptations to conditions in host-species (not parasite) colonies.

In these host species, polygyny involves the acceptance of newly mated young queens in existing colonies. Simultaneously, polydomy involves a more or less continual exchange of workers, queens, and brood among nests; and such commerce requires workers in one nest to accept workers, queens, and brood from other nests of the same colony (Alloway *et al.* 1982). An incidental effect of these characterstics of host-species colonies is to produce a worker caste which is vulnerable to enslavement. Of course, a second effect of polydomy is to produce a worker caste which tends to organize multiple-nest colonies; and life in multiple nests may be disadvantageous to slave-makers. In other words, *Harpagoxenus americanus* parasitizes the labor of workers which possess a "mixed bag" of behavioral characteristics. Some of these characteristics may facilitate enslavement, while others may produce inefficient slave-maker colonies. However, the assertion that host-species workers have evolved to be inefficient slaves seems only a little more likely than the assertion that they have evolved to be slaves at all.

SUMMARY

Colonies of the slave-making ant, *Harpagoxenus americanus* (Emery), and two of its host species (*Leptothorax ambiguus* Emery and *L. longispinosus* Roger) were observed under "seminatural" conditions, in which the ants lived in artificial nests arranged to reconstruct the spatial relationships among their natural nests. Some of the slave-maker and host-species colonies were polydomous., In some polydomous slave-maker colonies, the slaves carried all the *H. americanus* workers into one nest before the onset of raiding. When thus assembled, the slave-makers efficiently captured

brood from nearby host-species colonies. In other polydomous colonies where the slave-makers remained in more than one nest, the parasites conducted unco-ordinated raids and incurred many casualties. Several kinds of slave aggression against the slave-makers are described. However, slaves "peacefully" augmented the slave worker forces of some incipient *H. americanus* colonies.

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