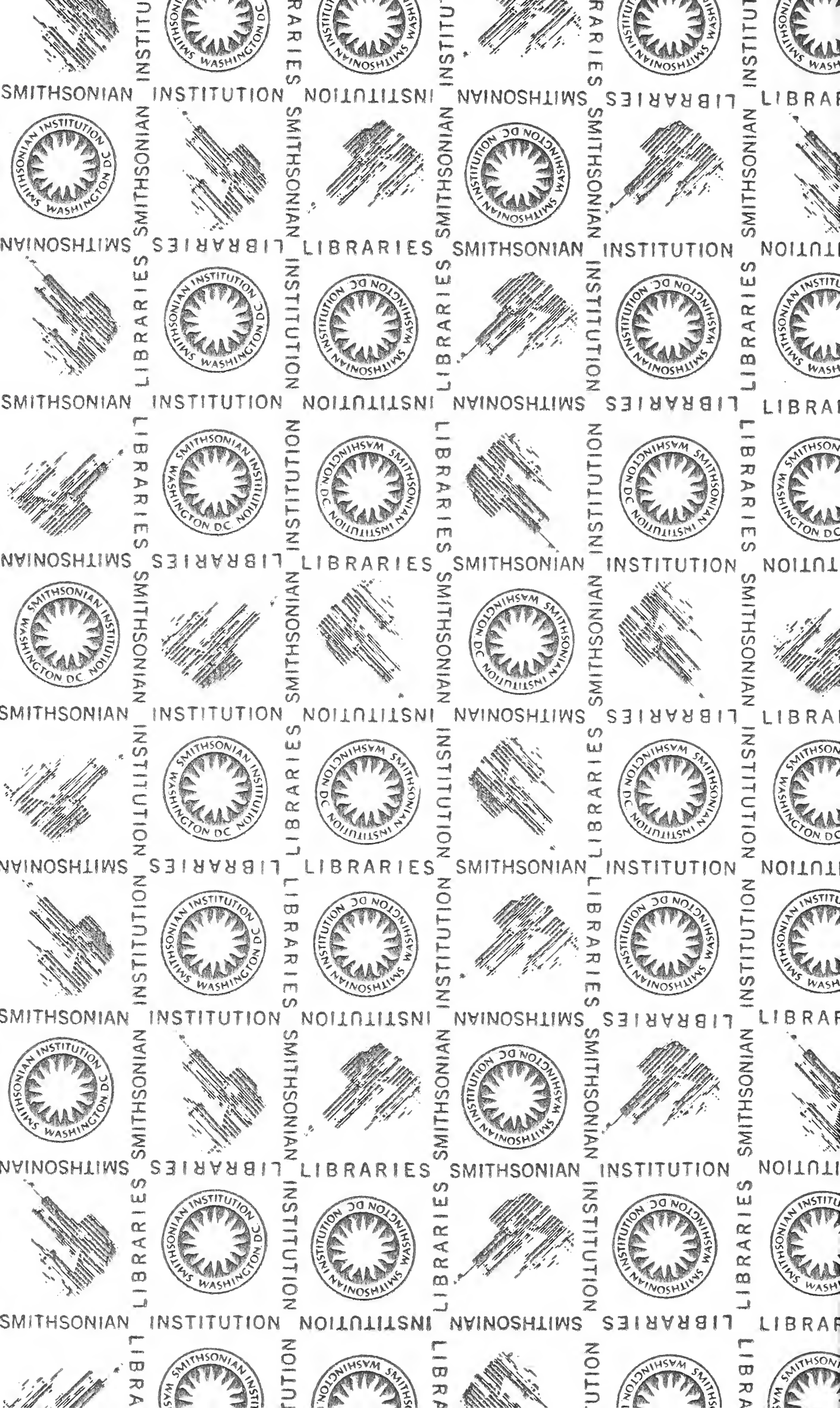
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PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 94 1987 No. 1-2

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Psyche, vol. 93, no. 3–4, for 1986, was mailed March 17, 1987

The Lexington Press, Inc., Lexington, Massachusetts

PSYCHE

Vol. 94 1987 No. 1–2

THE FOSSIL MEMBERS OF THE ANT TRIBE LEPTOMYRMECINI (HYMENOPTERA: FORMICIDAE)

By Cesare Baroni Urbani[1] and Edward O. Wilson[2]

In 1980 Baroni Urbani described *Leptomyrmex neotropicus* from 9 rather poorly preserved specimens clustered in a single piece of Dominican amber and hence presumed to be of Miocene age (the date estimated in Baroni Urbani and Saunders, 1982). The finding is of potential biogeographic importance because *Leptomyrmex,* and hence the very distinctive dolichoderine tribe Leptomyrmecini, is today limited to the Old World, in particular eastern Australia, New Caledonia, New Guinea, the Aru Islands, and the Moluccas. A second genus, *Leptomyrmula,* had previously been described from the Miocene amber of Sicily (Emery, 1891, 1912). It thus appears that an entire tribe was once almost worldwide but has since retreated not only from Europe but the entire Western Hemisphere. Wilson (1985a) doubted Baroni Urbani's tribal placement of the Dominican amber specimens. He found a worker in Dominican amber that superficially resembles *Leptomyrmex,* sharing the same distinctively elongated body form, mesothoracic constriction, petiole, tapered neck, and bulging eyes located toward the rear of the head, but actually belongs to the *Camponotus branneri* group. He suggested that *Leptomyrmex neotropicus* might be the same species. In the meantime, Schlee (1984) published a color photograph of another Dominican amber piece containing four presumed *Leptomyrmex* workers. This example is now preserved in the collection of

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Manuscript received by the editor February 17, 1987.

the Museum für Naturkunde, Stuttgart, with the reference number Do-4931-M. He has also provided us with four more workers, in a piece labeled Do-4484-M.

Baroni Urbani was right. The additional, better preserved workers are identical or close to *L. neotropicus,* and prove to belong to the Leptomyrmecini beyond any reasonable doubt. In addition to being so close in overall habitus to the living species of *Leptomyrmex* as to fall easily within the limits of this genus, the material shows the following distinctive traits in common with that Old World genus:

(1) Slit-shaped anal orifice.

(2) Masticatory border of mandibles smoothly rounded at the basal angle and lined with more than 15 denticles of uniform size, as opposed to fewer than 10 teeth, usually 5–6, decreasing in size from apex to base in species of *Camponotus.*

(3) Anteriormost point of antennal socket very close to the posterior clypeal border (in *Camponotus* the two are widely separated).

(4) Large metapleural gland orifice and prominent bulla (in *Camponotus* bulla small and orifice absent).

(5) Metathoracic spiracles on dorsum of alitrunk (usually lateral in *Camponotus*).

In addition, Wilson has acquired a male that appears to be a leptomyrmecine, although it possesses at least one trait (absence of the radial cell) that might eventually justify separating it at the generic level from both *Leptomyrmex* and *Leptomyrmula.*

Status of *Leptomyrmex neotropicus* Reexamined

The main features of a well-preserved *Leptomyrmex* are depicted in Figure 1. As noted by Baroni Urbani (1980) for the *L. neotropicus* types and confirmed with the new worker specimens, the habitus of the fossil species is closest to *L. fragilis* (= *L. gracillimus*) of New Guinea, Ceram, and Aru among the living species. This assessment is based on the revision of *Leptomyrmex* by Wheeler (1934) and the examination of large new collections of that genus placed in the Museum of Comparative Zoology during the ensuing fifty years. *L. neotropicus* differs from *fragilis* in its smaller size, even narrower head, projection of the compound eyes beyond the lateral borders of the head, and more concave masticatory borders. In a genus with a relative scarcity of worker characters, the small size is especially notable. The specimen shown in Figure 1 possesses the following

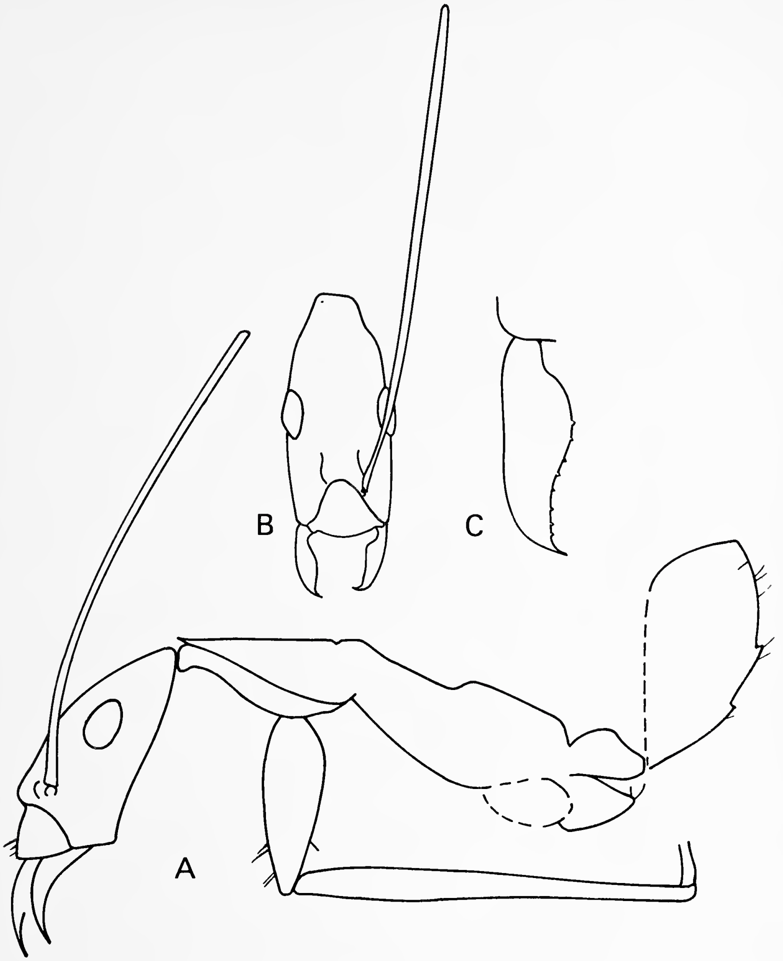


Figure 1. *Leptomyrmex neotropicus* worker from Miocene amber of the Dominican Republic: A, side view of entire body; B, frontal view of head; C, enlarged view of right mandible tilted anteriorly to give a full frontal aspect.

measurements: Head Length (excluding mandibles) 1.50 mm, Head Width (across and including eyes) 0.72 mm, Scape Length 2.48 mm, Eye Length (longest axis) 0.31 mm, total length (including mandibles) 5.6 mm. A second specimen is smaller: Head Length 1.30 mm, total length 4.6 mm. The four Stuttgart specimens embedded in a single amber piece (Museum reference number Do-4931-M) yielded the following measurements: Head Length 0.80–0.83 mm (4 specimens measured), Head Width 0.52 mm (one specimen measured), Scape Length 1.56–1.66 mm (5 scapes in 3 specimens measured), Eye Length 0.14–0.16 mm (3 eyes on 3 specimens measured), Total Length 4.8–5.5 mm (4 specimens measured). Three of those in piece number Do-4484-M possessed the following measurements: Head Length 1.20–1.36 mm, Head Width 0.72–0.84 mm, Scape Length 2.40–2.48 mm, Eye Length 0.24–0.26 mm. These dimensions are at the extreme lower end of the variation showed by the extant *Leptomyrmex,* represented by *L. mjobergi* of Queensland. Among other important character states of *L. neotropicus* with reference to the extant *Leptomyrmex* are the lack of hairs on the compound eyes, the almost completely hairless body surface, the narrowly constricted occiput, and the apparently light, uniform body color.

The male that we have tentatively associated with *Leptomyrmex neotropicus* is illustrated in Figure 2. This specimen is similar to *Leptomyrmex* and *Leptomyrmula* in several important respects and is appropriately placed in the tribe Leptomyrmecini, whether it is really the male of *L. neotropicus* or not. The leptomyrmecine traits are as follows: exceptionally slender body form and overall habitus similar to *Leptomyrmex* and *Leptomyrmula;* antennae very long; venation reduced and the stigma vestigial or absent. The genitalia unfortunately cannot be studied.

There are also some important differences. First, consider the venation (see Figure 3). Where extant *Leptomyrmex* species have a peculiarly narrow radial cell, *Leptomyrmula maravignae* has a wider and hence more "ordinary" radial cell, and *L. neotropicus* has no radial cell at all. Living *Leptomyrmex,* with the exception of *L. fragilis,* possess a stigmal appendage ("pterostigmal appendage" of Wheeler, 1934), a unique bladder-like structure extending from the position of the vestigial stigma out into the radial cell. This structure is absent in *Leptomyrmula maravignae* and the putative *Leptomyrmex neotropicus.* In the extant *Leptomyrmex,* the antennae are about 0.7–0.9× as long as the body; in *Leptomyrmula maravignae* they are about 0.5× as long; and in *Leptomyrmex neotropicus* they are about equally long.

The absence of the stigmal appendage and an exceptionally slender body form are shared by the male of *Leptomyrmex neotropicus* with the male of the living *L. fragilis,* but there the resemblance ends. *L. neotropicus* is much smaller than *L. fragilis,* has a

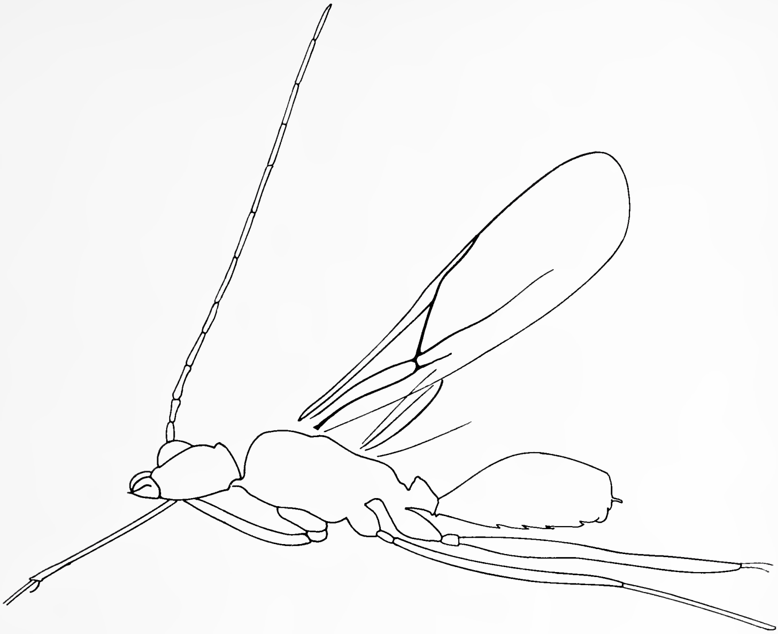


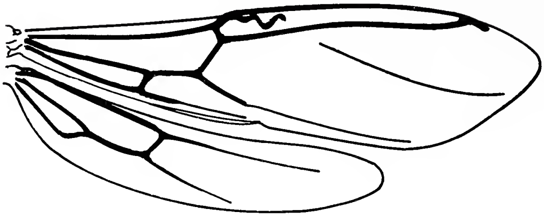
Figure 2. Leptomyrmecine male from the Dominican amber tentatively associated with *Leptomyrmex neotropicus.*

convex (as opposed to concave) prothorax, lacks the radial cell, and has more fully developed, denticulate mandibles. The mandibular form of *L. neotropicus* is shared with *L. erythrocephalus* and *L. nigriventris* among living species. *L. fragilis* has thinner, strap-like, toothless mandibles; this trait is shared by *cnemidatus, darlingtoni, mjobergi, pallens, tibialis, varians,* and *wiburdi* among the extant *Leptomyrmex.*

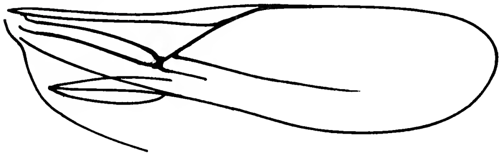
Discussion

The leptomyrmecine male, whether *Leptomyrmex neotropicus* or not, may be sufficiently different from the living *Leptomyrmex* and Sicilian amber *Leptomyrmula* to warrant separation as a distinct genus. However, we do not believe it prudent to take this step until enough material has accumulated to make the worker-male association more probable, and to better estimate the extent of variation in both castes.

Leptomyrmex tibialis



Leptomyrmex neotropicus



Leptomyrmula maravignae

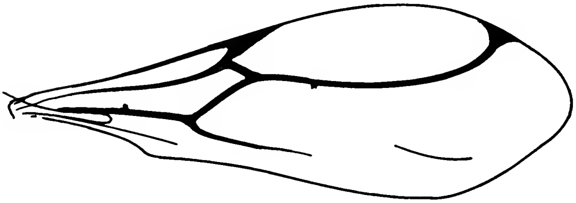


Figure 3. Wings of males of the living *Leptomyrmex tibialis* of Australia (Wheeler, 1934), *Leptomyrmula maravignae* of the Sicilian amber (Emery, 1891), and the putative *Leptomyrmex neotropicus.*

The picture remains puzzling. If *Leptomyrmex neotropicus* is really cognate with the living Indo-Australian *Leptomyrmex,* that is, derived from an immediately common ancestor, then the Leptomyrmecini have undergone a dramatic retreat since later Tertiary times. The only other ant group with a comparable history is the Aneuretinae, which once ranged through Europe (Baltic amber, Oligocene; see Wheeler, 1914) and North America (Florissant shales, Oligocene; see Carpenter, 1930), but now is known only from *Aneuretus simoni* of Sri Lanka in the living world fauna (Jayasuriya and Traniello, 1985). The peculiarity of the leptomyrmecine case is heightened by the distinctively modern character of the Dominican amber fauna in which it occurs: of 37 genera and well-defined subgenera of ants recorded to date, 34 have survived somewhere in the New World tropics; only three are absent, and these are extinct everywhere in the world (Wilson, 1985b).

It is of course possible that *Leptomyrmex neotropicus* represents a wholly convergent line to the Old World "true" Leptomyrmecini, but we consider that unlikely. The character states possessed in common seem too numerous and detailed to be convergent. However, the matter will be settled wih confidence only with the acquisition and study of larger series.

SUMMARY

Additional specimens have confirmed the existence of the ant tribe Leptomyrmecini in Miocene amber of the Dominican Republic. The workers of the species, *Leptomyrmex neotropicus,* are not distinguishable at the generic level from the living *Leptomyrmex* of Australia and Melanesia, but the male tentatively associated with the workers has peculiarities in wing venation that may eventually justify a separation from *Leptomyrmex* as well as from *Leptomyrmula* of the Miocene Sicilian amber. This is the only higher ant taxon other than the subfamily Aneuretinae known to have gone extinct in the New World while surviving in the Old World.

ACKNOWLEDGMENTS

We are grateful to Major Jake Brodzinsky of Amberica, Inc., George Poinar of the University of California, Berkeley, and Dieter Schlee of the Museum für Naturkunde, Stuttgart, for supplying the material used in this study.

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PSEUDACTEON OBTUSUS (DIPTERA: PHORIDAE) ATTACKING *SOLENOPSIS INVICTA* (HYMENOPTERA: FORMICIDAE) IN BRAZIL*

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Although parasitism of ants (Hymenoptera: Formicidae) by phorid flies (Diptera: Phoridae) has been reported by a number of investigators, their behavior is still poorly understood (Pergande, 1901; Wasmann, 1918; Borgmeier, 1925, 1931, 1963, 1969; Donisthorpe, 1927; Steyskal, 1944). Recently Williams et al. (1973), Williams and Whitcomb (1974) and Williams (1980) reported on two genera of phorids, *Pseudacteon* and *Apodicrania,* that attack fire ants in South America. They noted that *Apodicrania* larvae were endoparasites of fire ant larvae (*Solenopsis invicta*) while sixteen species of the genus *Pseudacteon* seem to parasitize workers of the *Solenopsis saevissima* complex. Although attacks by *Pseudacteon* on fire ants have been observed, evidence of actual parasitism (i.e. oviposition by the parasite) is lacking. Here, we report field observations of *Pseudacteon* attack on foraging *S. invicta* workers and document parasite oviposition on a host ant. Our observations indicate that the parasite preferentially attacks major workers of the host species. Possible reasons for this caste-bias are discussed.

Data were collected on April 18 (16:00–16:30), April 19 (11:00–15:30) and on April 24 (15:00–17:00), 1985 in Caceres, Mato Grosso, Brazil during studies of ant species competing for baits. At this time the phorid flies, *Pseudacteon obtusus* Borgmeier were observed hovering over workers of the fire ant *Solenopsis invicta* Buren as they fed at bait stations or moved along the foraging trails. Between one and four *P. obtusus* were observed during any one observation period. Only a few attempts ($n = 3$) were made by phorids to attack minor workers, and in these cases two of the minor workers escaped by crawling under debris, leaves or grass, while the

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**Manuscript received by the editor October 8, 1986.*

third escaped by dispersing venom in the air by raising and vibrating its gaster (i.e., "gaster-flagging", Obin and Vander Meer, 1985). The attacking phorid would then fly in search of another potential host worker, and the minor worker would resume foraging. In contrast, no major workers displayed any defensive behavior such as gaster-flagging, mandible gaping or lunging, although all of them tried to escape from attacking phorids. The major workers appeared "confused" by hovering phorids, moving off the foraging trail or away from the bait station into an open area (usually away from other workers). This action apparently benefited the parasite because the phorids closely pursued and attempted to oviposit only on major workers during this study (n = 10 attempts), even though minor workers clearly outnumbered major workers at the bait station and along the foraging trails.

In one particular case, we observed a major worker of *S. invicta* under continuous attack by a lone phorid. We collected both host and parasite, placed them in a 20 ml vial. Once in the vial, the phorid attempted repeatedly to land on the agitated worker which was running back and forth in the vial trying to elude the fly. After approximately 5 min, the phorid landed successfully on the posterior end of the hosts' head capsule, deposited one oval egg, and then began searching for an exit from the vial, paying no attention to the ant. The ant, however, attempted to remove the egg with its antennae and forelegs. However, the placement of the egg at the base of the head capsule near its junction with the thorax made it impossible for the ant to do so. After several minutes of persistent attempts to dislodge the egg, the parasitized ant ceased grooming activities. We do not know whether or not the egg would have been removed by nestmates had the worker returned to its nest. Replicates (n = 5) of the above procedure were conducted using newly-mated female sexuals and other *P. obtusus*. These *P. obtusus* displayed no visible attack or oviposition behaviors while enclosed in a vial with individual *S. invicta* queens.

During this study, five other species of ants were observed foraging for baits in the study area. These included *Mycocepurus* sp., *Conomyrma* sp. A, *Conomyrma* sp. B, *Paratrechina longicornis,* and *Acromyrmex* sp.. However, only the *Solenopsis* workers were attacked by *P. obtusus.*

DISCUSSION

These observations represent the first, direct evidence that *P. obtusus* is parasitic; although other investigators have assumed this to be the case (Williams, 1980). Our observations also document *P. obtusus* attacks upon naturally occurring *S. invicta* workers at a distance from the fire ant nest. Previous studies (for example, Williams et al., 1973; Williams, 1980) have reported on attacks by phorids only on experimentally-disturbed fire ant mounds. Recently, however, Wojcik et al. (1986) discovered a single puparium of an unidentified phorid in a female alate.

Feener (1981) noted that phorids of the genus *Apocephalus* attack major workers of the ant *Pheidole dentata* and "stampede" the ant, thus overcoming its defensive behavior. *P. obtusus* appeared in our study to promote a similar response from its host. Parasitism of *P. dentata* also affected the competitive balance between it and *S. texana* (Feener, 1981).

Foraging *S. invicta* major workers appear more susceptible to successful attack by the phorid fly *P. obtusus* than workers of other size castes. This may be the result of larger ants presenting proximate, visual and/or chemical stimuli of greater magnitude than smaller ants. However, the fact that phorid females did not attack available sexuals which are as large or larger than majors suggests that other factors are involved. The preference for workers only is not unique to *P. obtusus.* Wasmann (1918) reported *P. formicarum* attacking only workers of *Lasius* spp. while ignoring winged males and females.

Defensive ability may be another factor. *S. invicta* major workers are less aggressive than minor and media workers (Wilson, 1978) and Vander Meer (unpublished data) has determined that the venom sacs of major workers contain significantly less venom alkaloids per mg ant than the venom sacs of other worker castes. Observations presented here suggest that such behavioral and physiological differences may render major workers particularly susceptible to parasitization by *P. obtusus.* However, factors other than ant aggressiveness and deterrent capability may also contribute to caste-bias in host selection by *P. obtusus.* Perhaps most significant in this regard is the site of parasite oviposition. Compared to minor or media workers, major workers offer a larger area at the base of the head capsule for securing an egg. An additional factor promoting the caste-bias in host selection observed in this study may be that major workers provide more nutrition for developing parasite larvae than non-major workers. This would be especially the case if *P. obtusus* larvae develop only in the head, a pattern observed in other species of ant-specific phorids (Pergande, 1901).

Finally, major workers may represent a more reliable resource. They are the longest-lived of the worker castes (Porter and Tschinkel, 1985), and their relatively reduced aggressiveness renders them least likely of all workers to incur injury or death from fighting. Therefore we suggest that the probability of an individual host surviving the requisite period of parasite development in that host is, on average, greater for major workers than for other workers. If so, selection would favor phorids that parasitize major workers.

ACKNOWLEDGEMENT

We wish to thank M. S. Obin for his excellent suggestions and comments on the manuscript. We also thank F. C. Thompson, D. R. Smith, and J. C. Trager for the identifications of the phorids and ant specimens. We are grateful for the assistance received from Antonio Pereira, Jorge Rodrigues and EMBRAPA in Brazil. Finally, we appreciate the opportunity afforded us by the U.S. and Brazilian governments to visit and study in Brazil.

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NEW GENERA AND SPECIES OF TYRINI FROM AUSTRALIA (COLEOPTERA: PSELAPHIDAE)*

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While preparing a paper on the pselaphid genera of Australia, three groups of the Tyrini, subtribe Tyrina, were discovered which could not be placed within the current generic concepts of the Australian fauna. One of these groups appears to be congeneric with *Tyrogetus* Broun from New Zealand, while the other two represent undescribed genera. With the recognition of these taxa, the major generic components of the Tyrini appear to be described for Australia.

All measurements are in millimeters. Slides of cleared and disarticulated specimens were used to determine the patterns of foveation of the genera. Holotypes are placed in the Australian National Insect Collection, Canberra, or in the National Museum of Victoria, Abbotsford.

Tyrogetus Broun

Tyrogetus Broun is represented by two species from New Zealand, *optandus* Broun (figured by Jeannel 1962:448) and *palpalis* Broun. Three undescribed species from Tasmania are very close to these New Zealand species based on the suite of characters used to differentiate genera in the Tyrini. The two New Zealand species are easily separated by tergite I being five times the length of II, while the length of tergite I in the three Tasmanian species is about twice the length of II. The maxillary palpi of one Tasmanian species (*occidentalis* n. sp.) is relatively robust, while the palpi of the New Zealand species are more elongate and narrow, and the palpi of the two other Tasmanian species are the longest and narrowest. The relative lengths of the tergites and form of the maxillary palpi are

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*Scientific Contribution Number 1461 from the New Hampshire Agricultural Experiment Station.

Manuscript received by the editor January 5, 1987.

often used in conjunction with other characters to discriminate genera in the Tyrini. However, all other features used to separate tyrine genera are uniform in these species, and, coupled with the identical suite of foveae and quite similar general appearance, it is readily apparent that these five species form a monophyletic group. At this time I prefer to take a conservative course and place the undescribed Tasmanian species in *Tyrogetus* without division into subgenera or genera, at least until the New Zealand fauna is better known.

Tyrogetus Broun is characterized by: Body smooth, legs rugosely pebbled; head nude with vertexal foveae placed laterally above eyes, nude antero-median fovea at base of antennal tubercle, antennae with apical three flagellomeres forming club, segments II–IV of maxillary palpi elongate and basally pedunculate, 1 gular fovea; pronotum lacking antebasal foveae or sulcus, prosternal foveae present; elytra with two basal foveae; lateral mesosternal foveae broadly meeting internally, with small anterior fork, shallow median mesosternal fovea, lateral mesocoxal foveae placed posterior to mesocoxae, with median metasternal fovea; metasternum short, longitudinally tumid between meso- and metacoxae, metacoxae abruptly strongly protruding at junction with trochanters; abdomen with tergite I two to five times length of II, II–IV subequal, III shorter than IV, I with three basolateral foveae, anterolateral foveae small, II–IV with two baso-lateral foveae separated or partially fused, V with single baso-lateral fovea; sternites II–III deeply incised laterally at base (only visible on cleared specimens), incision joining globular invagination medially, IV–VI lacking basolateral foveae.

KEY TO TASMANIAN *TYROGETUS*

1. Fourth segment of maxillary palpi no more that three times as long as wide, basal third abruptly narrowed (Fig. 1); eyes with about 15 facets .... *occidentalis* n. sp.
   Fourth segment of maxillary palpi five times or more as long as wide, gradually narrowed (Fig. 5); eyes with 10 or fewer facets 2
2. Length 1.5–1.8; males with paired teeth at apex of fifth tergite (Fig. 7); southwestern Tasmania .... *howardi* n. sp.
   Length 1.3; male lacking teeth at apex of fifth tergite; northeastern Tasmania .... *minimus* n. sp.

Tyrogetus occidentalis n. sp.
(Figs. 1–4)

Length 1.68–1.77. Body with moderately dense appressed setae; maxillary palpi with last segment angulate and directed laterally in apical two-thirds, abruptly swollen at point of angulation; eyes with about 15 facets; elytra with discal stria extending past middle; tergite I twice length of II, II as long as IV, III three-fourths length of II, V with narrowly truncate apex, apex slightly indented; protrochanters with stout swollen ventral knob, profemora with flattened carina on inner margin from near base to middle, protibia with small spur at apex.

Males with sternites II-IV flattened medially, V with shallow longitudinal groove.

Females with sternites II-V medially convex.

Measurements of holotype: Maxillary palpi with fourth segment 0.06 wide, 0.16 long; tergite I 0.33 long, II 0.17 long, III 0.13 long, IV 0.18 long, V 0.07 long; carina on profemora 0.17 long.

Specimens examined, 6: HOLOTYPE male, *Tasmania,* Mt. Field National Park, near SE end Lake Fenton, 1000 m, I-30/II-5-1980, A. Newton & M. Thayer, *Nothofagus gunnii-Richea* spp.-*Arthrotaxis* spp.-*Phyllocladus asplen.* forest (ANIC). PARATYPES: 1 male, Hartz Mountains National Park, Hartz Road, 740 m, II-8/10-1980, *Eucalyptus-Nothofagus,* A. Newton & M. Thayer, berlese forest leaf & log litter (DSC); 1 male, Willie's Saddle, 9 km W Geeveston, 370 m, II-8/10-1980, A. Newton & M. Thayer, *Eucalyptus* forest, berlese forest leaf & log litter (AFN); 1 female, Great Lakes, C. Oke (MVMA); 1 male, 1 female, no locality, C. Oke collection (MVMA). Found in the southwestern half of Tasmania.

Discussion: This species is quite similar in general appearance to *palpalis* Broun. In *occidentalis* tergite I is shorter, flagellomere VII is wider than VI and forms the base of the antennal club, and the last segment of the maxillary palpi is expanded in the apical two-thirds. *Palpalis* has tergite I longer, flagellomere VII is barely wider than VI so the antennal club appears almost two-segmented, and the last segment of the maxillary palpi is expanded in the apical half.

Etymology: The name is derived from the distribution in the western portion of Tasmania.

Line to right of figures is equal to 0.1 mm.

Figs. 1–4. *Tyrogetus occidentalis* n. sp. 1. Dorsal view right maxillary palpus; 2. posterior view right profemur; 3. dorsal view tergite V; 4. right lateral and dorsal view male genitalia.

Figs. 5–8. *Tyrogetus howardi* n. sp. 5. Dorsal habitus; 6. dorsal view right maxillary palpus; 7. dorsal view tergite V; 8. right lateral and dorsal view male genitalia.

Tyrogetus howardi n. sp.
(Figs. 5–8)

Length 1.50–1.74. Body with sparse short appressed setae; eyes small, with 8–10 facets, maxillary palpi elongate-pedunculate, with stems longer than swollen areas, last segment narrowly swollen beyond midpoint; elytra with discal stria indistinct past middle; tergite I twice as long as II, II and IV subequal, III over half as long as II, V longitudinally carinate with two lateral teeth at apex; metasternum strongly tumid and carinate between meso- and metacoxae; profemora with narrow elongate oval smooth area on antero-mesal margin delimited by fine carina.

Males with sternites III–V barely flattened medially, VI with faint circular impression through entire length.

Females with sternites III-V convex medially.

Measurements of holotype: Maxillary palpi with fourth segment 0.03 wide, 0.24 long; tergite I 0.36 long, II 0.16 long, III 0.09 long, IV 0.15 long, V 0.07 long; smooth area on profemur 0.24 long.

Specimens examined, 9: HOLOTYPE male, *Tasmania,* Lower Gordon River, 42.43S 145.45E, 42.43S 145.50E, II-3-1977, Howard & Hill, HEC Survey, litter (ANIC). PARATYPES: 1 female, same data as holotype (ANIC); 1 female, same data except II-8-1977 (ANIC); 1 male, Lower Gordon River, 42.42S 145.53E, 42.41.5S 145.53E, II-3-1977, Howard & Hill, HEC Survey, litter (DSC); 1 female, Lower Gordon River, 42.42S 145.48E, 42.41S 145.49E, II-13-1976, Howard & HIll, HEC Survey, moss (DSC); 1 male, Lower Gordon River, 42.48.5S 145.51E, 42.48S 145.54E, III-1-1977, Howard & Hill, HEC Survey, moss (DSC); 1 female, same data except III-4-1977, litter (ANIC); 1 male, Willie's Saddle, 9 km W Geeveston, 310 m, II-8/10-1980, A. Newton & M. Thayer, *Eucalyptus* forest, berlese forest leaf & log litter (AFN); 1 male, Mt. Field National Park, Lake Dobson Road, 710 m, I-30/II-5-1980, A. Newton & M. Thayer, *Nothofagus-Eucalyptus* forest, berlese forest leaf & log litter (AFN). Found in the southwestern half of Tasmania.

Discussion: *Howardi* n. sp. shares with *minimus* n. sp. the reduced eyes and elongate palpi which are only narrowly enlarged apically. *Howardi* is larger than *minimus,* the last tergite of the male is produced into two teeth at the apex, and the aedeagus is deeply emarginate at the apex.

Etymology: Named for C. Howard, who collected many pselaphids during the H. E. C. Survey of the Lower Gordon River.

Tyrogetus minimus n. sp.
(Fig. 9)

Length 1.29. Body with sparse short appressed setae; maxillary palpi elongate-pedunculate, last segment with apical half narrowly enlarged, eyes with 6–7 facets; elytra with discal stria not reaching to middle; tergite I twice as long as II, II almost twice as long as III, II and IV subequal, V with strong median carina through apical half of length; metasternum short, strongly tumid between meso- and metacoxae.

Males with transverse impression through length of sternite V.

Females unknown.

Measurements of holotype: Maxillary palpi with fourth segment 0.04 wide, 0.24 long; tergite I 0.28 long, II 0.13 long, III 0.07 long, IV 0.11 long, V 0.06 long.

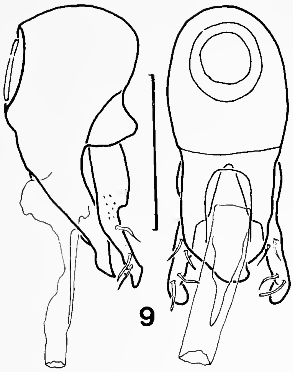
Specimen examined: HOLOTYPE male, *Tasmania,* 4.4 km SE Weldborough, 460 m, II-12/14-1980, A. Newton & M. Thayer, *Nothofagus,* etc. forest, berlese forest leaf & log litter (ANIC). Found in northeastern Tasmania.

Discussion: Quite similar in general appearance to *howardi* n. sp. by the reduced eyes and narrowly swollen maxillary palpi. Separated by the smaller size, simple apex of the last male tergite, and the broadly protruding apex of the aedeagus.

Etymology: The name was suggested by the small size of this species.

Tasmanityrus n. gen.

Tyromorphus auricomus Lea is an anomaly in *Tyromorphus* Raffray (17 species, Australia and Tasmania). It is somewhat similar in general appearance to the members of *Tyromorphus,* but differs conspicuously in the form of the maxillary palpi, which are elongate and pedunculate in *auricomus* (Fig. 10) and are radically different from the short, stout apical segments in *Tyromorphus* (Fig. 11). It is surprising that Lea placed *auricomus* in this genus, since the palpal form actually approaches that of *Gerallus* Sharp (8 species, Australia and Tasmania), with the fourth palpal segment of *Gerallus* being more fusiform and only narrowly pedunculate at the base (Fig. 12).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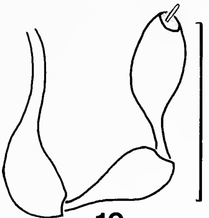
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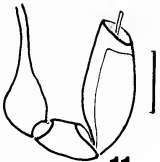
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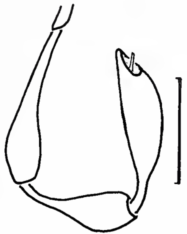
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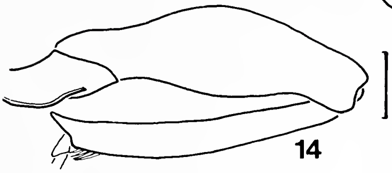
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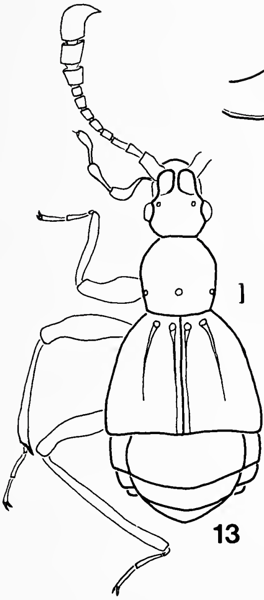
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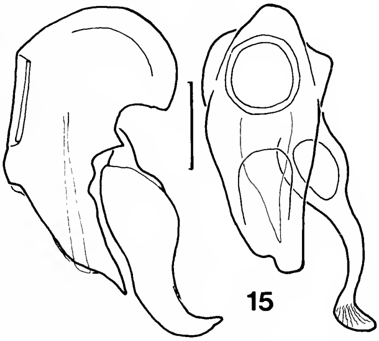
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Fig. 9. *Tyrogetus minimus* n. sp., right lateral and dorsal view male genitalia.
Fig. 10. *Tasmanityrus auricomus* (Lea), dorsal view right maxillary palpus.
Fig. 11. *Tyromorphus comes* (Schaufuss), dorsal view right maxillary palpus.
Fig. 12. *Gerallus palpalis* (King), dorsal view right maxillary palpus.
Fig. 13–15. *Tasmanityrus hilli* n. sp. 13. Dorsal habitus; 14. posterior view right middle leg; 15. right lateral and dorsal view male genitalia.

The suite of male characters used in discrimination of species of *Gerallus* and *Tyromorphus* occur in different areas of the body for each genus. *Tasmanityrus* possesses only a few simple male characters on the mesotrochanters and mesotibiae, which occur in many other genera, but with the unique feature of having lost either the right or left paramere. The remaining paramere is more developed than in groups with two parameres, and projects to either side. In *Gerallus* the parameres are free and elongate, while in *Tyromorphus* they are reduced and symmetrical. Based on the aedeagal characters, the male cuticular modifications, and the palpal form, it is clear that this is a monophyletic group of seven very similar species which is perhaps closest to, but distinct from, *Gerallus.*

Type species, *Tyromorphus auricomus* Lea. Gender of genus, masculine.

Tasmanityrus n. gen. is characterized by: head with nude vertexal foveae, paired gular foveae, segments II-IV of maxillary palpi clearly pedunculate at base, antennal club of last three flagellomeres; prothorax with small median and lateral antebasal foveae, lacking transverse antebasal sulcus, procoxal foveae present; elytra with two large basal pubescent foveae, discal stria distinct past middle of elytra; tergite I with three basolateral foveae, anterior foveae small, II–V with single basolateral fovea; sternites II-III and V with deep sulci at basolateral margins extending medially and then abruptly curving anteriorly, II with large baso-lateral foveae medial to sulcal incision, with deep transverse sulcus between medial foveae, two teeth projecting anteriorly from posterior margin of sulcus at inner margin of metacoxae; mesosternum with large lateral mesosternal foveae meeting medially, with small anterior branches, median mesosternal fovea present, lateral mesocoxal foveae present, median metasternal fovea present.

Females are very similar and are associated with males solely on the basis of identical collection data. The genitalia of all males, except for those of *hilli* n. sp. which have differently modified male mesotrochanters, were extracted to check identification. Two species were collected at several sites, but the data associated with the specimens collected by John Kethley indicate that these species were found in different leaf litters. The following key is based only on male features. Males may be recognized by the modified mesotrochanters, the large apical mesotibial spur, and sternites medially flattened to concave. Also, males tend to have the outer face of the mandibles bearing a more conspicuous medial tooth.

KEY TO SPECIES OF *TASMANITYRUS* (MALES)

1. Mesotrochanters carinate ventrally (Fig. 14), mesotibial spurs small, barely longer than first mesotarsomeres ...... *hilli* n. sp.
   Mesotrochangers with ventral tooth (Fig. 16), mesotibial spurs 1.4× or more as long as first mesotarsomeres 2
2. (1) Apical flagellomeres at most barely curved ventrally in apical half, ventral margin nearly straight; northeastern Tasmania .... *simplicis* n. sp.
   Apical flagellomeres strongly curved ventrally toward apex, outline strongly concave in lateral view (Fig. 13) 3
3. (2) Right paramere developed, longer than penis (Fig. 17); southwestern Tasmania...................... *newtoni* n. sp.
   Left paramere developed 4
4. (3) Penis apex acute, paramere abruptly curved laterally at apex (Fig. 19); southwestern Tasmania .... *auricomus* (Lea)
   Penis apex broadly truncate or broadly asymmetrical, paramere differently formed (Figs. 20–22)............................5
5. (4) Mesotrochanteral spurs and apical spur of mesotibiae same length; northeastern Tasmania............... *orientalis* n. sp.
   Mesotrochanteral spurs at most two-thirds length of apical spur of mesotibiae 6
6. (5) Penis apex symmetrical, paramere broadly rounded to medial point; southwestern Tasmania .... *thayeri* n. sp.
   Penis apex asymmetrical with left margin protruding, paramere apex truncate and acutely angled laterally; northwestern Tasmania .... *septentrionalis* n. sp.

Tasmanityrus hilli n. sp.
(Figs. 13–15)

Length 1.83–2.01. Male with deep oblique ventral impression on last flagellomere, penultimate flagellomere asymmetrical, obtusely produced on ventral margin; mesotrochanters carinate ventrally, mesotibiae with apical spur as long as first tarsomere, spur acutely pointed at apex; aedeagus with asymmetrical apex, right paramere strongly developed, flattened and twisted ventrally, expanded at apex.

Measurements of holotype: Flagellomere VII 0.10 wide, 0.11 long; VIII 0.11 wide, 0.12 long; IX 0.12 wide, 0.24 long; mesotibial spur 0.05 long, first mesotarsomere 0.06 long.

Specimens examined, 109: Holotype male, *Tasmania,* W side Lake St. Clair, c. 750 m, I-25/29-1980, *Nothofagus,* etc., berlese leaf & log litter (ANIC). Paratypes: 4 males, 7 females, eutopotypical (AFN, DSC); 1 male, 3 females, St. Clair National Park, nr. Echo Point, II-11-1977, J. Kethley, *Nothofagus cunninghami* litter with fungal mat. (golden) (FMNH); 1 male, 5 females, Zeehan-Renison Bell St. Res., Scenic Drive, 250 m, II-18-1980, A. Newton & M. Thayer, *Nothofagus,* etc. (AFN); 1 male, 3 females, 10 mi SE Smithton, Savage River, III-5-1977, J. Kethley, very dry *Nothofagus cunninghami* litter (FMNH); 1 male, 40 km SW Smithton, III-4-1977, J. Kethley, *Acacia melanoxylon* litter (FMNH); 28 males, 54 females, Lower Gordon River, many different latitude and longitude records, II-11-1976, I-21/III-1-1977, I-1978, Howard & Hill, HEC Survey, moss, litter (ANIC, DSC). This species consists of most of the type-series of *T. auricomus* (Lea) from Waratah (ANIC, SAMA). Found in the southwestern two-thirds of Tasmania.

Discussion: The males are easily separated from the other species by the carinate mesotrochanters. Most similar to *newtoni* n. sp. by the form and development of the right paramere, and the oblique impression on the venter of the apical flagellomere.

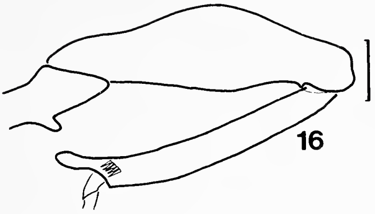
Etymology: Named for L. Hill, who collected many pselaphids during the HEC Survey on the Lower Gordon River.

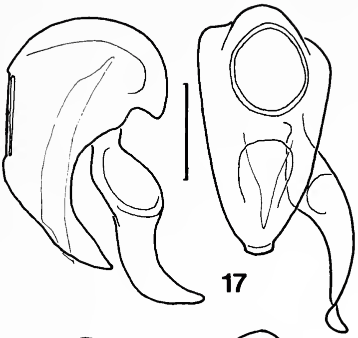
Tasmanityrus newtoni n. sp.
(Figs. 16–17)

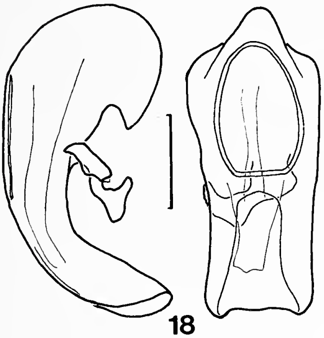
Length 1.74–1.95. Male with apex of last flagellomere curved ventrally, acute, venter impressed in apical half, penultimate flagellomere somewhat flattened dorso-ventrally but otherwise symmetrical; mesotrochanters with ventral spine near base, mesotibiae with apically spatulate to pedunculate spur, almost twice as long as first tarsomere; aedeagus with symmetrical apex, right paramere strongly developed, flattened and twisted ventrally to subacute apex.

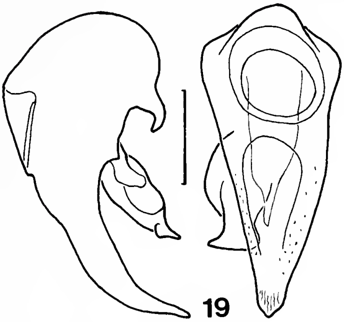
Measurements of holotype: Flagellomere VII 0.11 wide, 0.11 long, VIII 0.13 wide, 0.11 long, IX 0.14 wide, 0.24 long; mesotrochanteral spur 0.04 long, mesotibial spur 0.08 long, first tarsomere 0.05 long.

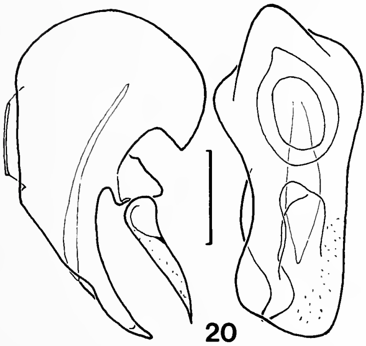
Specimens examined, 115: Holotype male, *Tasmania,* Mt. Field National Park, Lake Dobson Road, 610 m, I-30/II-4-1980, A. Newton & M. Thayer, *Nothofagus-Eucalyptus* forest, berlese leaf & log











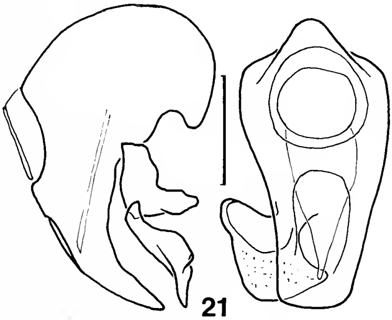


Fig. 16–17. *Tasmanityrus newtoni* n. sp. 16. Posterior view right middle leg; 17. right lateral and dorsal view male genitalia.

Fig. 18. *Tasmanityrus simplicis* n. sp., right lateral and dorsal view male genitalia.

Fig. 19. *Tasmanityrus auricomus* (Lea), right lateral and dorsal view male genitalia.

Fig. 20. *Tasmanityrus orientalis* n. sp., right lateral and dorsal view male genitalia.

Fig. 21. *Tasmanityrus thayeri* n. sp., right lateral and dorsal view male genitalia.

litter (ANIC). Paratypes: 1 male, 2 females, eutopotypical (DSC); 1 male, 3 females, same data except, 710 m, I-30/II-5-1980 (AFN); 3 males, 1 female, Willie's Saddle, 9 km W Geeveston, 310 m, II-8/10-1980, A. Newton & M. Thayer, *Eucalyptus* forest, berlese forest leaf & log litter (AFN, ANIC); 1 male, The Gap, Florentine Road, 15 km WNW Maydena, 600 m, II-1-1980, A. Newton & M. Thayer, *Nothofagus,* etc., berlese forest leaf & log litter (AFN); 2 males, 2 females, Florentine Valley, 29.2 km WNW Maydena, on Eleven Road, 460 m, II-1/6-1980, A. Newton & M. Thayer, *Nothofagus,* berlese forest leaf & log litter (AFN, DSC); 11 males, 8 females, 22 km NW Maydena, Florentine Valley, 700′, II-15-1977, J. Kethley, litter of *Eucalyptus regnans* & *Dicksonia antarctica* in depression (DSC, FMNH); 1 male, 3 females, same data except, litter base of *Eucalyptus* (FMNH); 1 male, same data except, II-14-1977, *Nothofagus cunninghami* litter at base of log (FMNH); 3 males, 28 km NW Maydena, Derwent Valley, 800′, II-16-1977, J. Kethley, mixed litter *Nothofagus cunninghami* & *Atherosperma moschatum* (FMNH); 1 male, Hartz Mountains National Park, Hartz Road, 740 m, II-8/10-1980, A. Newton & M. Thayer, *Eucalyptus-Nothofagus* forest, berlese forest leaf & log litter (AFN); 1 male, 1 female, Hastings St. Res., near Newdegate Cave, 130 m, II-9-1980, A. Newton & M. Thayer, trapped in floating debris, forest stream (AFN); 6 males, 16 females, Lower Gordon River, 42.56S 145.50E, 42.54S 145.54E, II-18-1977, Howard & Hill, HEC Survey, litter (ANIC, DSC); 1 male, 3 females, same data except, 42.51.5S 145.48E, 42.40.5S 145.51.5E (ANIC); 5 males, 12 females, same data except, 42.48.5S 145.51E, 42.48.5S 145.54E, III-4-1977 (ANIC, DSC); 1 male, 3 females, Mt. Wellington, XII-24/26-1978, L. Hill (ANIC); 4 males, 6 females, 10 km NW Hobart, Mt. Wellington, I-27-1977, litter under *Dicksonia antarctica* (FMNH); 1 male, Mt. Wellington, Griffith (SAMA); 2 males, 6 females, Mt. Wedge, XII-8-1982, S. Endrody-Younga, *Nothofagus* litter (TMSA); 1 male, 2 females, no locality (MVMA). Found in the southwestern half of Tasmania.

Discussion: The males are most similar to those of *hilli* by the form and development of the right paramere. *Newtoni* is easily separated from *hilli* by spurred mesotrochanters, long spatulate to pedunculate mesotibial spurs, and symmetrical penis apex.

Etymology: Named for A. F. Newton, Jr., who has collected many interesting Pselaphidae in Australia.

Tasmanityrus simplicis n. sp.
(Fig. 18)

Length 1.95–2.16. Males with ventral margin of apical flagellomere straight or only slightly curved; mesotrochanters with ventral spine near base, mesotibiae with long curved spur narrowly rounded at apex, spur almost half again as long as first mesotarsomere; aedeagus with apex symmetrical, probable right paramere short, strongly recurved to left.

Measurements of holotype: Flagellomere VII 0.09 wide, 0.11 long, VIII 0.10 wide, 0.10 long, IX 0.12 wide, 0.24 long; mesotrochanteral spur 0.02 long, mesotibial spur 0.07 long, first mesotarsomere 0.05 long.

Specimens examined, 9: HOLOTYPE male, *Tasmania,* Mt. Barrow Road, 890 m, II-15/17-1980, A. Newton & M. Thayer, *Nothofagus,* etc., berlese forest leaf and log litter (ANIC). PARATYPES: 1 male, 3 females, eutopotypical (AFN, ANIC); 3 males, 1 female, track off Mt. Barrow Road, 780 m, II-15/17-1980, A. Newton & M. Thayer, *Nothofagus,* etc., berlese forest leaf & log litter (AFN, DSC). Found in the northeastern portion of Tasmania.

Discussion: Unique in the simple apical flagellomeres of the male, right paramere strongly recurved, and broad symmetrical apex of the aedeagus.

Etymology: The name is derived from the simple apical flagellomeres.

Tasmanityrus auricomus (Lea), n. comb.
(Figs. 10, 19)

Tyromorphus auricomus Lea 1911: 766, pl. 21, fig. 9. Holotype locality: Waratah, Tasmania. Holotype in South Australian Museum, Adelaide (SAMA).

Length 1.83–2.01. Males with last flagellomere curved ventrally to point at apex, with oblique ventral impression, impression and flattened adjacent portions of flagellomeres VII–VIII roughened, flagellomere VIII obtusely protruding on ventral margin; mesotrochanters toothed near base, mesotibiae with spatulate apical spur, spur half again as long as first mesotarsomere; aedeagus with symmetrical apex, left paramere developed, short and laterally curved abruptly to acute point at apex.

Measurements of specimen from Rufus Canal: Flagellomere VII 0.09 wide, 0.12 long, VIII 0.10 wide, 0.12 long, IX 0.12 wide, 0.26

long; mesotrochanteral spur 0.04 long, mesotibial spur 0.08 long, first mesotarsomere 0.05 long.

Specimens examined, 33: Rufus Canal, 13.5 mi WNW Derwent Bridge, 800 m, I-26/28-1980, A. Newton & M. Thayer, *Nothofagus* rainforest, berlese forest leaf & log litter; 28 km NW Maydena, Derwent Valley, 800′, II-16-1977, J. Kethley, mixed litter *Nothofagus cunninghami* & *Atherosperma moschatum* on slope; Gordon River Road, 0.8 km W Florentine River, 550 m, II-3-1980, A. Newton & M. Thayer, *Nothofagus,* etc., berlese forest leaf & log litter; same data except, near Little Florentine River, 440 m; The Gap, Florentine Road, 15 km WNW Maydena, 600 m, II-1-1980, A. Newton & M. Thayer, *Nothofagus,* etc., berlese forest leaf & log litter; Florentine Valley, 22 km SW Maydena, 700′, II-15-1977, J. Kethley, ex: myrtle log and root mat; W side Lake St. Clair, c. 750 m, I-25/29-1980, A. Newton & M. Thayer, *Nothofagus,* etc., wet leaves and floral debris, forest stream; Lake St. Clair National Park, S end Lake St. Clair, II-7-1977, J. Kethley, litter under *Calystomen veridifloris;* 40 km SW Smithton, III-4-1977, J. Kethley, *Acacia melanoxylon* litter; 64 km S Smithton; III-3-1977, J. Kethley, litter of *Nothofagus cunninghami* under ground fern, *Blechnum* sp. There is a specimen labeled as the holotype ("TY") by Lea on a card bearing four specimens (two males, two females) from Waratah, although this designation was not mentioned in the description. This specimen is accepted as the holotype. The male paratype on the card is a specimen of *hilli* n. sp, as are the paratypes from Waratah in the ANIC. The paratypes from the other type localities (Ulverstone, Mt. Wellington, Hobart) have not been seen. Specimens are present in the collections of: AFN, ANIC, DSC, FMNH, SAMA. Found in southwestern Tasmania.

Discussion: Closest to *thayeri* n. sp. and *orientalis* n. sp. by the development of the left paramere. Separated by the spatulate mesotibial spur, protruding ventral apical margin of flagellomere VIII, and narrowed penis apex.

Tasmanityrus orientalis n. sp.
(Fig. 20)

Length 1.77–1.89. Males with oblique ventral impression on last flagellomere, sharply curved ventrally to point, flagellomere VIII only slightly protruding on ventral apical margin, nearly symmetrical; mesotrochanters with long spine near base, mesotibiae with long thick apical spur half again as long as first mesotarsomeres; aedeagus with broad asymmentrical apex, left paramere strongly developed, curved laterally and narrowing to point.

Measurements of holotype: Flagellomere VII 0.09 wide, 0.09 long, VIII 0.12 wide, 0.10 long, IX 0.13 wide, 0.26 long; mesotrochanteral spur 0.09 long, mesotibial spur 0.10 long, first mesotarsomere 0.05 long.

Specimens examined, 5: HOLOTYPE male, *Tasmania,* 4 km SE Weldborough, 450 m, II-12/14-1980, A. Newton & M. Thayer, *Nothofagus,* etc., berlese forest leaf & log litter (ANIC). PARATYPES: 1 female, eutopotypical (ANIC); 2 males, 1 female, same data except 4.4 km SE Weldborough, 460 m (AFN, DSC). Known from northeastern Tasmania.

Discussion: Closest to *thayeri* by the strong development of the left paramere, but easily distinguished by the asymmetrical penis apex and form of the paramere.

Etymology: The name is derived from its collection in northeastern Tasmania.

Tasmanityrus thayeri n. sp.
(Fig. 21)

Length 1.95–2.10. Male with apical flagellomere curved abruptly near apex to point, flagellomere VIII with ventral margin barely protruding at apex; mesotrochanters with ventral spine near base, mesotibiae with spatulate apical spur, spur half again as long as first tarsomere; aedeagus with broadly truncate apex, left paramere strongly developed, abruptly enlarged in apical half.

Measurements from holotype: Flagellomere VII 0.11 wide, 0.10 long, VIII 0.12 wide, 0.09 long, IX 0.13 wide, 0.22 long; mesotrochanteral spur 0.03 long, mesotibial spur 0.08 long, first mesotarsomere 0.05 long.

Specimens examined, 12: HOLOTYPE male, *Tasmania,* Mt. Field National Park, Lake Dobson Road, 240 m, I-30/II-5-1980, A. Newton & M. Thayer, wet sclerophyll, berlese forest leaf & log litter (ANIC). PARATYPES: 3 males, 5 females, eutopotypical (AFN, ANIC, DSC); 1 male, Florentine Valley, 10 km NW Maydena, II-14-1977, J. Kethley, ex: *Eucalyptus* litter & soil under log (FMNH); 1 male, Maydena, ANM Forest Station, 600′, II-13-

1977, J. Kethley, conc. pine litter (FMNH). One male specimen with weakly sclerotized genitalia is identified as this species but is not a designated paratype: E of Tooms Lake, IV-14-1977, L. Hill, litter ex: dry sclerophyll forest *Eucalyptus obliqua* (FMNH). Found in southern Tasmania.

Discussion: Close to *septentrionalis* and *orientalis* by the development of the left paramere and the broad penis apex. The broad symmetrical penis apex places *thayeri* closest to *simplicis,* but the form of the paramere and curved last flagellomeres easily separates these two species.

Etymology: Named for M. K. Thayer, who has collected many species of Pselaphidae in Australia.

Tasmanityrus septentrionalis n. sp.
(Fig. 22)

Length 1.86. Males with apex of last flagellomere curved ventrally, acute, venter impressed in apical half, penultimate flagellomere with antero-ventral angle at apex projecting; mesotrochanters with ventral spine near base, mesotibiae with long spatulate spur twice as long as first tarsomere; aedeagus with broad asymmetrical apex, left apical margin projecting, right paramere truncate at apex, acutely projecting laterally.

Measurements of holotype: Flagellomere VII 0.10 wide, 0.11 long, VIII 0.12 wide, 0.10 long, IX 0.13 wide, 0.23 long; mesotrochanteral spur 0.03 long, mesotibial spur 0.09 long, first mesotarsomere 0.04 long.

Specimen examined: HOLOTYPE male, *Tasmania,* 34 km W Smithton, Dismal Swamp, II-26-1977, J. Kethley, mixed *Nothofagus cunninghami* & *Acacia melanoxylon* litter, base of *Nothofagus cunninghami* (ANIC). Found in northwestern Tasmania.

Discussion: The broad asymmetrical penis apex places this species closest to *orientalis,* with the apex being slightly produced on the left rather than right side. The form of the paramere easily separate the two species, with the paramere of *septentrionalis* being stouter and much more abruptly angulate at the apex.

Etymology: Named for its collection in extreme northwestern Tasmania.

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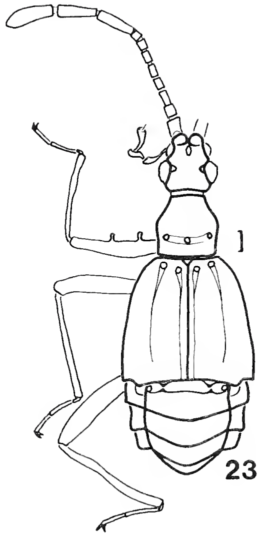

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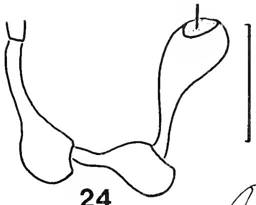

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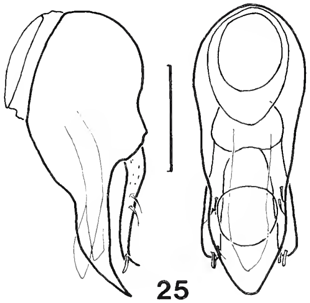

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Fig. 22. *Tasmanityrus septentrionalis* n. sp., right lateral and dorsal view male genitalia, paramere detached.

Fig. 23–25. *Chasoke victoriae* n. sp. 23. Dorsal habitus; 24. dorsal view right maxillary palpus; 25. right lateral and dorsal view male genitalia.

Chasoke n. gen

This genus cannot be placed near any of the genera of Tyrini from Australia and New Zealand, or indeed near any of the Ethiopian or Neotropical genera discussed and figured by Jeannel (1959, 1962). The offset insertion of the last segment of the maxillary palpus (Fig. 24), and large narrow apical flagellomeres (Fig. 23) are suggestive of some members of the Ctenistini. However, it lacks any evidence of lateral spines or setaceous projections on the maxillary palpi, and also lacks squamous pubescence except in the vertexal foveae. *Chasoke* is readily recognizable in the Australian fauna by the form of the maxillary palpi, pronotum with an antebasal transverse sulcus, and the pubescent vertexal foveae adjacent to the eyes.

Type species, *Chasoke victoriae,* n. gen., n. sp. Gender, masculine.

Chasoke n. gen. is characterized by: Antennae with long narrow club of 3 flagellomeres, maxillary palpi pedunculate basally, third and fourth segments bowed medially, large pubescent vertexal foveae adjacent to large eyes, small nude fovea at base of antennal tubercle, single gular fovea; pronotum with antebasal transverse sulcus, medial and lateral foveae in sulcus, procoxal foveae present; elytra with two basal foveae, discal stria extending through two-thirds of elytral length; median mesosternal fovea forked with forks widely separated at base, lateral mesosternal foveae forked medially and anteriorly, mesocoxal foveae present, single metasternal fovea; tergites I-IV subequal in length, I-III with three baso-lateral foveae, posterior lateral foveae quite small on II-III, IV with two baso-lateral foveae, V with single lateral fovea, I and II with pair of opposing teeth extending over medial baso-lateral foveae at end of basal impression; sternites II-V with large medio-lateral foveae, III-V with small baso-lateral foveae at margin, II with large globular invagination connected to margin by sulcus, III with small sulcus extending from margin and curved anteriorly; aedeagus with elongate symmetrical parameres.

Chasoke victoriae n. gen., n. sp.
(Figs. 23–25)

Length 1.72–2.25. Males with flagellomeres VII-IX narrow and elongate, VII and VIII about four times as long as wide; abdominal apex narrowly rounded, tergite V pointed apically, sternites II–VI lightly flattened medially; protrochanters with ventral knob, profemora with two widely spaced ventral knobs in basal half.

Females with flagellomeres VII-IX wider and shorter, VII no more than three times as long as wide, VIII only twice as long as wide; abdomen broadly rounded at apex, tergite V slightly tumid medially; knobs of protrochanters and profemora as in males.

Measurements of holotype: Flagellomere VII 0.7 wide, 0.29 long, VIII 0.08 wide, 0.27 long, IX 0.11 wide, 0.31 long; knobs of right profemur 0.08 and 0.24 from base.

Specimens examined, 5: HOLOTYPE male, *Victoria,* Australian Alps, I-1943, C. Oke and M. T. Higgenbotham (MVMA). PARATYPES: 1 male, Australian Alps, V, C. Oke (MVMA); 1 male, Balook, IV-26-1943, C. Oke (DSC); 1 male, 1 female, no locality data (MVMA). Known only from Victoria.

Etymology: The generic name is derived from that of the principal collector of the type series, Charles Oke, and the specific name from the state in which the specimens have been collected.

ACKNOWLEDGMENTS

I would like to thank the following individuals for the loan of specimens in their care, and the abbreviation for the collections in which specimens are placed follows their affiliation: John F. Lawrence, C.S.I.R.O, Canberra, Australia (ANIC); A. Neboiss, National Museum of Victoria, Abbotsford, Australia (MVMA); S. Endrody-Younga, Transvaal Museum, Pretoria, South Africa (TMSA); A. F. Newton, Field Museum of Natural History, Chicago, arranged the loan of material from that institution (FMNH) and from his private collection (AFN); E. G. Matthews, South Australian Museum, Adelaide, Australia (SAMA), assisted by the loan of the holotype and part of the type-series of *Tyromorphus auricomus* Lea. Some material is retained in the collection of the author (DSC). J. C. Watt and R. C. Craw, D.S.I.R., Auckland, New Zealand, helped greatly by the loan of specimens of *Tyrogetus palpalis* Broun and other representatives of the New Zealand Tyrini. J. F. Burger and R. M. Reeves, University of New Hampshire, kindly read the manuscript.

SUMMARY

The New Zealand tyrine genus *Tyrogetus* Broun is now recorded from Tasmania with the description of three new species; *occidentalis* n. sp., *howardi* n. sp., *minimus* n. sp. Two new genera of Tyrini

are described. *Tasmanityrus* n. gen., is proprosed for *Tyromorphus auricomus* Lea n. comb., and six new species from Tasmania: *hilli* n. sp., *newtoni* n. sp., *simplicis* n. sp., *orientalis* n. sp., *thayeri* n. sp., *septentrionalis* n. sp. *Tasmanityrus* is placed nearest *Gerallus* Sharp. *Chasoke victoriae* n. gen., n. sp., from Victoria cannot be placed near any particular genus at this time.

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AFFINITIES OF THE FOSSIL WASP, *HOPLISIDEA KOHLIANA* COCKERELL (HYMENOPTERA: SPHECIDAE: SPHECINAE)

By A. S. Menke[1] and A. P. Rasnitsyn[2]

The fossil wasp, *Hoplisidea kohliana,* was described by Cockerell (1906) from a single specimen taken from the "Miocene" shales of Florissant, Colorado. These deposits are now regarded as Lower Oligocene (MacGintie, 1953). Cockerell placed *Hoplisidea* in the "Nyssonidae" and related it to the "Gorytinae." He compared it with *Gorytes mystaceus* (now *Argogorytes*) and *Gorytes quadrifasciatus,* and stated that it came closest to *"Hoplisus"* (now *Gorytes*) in hindwing venation and general habitus.

The specimen (MCZ type #2018) is a large wasp (20 mm long) preserved venter up (fig. 1). Unfortunately the antennae were not preserved. The mandibles are long and sickle-like. The occipital carina is a complete circle tangential with the hypostomal carina. One pair of wings is nearly intact—at least the venation is clear (fig. 2). The stigma is narrow and elongate. There are 3 submarginal cells, the second of which receives both recurrent veins. The basal vein of the forewing is interstitial with cu-a, and it meets the subcosta well basad of the stigma. There is a forewing cloud through the marginal and submarginal cell area. The hindwing media diverges from M + Cu at crossvein cu-a. Unfortunately, the anal area of the hindwing is missing. The thorax and underside of the head are covered with long setae indicating that the wasp was fairly hairy. Similar long setae are visible on the abdominal sterna, but on III-V they seem restricted to a transverse row near the apex of each segment. The legs appear smooth, without obvious serration, and are rather slender. The coxae and femora have long setae, and one dislocated tarsus is spinose. The coxae are contiguous. The number of midtibial spurs and claw details are unclear. The connection between the gaster and propodeum is not clearly visible, but based on the shape of segment I, there was evidently a short petiole (dotted

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Manuscript received by the editor May 18, 1986

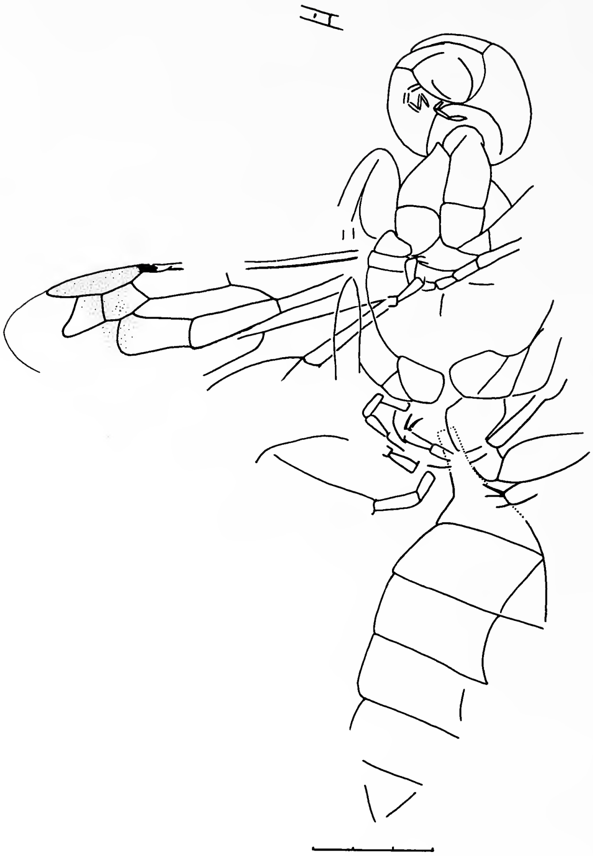

Fig. 1. Line drawing of type specimen of *Hoplisidea.* Scale = 3 mm.

lines on fig. 1 indicate probable petiole configuration). Only 6 gastral segments can be distinguished, but it is uncertain whether the specimen is a female.

Evans (1966) examined the type and discussed the wasp's probable affinities in some detail. He cast doubt on the fossil's relationship with the Gorytini because of wing venation (the position of the basal vein and divergence of the hindwing media). Evans suggested that the general wing pattern was more reminiscent of the family Tiphiidae. He concluded that in general body form, hairiness, and forewing venation, *Hoplisidea* resembled males of the genus *Anthobosca.* It should be pointed out here that females of *Anthobosca*

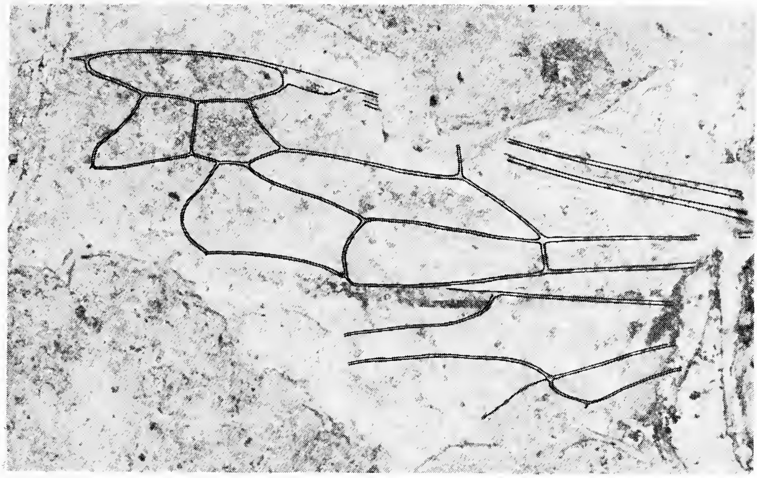

Fig. 2. Photograph of wings of *Hoplisidea* with veins inked in for clarity.

After examining the type, we are struck by the similarity of its venation pattern and cell shape with members of the sphecid tribe Sceliphrini. The forewing cloud enhances this perception because species of some sceliphrin genera (*Podium, Trigonopsis, Penepodium* and a few *Chalybion*), are similarly endowed. Figure 18 B in Bohart and Menke (1976), which is of a species of *Sceliphron,* is quite similar to the forewing of *Hoplisidea.* There is congruence in have very stout fossorial legs; thus *Hoplisidea,* because of its slender appendages, would have to be a male. Evans pointed out that the hindwing venation of *Anthobosca* (media diverges well before crossvein cu-a) contradicted a relationship with *Hoplisidea.* To this we can add that *Anthobosca* males (as well as females) have serrate tibiae, but the fossil's legs are apparently smooth, although the teeth would be hidden when viewed from certain angles. But more importantly, after comparing the wings of *Hoplisidea* with *Anthobosca* males, we fail to see the resemblance suggested by Evans. The cell shape and termination point of the recurrent veins are quite different. On the other hand, according to Evans, there is apparently considerable variability of these characters within *Anthobosca.* Evans' closing comment was "I consider it much more probable that it *[Hoplisidea]* is a tiphiid wasp not unrelated to *Anthobosca.*"

the long, narrow stigma and the shape of the submarginal cells. The forewings of other sceliphrin genera (*Chalybion, Podium, Trigonopsis*) are somewhat similar, but the 3rd submarginal cell is generally longer, and the shape of the 2nd varies. All of these wasps (except *Trigonopsis*) have long setae on the head and thorax. The hindwing venation of *Hoplisidea* is similar to the basic sceliphrin pattern: the media diverges at or very close to crossvein cu-a. The large, slender body of *Hoplisidea* and its sickle-like mandibles also agree with the character states of the Sceliphrini. The inability to discern the nature of the abdominal petiole is disconcerting, but it is clear that the petiole was short, about the length of the hindcoxa. The petiole is longer than the hindcoxa in most of the sceliphrin genera discussed above. On the other hand, in the most primitive members of the tribe such as *Stangeella* and *Chlorion,* the petiole is about as long as the hindcoxa. But the shape of the forewing submarginal cells in these genera is different from *Hoplisidea.* The preponderance of evidence suggests to use that *Hoplisidea* is most likely a sphecid wasp whose affinities are with the tribe Sceliphrini, rather than a tiphiid, but it does not appear to represent a living genus.

We thank Frank Carpenter, Museum of Comparative Zoology, Harvard University, for lending the type specimen of *Hoplisidea* for study; and Ronald Hodges, Systematic Entomology Laboratory, U.S. Dept. of Agriculture, and R. M. Bohart, Univ. of California, Davis, for commenting on the manuscript.

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HOST SPECIFICITY IN RAIDING BEHAVIOR OF THE SLAVE-MAKING ANT *POLYERGUS LUCIDUS*

By Linda Goodloe,[1] Raymond Sanwald,[2]
and Howard Topoff[3]

In the pine barrens of Suffolk County, New York, at least three species of *Formica* (subgenus *Neoformica*) are used as slaves by the obligatory slave-making ant *Polyergus lucidus.* In any single nest, however, only one slave species may be found. This contrasts with the sympatric, facultative slave-making ants of the genus *Formica* (subgenus *Raptiformica*) in which single colonies often contain two or more species of slaves. The slave species exclusivity of *P. lucidus* might result in two ways: (1) raids could be made to only one slave species of the four available; or (2) raids could be made to more than one slave species, but the captured pupae could be consumed differentially by the resident slaves, favoring the survival to eclosion of only one slave species. This paper reports the results of a study demonstrating that colonies of *P. lucidus* will, if given a choice, raid only colonies of the slave species already present in the mixed nest. Since scouts typically lead nestmates to target *Formica* nests (Cool-Kwait & Topoff, 1984), this selective process must occur through the perceptions and actions of the scouts.

METHOD

The field study was conducted on a two-acre site in Suffolk County previously described in Goodloe & Sanwald (1985). Two colonies of *P. lucidus* were collected in late spring of 1985 near Rocky Point, N.Y. One colony, P/S#1, contained slaves of the species *Formica schaufussi,* and the other, P/N#10 contained *Formica nitidiventris* slaves. Each colony was placed in a portable artificial

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Manuscript received by the editor October 18, 1986.

nest contained within a 61 × 43 × 10 cm plywood box. The nest consisted of a plastic box filled with moistened dirt inserted into a larger plywood box and having a single entrance/exit hole. A similar entrance/exit hole from the plywood box to the outside was closed with a plastic plug which could be removed to allow raiding to occur. The lid of the plywood box was removable to allow examination of the nest and the acitivity of *P. lucidus* workers prior to raiding. A cardboard cover was placed over the plastic nest box to prevent disturbing the colony when the lid was lifted, and was removed only when the interior of the nest was examined.

Experience has shown that very large colonies of *P. lucidus* are able to make multiple raids in a single day (Sanwald, unpublished observations). To maximize the frequency of raids for this study, each colony was expanded, prior to the beginning of the experiment, by the addition of slave-makers and slaves of the appropriate species. The colonies were expanded until each included approximately 1300 raiders and 4000 slaves at the beginning of the raiding season. Normal colonies usually contain several hundred slave-makers and slavs. This mixing procedure was possible because *P. lucidus* workers and slaves from different colonies can be successfully mixed when they are from colonies containing the same slave species (Goodloe & Sanwald, unpublished data). Such mixes between any combination of adult slaves and slave-makers from colonies using different slave species have been impossible to achieve.

Initially, each colony contained a single *P. lucidus* queen. The artificial colonies were kept indoors and observed until larvae appeared in the nest, from which time the colonies were allowed opportunities to raid.

A fixed location was chosen on the two-acre site from which raids were allowed to occur. On every day when weather was favorable for raiding, between 1300 and 1400 hr, one of the colonies was brought outside and placed at this location. The plug was removed to allow passage in and out of the artificial nest. To prevent slaves from initiating an emigration out of the artificial nest, all emerging slaves were retrieved by hand and returned to the artificial nest at the end of the day. All *P. lucidus* workers, by contrast, were allowed to pass in and out so that raids could occur.

Observations were made until the raiders had returned from any raids that occurred and activity of the slave-makers in and out of the nest ceased. The artificial nest was then replugged and returned inside until the next raiding opportunity. The two colonies were allowed to raid on alternate days at the fixed location within the constraints of differences in time of onset of raiding activity.

Samples of slave species workers were taken from each raided colony, when possible, for identification (see Appendix). Data were analyzed using the binomial test for large samples to determine if the choice of species raided was non-random. Expected P for random choice was set at .5 because both slave species were equally available to the raiders.

RESULTS AND DISCUSSION

The results of this study are summarized in Table 1. Between June 1 and August 3, 1985, Colony P/S#1, containing *F. schaufussi* slaves, made 45 raids. Samples of raided workers were obtained for 44 of these raids. In the blind identification of samples, 43 were determined to be *F. schaufussi* and one was *F. nitidiventris.* Choice of host species to raid was non-random ($p < .00003$, $n = 44$).

Colony P/N#10, containing *F. nitidiventris* slaves, conducted a total of 32 raids. Worker specimens were obtained for 28 of the raided colonies. Of these, 25 were identified as *F. nitidiventris,* one as *F. schaufussi,* and two as indeterminate, possible *F. incerta.* Again choice of host species was non-random ($p < .00003$, $n = 28$). The raid of P/S#1 on the *F. nitidiventris* netted approximately 50 pupae, while the raid of P/N#10 on the *F. schaufussi* nest netted 5 pupae. These numbers are low, but there is no evidence to determine whether the raiders were less interested in the pupae of these species or if the raided nests were already depleted of pupae.

Table 1. Slave species raided by *P. lucidus* colonies.

	Same	Different	Intermediate***	Total
P/S#1*	43	1	0	44
P/N#10**	25	1	2	28

**P. lucidus* colony with *F. schaufussi* slaves
***P. lucidus* colony with *F. nitidiventris* slaves
***intermediate in characters between the two slave species

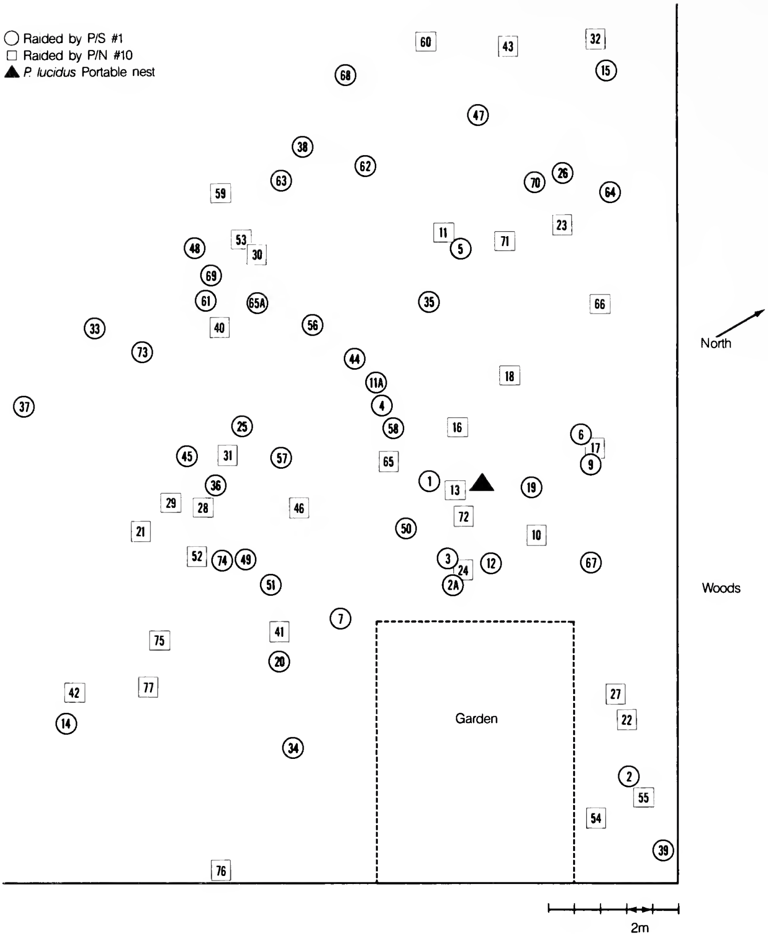

Fig. 1 Spatial distribution of raids by *Polyergus lucidus*. Numbers represent temporal order of raids during the 1985 season.

A more impressive demonstration of the species exclusivity of raiding in these colonies can be seen in Figure 1, where a spatial distribution of the raids is shown. The raided nests constitute a majority (estimated to be at least 75%) of the total available slave species nests in the described area.

There was no overlap between the two raiding colonies: none of the slave species nests were raided by more than one *P. lucidus* colony although several colonies were subjected to multiple raids by the same colony. P/S#1 raided slave colony #1 four times, colony #11A three times, and colonies #5, #9, #11, #34, #50, and #61 twice. P/N#10 raided slave colony #41 three times, and colonies #19, #21, and #58 twice.

It is clear from this study that raids are conducted almost exclusively to colonies of the same slave species found in the raiders' home nest. However, this experiment addressed the question of whether preference would be shown given abundant and equal availability of both species. Yet to be explored is the question of whether the raiders would choose alternative targets if the preferred slave species was absent.

Additional evidence has indicated that pupae of a slave species other than the species present in a given *P. lucidus* nest are more likely to be consumed (Goodloe and Topoff, unpublished data). Thus it seems unlikely that workers of any slave species other than the original host species will survive in the nest.

Goodloe and Sanwald (1985) demonstrated that newly mated *P. lucidus* queens, given a choice between a colony of the slave present in their nest of origin and a colony of another equally available slave species, will choose to invade the former. Although the mechanism by which raiders and queens acquire their preferences is unknown, imprinting is a likely possibility. For several *Formica* species, newly eclosed workers imprint to the species of pupae present during their first 15 days (Jaisson, 1975; Le Moli & Passetti, 1977; Le Moli & Mori, 1982). Perhaps *P. lucidus* queens and workers imprint to the slave species present at the time of their eclosion. The next step will be to determine if *P. lucidus* female alates are influenced, in their mate choice, by the host species in the male's colony of origin.

ACKNOWLEDGEMENTS

This research was supported by NSF grant #BNS-8402041. We thank Stefan Cover of the State University of New York at Stony Brook for his identification of *Formica* specimens and his most helpful discussion and comments on this manuscript.

APPENDIX

Identification of Slave Species

Currently existing published keys proved insufficient to distinguish *Neoformica* species. Specimens obtained from raided nests were identified, without knwoledge of the slave species of the raiders, according to the following criteria:

1) *Formica schaufussi:* Specimens reddish to yellowish brown on the head and alitrunk (=thorax). Gaster usually darker. Head and alitrunk usually concolorous, head sometimes slightly darker, never as dark as gaster. Body size typically large.

2) *Formica nitidiventris:* Specimens distinctly brown. In mature workers head and gaster shiny medium brown, alitrunk sometimes concolorous, sometimes lighter with brown infuscation on dorsal surface. Younger workers usually have a lighter alitrunk: yellowish brown with brown infuscation on the dorsal surface. Body size usually small to medium.

3) Specimens fitting into neither of the above categories. These ants have the dark heads and gasters characteristic of *Formica incerta* but there are too few workers in the samples to provide confidence in this label. The alitrunk color is yellowish or reddish yellow but dark infuscation appears on some specimens.

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NEW *PRAESTOCHRYSIS* AND NOTES ON DESCRIBED SPECIES FROM THE ORIENTAL REGION (HYMENOPTERA, CHRYSIDIDAE)*

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The genus *Praestochrysis* Linsenmaier is distinguished by having 5 distinct teeth on tergum III and a rather stout antenna. In any case the latter has flagellomere I less than 3 times as long as broad. Bohart (1986, Insecta Mundi 1:148-154) gave a key to species of the Ethiopian Region. One additional species, *lamborni,* is here described from that region. It keys out to couplet 6 in the 1986 paper but differs in having no transverse frontal carina.

Abbreviations used in the following descriptions are: F-I, etc., flagellomeres; TFC, transverse frontal carina; MOD, median ocellus diameter; T-I, etc., terga; S-II, sternum.

Praestochrysis lamborni Bohart, new species

Male holotype: Length 7.5 mm. Body moderately stout, green, midscutum mostly purple, F-I-II green in front, wings weakly stained. Punctures moderately small and close. Head 1.25× as broad as long (fig. 2a); F-I 1.7× as long as broad (fig. 2d), F-II as broad as long, F-V twice as broad as long; scapal basin short and broad, polished above and in middle one-third below, rest punctate, frons 1.8× as broad at malar space as at its least width; TFC absent, midocellus lidded, malar and subantennal spaces each about 1 MOD; pronotum about as long as scutellum, median groove weak; metanotum rounded (fig. 2c); mesopleuron edentate, scrobal and episternal sulci distinct; propodeal projection sharp, incurved behind; T-II without midcarina; T-III evenly convex before weakly developed pit row, lateral margin a little convex, 5 short, sharp distal teeth (fig. 2b); S-II spots small, triangular, nearly touching (fig. 2e).

Female. About as in male. T-III lateral margin slightly angled out, submedian teeth twice as long as others (fig. 2b).

**Manuscript received by the editor March 3, 1987.*

Holotype male, Malawi: Mangoche (Fort Johnston), I-14-34, emerged from flat moth cocoon on tree bark (W. A. Lamborn, OXFORD). Paratypes, 11 males, 29 females, same data as holotype (Oxford Museum, Bohart Museum); 3 males, 4 females, Malawi: Mzeze, 45 mi n. Mangoche, emerged from flat moth cocoons on tree bark (W. A. Lamborn, Oxford Museum, Bohart Museum, other major museums).

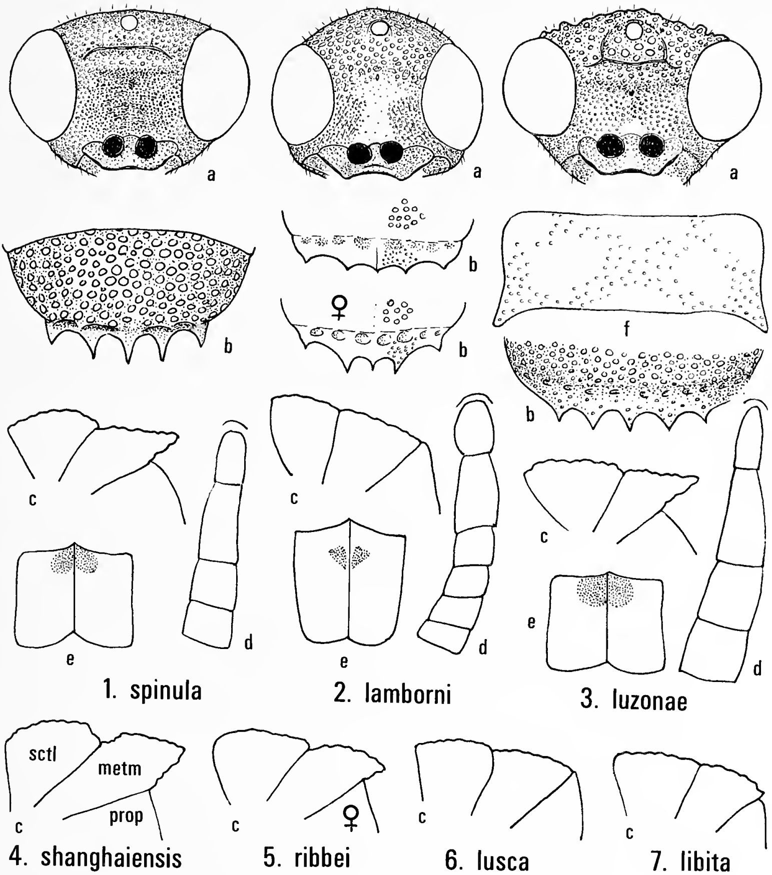
Discussion. The rounded metanotum, 5 distal teeth on T-III, and broadened flagellum are characters found also in *micromorpha* Mocsáry and *africanum* Buysson. However, both of these species have a definite TFC. In addition the *micromorpha* F-I is only 1.4× as long as broad instead of 1.7 as in *lamborni.* Also, in *africanum* the malar space is more than 2 MOD instead of only 1 MOD, and the lateral margin of T-III is not at all bent outward. The species is named for W. A. Lamborn, who collected the long type series.

Praestochrysis luzonae Bohart, new species

Male holotype: Length 7.5 mm. Body stout, green; deep purple across vertex, on scutum, and at base of T-III; T-III mostly bluish; F-I green in front; wings brown. Punctures coarse, close on vertex, widely separated by 4 smooth swellings on pronotum (fig. 3f), mostly a puncture diameter apart on rest of notum and terga. Head 1.55× as broad as long (fig. 3a), with prominent rugosities on vertex near eyes; F-I about twice as long as broad (fig. 3d), F-V 1.4× as broad as long; scapal basin short and broad, rather closely punctate; TFC broadly M-like (fig. 3a), branching above to nearly enclose midocellus and form a lid behind it; malar space 2.1 MOD; subantennal space 1 MOD; pronotum as long as scutellum, no median groove; metanotum with a flat, subtriangular mucro (fig. 3c); mesopleuron edentate but with prominent carinae below large scrobal sulcus, episternal sulcus deep and punctate; propodeal projection large, acute, slightly convex behind; T-II without midcarina; T-III evenly convex before weakly developed pit row (fig. 3b), pits unevenly shaped, mostly broader than long, lateral margin of III nearly straight, 5 sharp distal teeth, outer pair shortest; S-II spots rounded, touching (fig. 3e).

Female. Unknown.

Holotype male, Philippines: Luzon, Los Banos, IV-19-60 (A. Ojamin; U.S. National Museum, Washington).



Figures 1–7. *Praestochrysis.*

In all figs.: a, face; b, T-III dorsal; c, outline of scutellum, metanotum and propodeum, lateral; d, petiole and basal flagellomeres; e, sternum II; f, pronotum, dorsal; sctl, scutellum; metm, metanotum; prop, propodeum. Figures not drawn to scale, 2b and 5c are based on females, other figures based on males, those of 1–3 are from holotypes.

Discussion. The 4 large and polished pronotal convexities are distinctive. Also, the rough projections behind the eyes have not been seen in any other *Praestochrysis.*

Praetochrysis spinula Bohart, new species.

Holotype male. Length 7 mm. Body stout, blue green with extensive dark purple on vertex, notum, and terga, F-I green in front, wings light brown. Punctures medium coarse and fairly close on vertex and notum, coarse and separated by about a puncture diameter on terga. Head 1.5X as broad as long (fig. 1a); F-I 2.1X as long as broad (fig. 1d), F-V 1.4X as broad as long; scapal basin rather finely punctate, punctures arranged in a somewhat crossridged pattern; TFC prominent, nearly straight, downturned laterally (fig. 1a), backward branches weak, midocellus not lidded; malar space 2.5 MOD; subantennal space 0.8 MOD; pronotum as long as scutellum, no median groove; metanotum with a subtriangular, distally rounded, dorsally flattened mucro (fig. 1c); mesopleuron with a well-formed scrobal sulcus, areolate below, episternal sulcus discernible but weak; propodeal projection stout, sharply pointed, evenly convex behind; T-II without a midcarina; T-III rather evenly and strongly convex, pit row obsolete, lateral margin of III a little convex, 5 sharp and slender teeth, outer pair shortest (fig. 1b); S-II spots rounded, touching (fig. 1e).

Female. Unknown.

Holotype male, Sri Lanka (DAVIS).

Discussion. The long T-III teeth, obsolete pit row, medially straight TFC, and flattened mucro distinguish this species. The Taiwanese *basilacuna* Sugihara has similar T-III teeth but the pit row is better developed, TFC is medially incised, and the metanotal mucro is longitudinally furrowed. Also, it is a larger species, 9–13.5 mm long.

Notes on Oriental *Praestochrysis*

While studying Oriental *Praestochrysis,* I have noted several characters of key value. The presence or absence of a metanotal projection is a prime distinguishing feature. A large such projection is often present in *Praestochrysis* (figs. 1, 3, 4, 5) as in *basilacuna*

(Sugihara), *crassiscuta* (Mocsáry), *fumipennis* (Smith), *lachesis* (Mocsáry), *luzonae* Bohart, *palawanensis* (Mocsáry), *ribbei (Mocsáry)*, *sarawakensis* (Mocsáry), *shanghaiensis* (Smith), *spectabilis* (Mocsáry), and *spinula* Bohart. On the other hand, several species have little or no metanotal projection (figs. 6, 7). These are *amoenula* (Mocsáry), *furcifera* (Bingham), *libita* (Buysson), and *lusca* (Fabricius). Other characters are the presence of 2 large mesopleural teeth *(crassiscuta* and *spectabilis),* a strong sublateral pronotal carina *(lusca)*, pronotum with 4 smooth humps *(luzonae),* F-1 hardly longer than the pedicel *(lachesis),* and T-III teeth unusually long *(basilacuna, spinula).*

SUMMARY

Three new species of the chrysidid genus, *Praestochrysis,* are described and figured: *lamborni* from Malawi, *luzonae* from the Philippines, and *spinula* from Sri Lanka. Notes are given on previously named species from the Oriental Region.

A NEW SPECIES OF *PROTOSMIA* DUCKE FROM SPAIN WITH NOTES ON RELATED SPECIES (HYMENOPTERA: MEGACHILIDAE)[1]

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A trap-nesting program in northern Spain undertaken in cooperation with Dr. Enrique Asensio (Instituto Nacional de Investigaciones Agrarias, Valladolid) over the past few years has resulted in numerous nests of megachilids. One of these represents a new species of *Protosmia* Ducke. It is described here in order to make the name available for the description of its nesting biology, and is named in honor of Dr. Asensio, in recognition of his considerable help in this trap-nesting study.

In the following description, abdominal segments are numbered based on the metasoma; expressions in parentheses in the description of the male represent departures among male paratypes from characteristics described for the holotype.

Protosmia asensioi, new species
(Fig. 1–4)

Male. Length, 5 mm (3.5–5 mm); forewing length, 2.5 mm (2–2.5 mm). Black except: eyes, tegula, distal tarsal segments, sterna III, IV brown; tergum VII, sterna V–VIII yellowish; posterior margin of sternum I hyaline. Wings hyaline, venation black except costa brown. Pubescence white except off-white on clypeus, interantennal area, vertex, scutum, scutellum; dense on lower half of face, dorsal pronotal angle, scutellum; distinct apical fasciae laterally on terga I, II, nearly complete on tergum III, faint on tergum IV.

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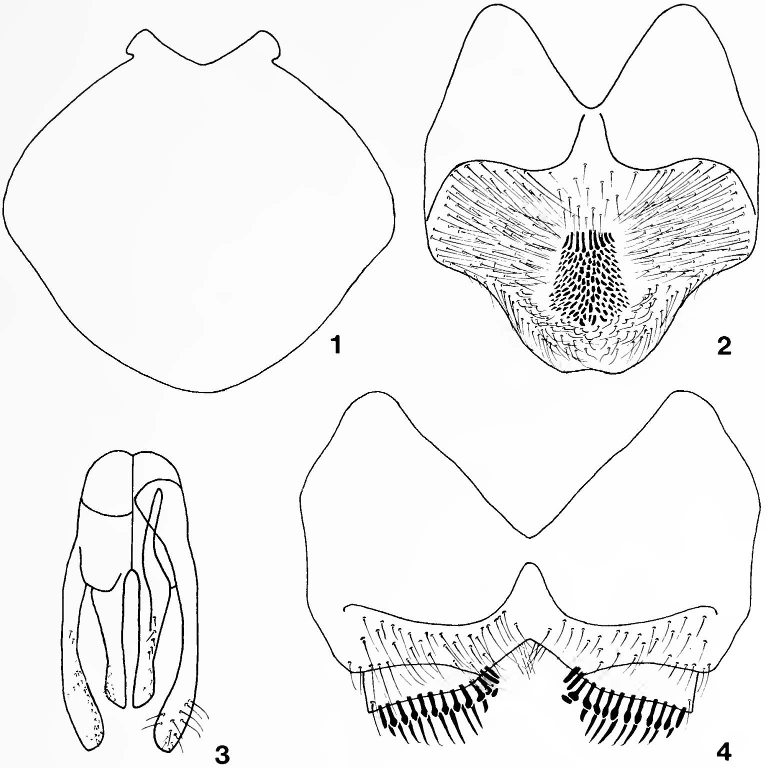
[1] This is a contribution from the Utah Agricultural Experiment Station, Utah State University, Logan, Utah 84322-4800, Journal Paper No. 3091, and USDA-Agricultural Research Service-Bee Biology & Systematics Laboratory, Utah State University, Logan, Utah 84322-5310.

Manuscript received by the editor January 19, 1987.

Head as long as broad; interocellar distance less than ocellocular distance, slightly greater than ocelloccipital distance; length of median flagellomeres one and one-half times width, clypeus slightly convex in profile, margin crenulate; mandible bidentate, upper tooth slightly acute; labrum slightly convex on apical margin, surface impunctate medially, sparsely haired; mouthparts in repose reaching past base of forelegs; scutellum slightly convex; metanotum oblique in profile; basal area of propodeum sloping, with fine longitudinal carinules; forebasitarsus linear, without acute apical angle; foretarsomere II not greatly expanded, longer than wide; tergum VI basolaterally with long, narrow, poorly sclerotized lobe hidden in normal view, apical margin with slight median lobe, lateral corner rounded; tergum VI hidden; sternum I with margin roundly convex (Fig. 1), surface under margin covered with dense, velvety pubescence; sternum II depressed medially, covered with dense, velvety pubescence where normally covered by sternum I, apical margin of sternum II narrowly, shallowly incurved laterally, widely, shallowly incurved medially, margin with long fringe of medially-directed hair; sternum II depressed, laterally bordered by narrow hyaline flange, apical margin narrowly hyaline with long fringe of medially curving hair interior to shallow lateral notch; disk of sternum IV sparsely pubescent, margin broadly convex with sharp lateral notch, submedially with small tuft of hair directed obliquely toward middle; sternum V as in Fig. 2; sternum VI as in Fig. 3; sternum VIII rounded apically; genitalia as in Fig. 4.

Female. Length, 4.5–5 mm; forewing length, 2.5–3 mm. Color as in male except: posterior margins of terga II, III, sometimes I, sterna I–V brown; mandible subapically reddish. Pubescence white; dense on lower paraocular area, dorsal pronotal angle, tip of pronotal lobe, posterior half of scutellum, metanotum medially, propodeum dorsolaterally; apical fasciae present on terga I–III, fascia on tergum I thick, broadly interrupted, becoming progressively thinner, less interrupted on terga II, III until thin, complete, sometimes indistinct on tergum IV; scopa white.

Head slightly longer than broad; distances on vertex as in male; length of flagellomere V less than width, flagellomeres VI–IX as long as wide; clypeus slightly convex in lateral view, margin slightly crenulate; mandible slender, not elongate, tridentate, distance between apices of lower and middle teeth slightly less than distance between apices of middle and upper teeth, acetabular carina reaching apical half of mandible, acetabular interspace finely, densely



Figs. 1–4. *Protosmia asensioi,* n. sp. Male. Fig. 1, sternum I. Fig. 2, sternum V. Fig. 3, sternum VI. Fig. 4, genitalia.

punctate, without ridges or shiny areas, basal portion of outer ridge curved dorsally, not reaching acetabular carina; labrum not elongate, not thickened apically, with strong medial tuft arising just basad of apical margin; mouthparts without modified hairs, maxillary palpi four-segmented; gena as wide as eye, ventrally with few long mesally curved hairs; hypostomal carina low, evenly raised throughout; thorax as in male; foretarsomere II as wide as long, asymmetrical, anteroapical angle slightly acute; sternum I without sharp transverse subapical carina.

Type Material. Holotype male: "39781C Rearing No.; SPAIN San Miguel de Bernuy, 14 km N Cantalejo, Reared E. Asensio/F.

Parker". 16 males, 18 females, San Miguel de Bernuy, 14 km N Cantelejo; 15 males, 11 females, Cantalejo, 50 km NNE Segovia; 10 males, 12 females, Fuentidueña, 66 km N Segovia; 10 males, 7 females, Aguilafuente, 37 km N Segovia. The holotype will be deposited in the collection of the U.S. National Museum (Washington, DC), paratypes in the collections of the British Museum (London), Museum National d'Histoire Naturelle (Paris), Natur-Museum Senckenberg (Frankfurt), Zoological Institute (Leningrad), E. Asensio, and the Bee Biology and Systematics Laboratory.

Discussion. Protosmia asensioi belongs to a group of poorly known and rarely collected Palearctic species. They are here included in *Protosmia* because they share with typical *Protosmia* a number of apomorphies including: fine transverse carinules on the pronotal lobe; hind coxa carinate; male tergum VI with lateral flap; male tergum VII and sterna V and VI hidden, not heavily sclerotized; female clypeus not overhanging labrum; female labrum with erect apical tuft of hair. Several of these characters are held in common with *Heriades,* but two, the transverse carinules on the pronotal lobe and the lateral flap on male tergum VI, are unique to *Protosmia.* Further, *Protosmia* lack distinctive characters found in *Heriades* such as the anteriorly carinate metanotum and the carinate basal propodeal zone.

Males of the *asensioi* group are abundantly distinct from typical *Protosmia.* Salient differences include the lack of a genal crease, median flagellomeres longer than broad, margin of tergum VI laterally rounded rather than angled, sternum I without a large ventral projection, and margin of sternum II with a fringe of long hair and without a deep median notch. Females, however, are not so easily differentiated. In fact, the only differences discovered, and these are slight, seem to be smaller body size, distance between mandibular teeth nearly equal, upper mandibular cutting edge a distinct arc ending dorsally in slightly acute tooth, and the absence of narrow impunctate apical margins on terga I and II.

Besides *P. asensioi,* this group includes *P. minutula* (Perez) (= *Osmia cataniae* Strand, new synonymy), previously included in *Hoplitis (Micreriades)* (Tkalcu 1977); *P. decipiens* (Benoist), previously placed in *Heriades (Eutrypetes)* (Popov 1955) and known only in the female; *P. limbata* (Benoist), included by Mavromoustakis (1955) in *Chelostoma* and also known only from the female; and *P. pulex* (Benoist), known only in the male. (These are all new combinations based on a study of the types by T. Griswold.) Strand (1921) thought it likely that *Osmia cataniae,* based on a single male from Sicily, was a representative of *P. minutula,* but stated he was naming it in the event that it should be found distinct. The type of *O. cataniae* is severely damaged, with the head and most of the abdomen gone, but the first sternum, whose form is distinctive for each species in the group, is still intact. The shape of this segment is the same as found in the male syntypes of *P. minutula.* Further, the type of *O. cataniae* is from Sicily, where one of the syntype males of *P. minutula* was taken (Benoist 1928). On these grounds, it is here placed in synonymy with *P. minutula.*

Males of *P. asensioi* can be readily distinguished from *P. minutula* by the shorter antennal flagellomeres and by the less pronounced median lobe of tergum VI and from *P. pulex* by the dark tegula, the absence of wide translucent apical borders on the terga, and the lack of a shallow medioapical emargination on sternum I. Females of *P. asensioi* can be distinguished from other *Protosmia* by the following combination of characters: the convex clypeus, the structure of the mandibular carinae, the apical position of the labral hair tuft, the absence of modified hairs on the mouthparts, the oblique metanotum with medially dense pubescence, the distribution of apical fasciae on the terga, the absence of translucent margins on the terga, and the lack of a strong transverse carina on sternum I.

ACKNOWLEDGMENTS

The study of types was made possible by grant BSR-8313307 from the National Science Foundation. We wish to thank S. Kelner-Pillault (Paris) and J. Oehlke (Eberswelde) for the opportunity to study types; G. van der Zanden for comments on the type of *Osmia cataniae;* E. Asensio and W. Hanson for reviewing the manuscript.

SUMMARY

A new species of *Protosmia* Ducke reared from trap-nest stems in Spain, *P. asensioi,* is described. It is compared with *P. minutula* (Perez), (= *Osmia cataniae* Strand, new synonymy), *P. decipiens* (Benoist), *P. limbata* (Benoist), and *P. pulex* (Benoist), all new combinations. This group of closely related species is distinguished from typical *Protosmia.*

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NEW GENERA AND SPECIES OF NEOTROPICAL AMISEGINAE (HYMENOPTERA, CHRYSIDIDAE)*

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The Canadian National Collection (OTTAWA) has one of the largest, if not the largest collection of neotropical Amiseginae in the world. In a sample of about 700 unidentified specimens sent to me by Lubomir Masner from this collection there were many new taxa, including representatives of a new genus. In addition, material was borrowed from the Museum of Comparative Zoology, Harvard University (J. M. Carpenter), Cambridge, Massachusetts, the American Entomological Institute, Gainesville, Florida (H. Townes, GAINESVILLE), and the U.S. National Museum, Washington, D.C. (K. V. Krombein, WASHINGTON). The new species of *Adelphe* are described separately (Kimsey 1986). The remaining new taxa are included below.

The following abbreviations are used: F = flagellomere, MOD = midocellus diameter, PD = puncture diameter and T = gastral tergum.

Amisega Cameron

Amisega Cameron 1888: 457. Type: *Amisega cuprifrons* Cameron 1888: 457. Monotypic.

Mesitiopterus Ashmead 1902: 231. Type: *Mesitiopterus kahlii* Ashmead 1902: 231. Orig. desig. NEW SYNONYMY.

KEY TO SPECIES OF *AMISEGA*

1. Gaster with 4 visible terga, F-I parallel-sided and about 4× as long as broad, female 2
   Gaster with 4 visible terga, F-I bulging submedially and about 3.5× as long as broad, male 19
2. Legs, including coxae primarily dark brown, fore and midtibiae and tarsi often paler 3

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*Manuscript received by the editor February 10, 1987.

Legs, including coxae primarily yellow, apex of femora and some tarsomeres may be dark brown 10

3. Propodeal dorsal enclosures smooth and polished; mesopleuron about one-half punctate or less 4
   Propodeal dorsal enclosures finely wrinkled or scratched; mesopleuron less than one-third impunctate 7
4. Vertex, pronotum and scutum densely transversely striate, T-II with small basomedial area of punctures, gena finely scratched or striate between punctures . . . . *townsendi* (Ashmead)
   Vertex pronotum and scutum without dense transverse striate, T-II mostly punctate, gena smooth between punctures 5
5. T-II bronzy purple, scapal basin smooth without striation . . . . *aeniceps* Ducke
   T-II black, without metallic tints; scapal basin with extensive transverse striation 6
6. Propodeum bluer than rest of thoracic dorsum, T-II reddish laterally . . . . *rufilateralis* Kimsey
   Propodeum and thoracic dorsum concolorous, black with faint bluish tints; T-II entirely black . . . . *tenebrae* Kimsey
7. Notauli complete, clearly indicated; mesopleuron finely striate or cross ridged above scrobe 8
   Notauli incomplete or absent; mesopleuron smooth above scrobe 9
8. Scutal posterolateral corners protruding dorsally, toothlike; vertex, pronotum, scutum, scutellum and metanotum reddish coppery . . . . *cooperi* Krombein
   Scutal posterolateral corners not protruding dorsally; vertex, pronotum, scutum, scutellum and metanotum bluish green . . . . *mocsaryi* Ducke
9. Malar space about 1 MOD, scape and legs dark, blackish . . . . *evansi* Krombein
   Malar space 1.7–2.0 MOD, scape and at least coxae yellowish brown . . . . *chiapana* Kimsey
10. Propodeal dorsal enclosures finely wrinkled, striate or scratched 11
    Propodeal dorsal enclosures smooth, shiny 12
11. Propodeal dorsal enclosure finely wrinkled or scratched, posterior enclosure smooth; legs pale red or yellow except posterior half of hindfemur dark brown . . . *bicolor* Kimsey

Propodeal dorsal and posterior enclosures densely striate, legs reddish brown with hindleg darker......... *striata* Kimsey

12. F-I yellow 13
F-I dark brown...15

13. Pronotum lateral face punctate; mesopleuron rough with small punctures below scrobe along posterior margin; scape and pedicel yellow, flagellomeres becoming gradually darker toward apex of antenna .... *kahlii* Ashmead
Pronotum lateral face polished and impunctate, mesopleuron polished and impunctate below scrobe along posterior margin; F-I pale only or scape, pedicel and F-I-III yellow and apical flagellomeres dark brown, without gradual transition 14

14. Antenna with only F-I pale, scutellum extensively transversely striate between sparse punctures, thoracic dorsum bluish... ....*bennetti* Kimsey
Antennal scape through F-III yellow; scutellum smooth between sparse punctures, without transverse striae; thoracic dorsum bronze .... *flavicrus* Kimsey

15. Head and thorax bright coppery, propodeum green-tinted; forewing membrane with pale transverse medial band; hindfemoral apex dark brown .... *belizensis* Kimsey
Head, thorax and propodeum concolorous bluish green to green or propodeum bluer, forewing without pale band, hindfemur entirely yellowish or apex dark brown 16

16. Scape yellow to red, malar space 1.8–2.0 MOD long .... *floridensis* (Krombein).
Scape dark brown, malar space 1.0–1.5 MOD long 17

17. T-II blue; frons, vertex and postocellar area densely cross striate .... *perviridis* Kimsey
T-II black or dark brown; frons and vertex without cross striae, postocellar area with or without striae.................18

18. Legs entirely yellow .... *flavipes* Kimsey
Legs yellow, except femoral apices, base of hindtibia and hindtarsomeres dark brown .... *semiflava* Kimsey

19. Legs including coxae primarily pale red or yellow 20
Legs primarily dark brown, coxae always dark brown......23

20. Scape reddish, at least ventrally paler than flagellomeres....21
Scape and flagellomere concolorous dark brown 22

21. Scape paler and reddish apically, contrasting with dark brown

pedicel and flagellum; midocellus 2.5–3.0 MOD from ocular margin . . . . *kahlii* (Ashmead)

Scape reddish brown, pedicel and flagellum only slightly darker; midocellus 2.0–2.2 MOD from ocular margin . . . . *floridensis* (Krombein)

22\. Propodeal dorsal enclosure smooth, T-II blue medially, scutal punctures 0.5–2.0 PD apart and not striatiform . . . . *perviridis* Kimsey

Propodeal dorsal enclosure finely rugose, T-II black medially, scutal punctures contiguous and striatiform . . . . *bicolor* Kimsey

23\. Propodeal dorsal enclosures finely rugose or striate; mesopleuron rugose, striate or punctate below scrobe 24

Propodeal dorsal enclosures smooth; mesopleuron smooth, polished and impunctate below scrobe 27

24\. Scutal posterolateral corners projecting dorsally, wings with transverse submedial unstained area . . . . *cooperi* Krombein

Scutal posterolateral corners not projecting, wings evenly brown-stained 25

25\. Propodeal posterior enclosures smooth, scapal basin distinct with few scattered punctures and without distinct transverse striation, pronotum and scutum with large circular punctures and without striae, notauli deeply impressed . . . . *mocsaryi* Ducke

Propodeal posterior enclosures rugose or striate at least dorsally, scapal basin not clearly delimited and densely striate, pronotal and scutal punctures striatiform among transverse striate 26

26\. Face and thoracic dorsum covered with dense, linear, transverse striae, punctures tiny and 2–5 PD apart; scape reddish, paler than flagellum . . . . *striata* Kimsey

Face and thoracic dorsum with coarse, irregular, transverse striae, punctures medium-sized and nearly contiguous; scape dark brown or black concolorous with flagellum . . . . *chiapana* Kimsey

27\. T-II medially bright blue, purple or bronze 28

T-II medially black, without metallic tints 30

28\. Terga dorsally bronzy, scapal basin smooth without transverse striation . . . . *aeniceps* Ducke

Terga dorsally blue to purple, scapal basin with transverse striation 29

29\. Malar space shorter than 1.5 MOD; terga bright blue dorsally .... *similis* Kimsey

Malar space longer than 1.5 MOD; terga purplish dorsally.... .... *flavipes* Kimsey

30\. Fore and midtibiae dark brown, concolorous with femora; pronotum densely striate 31

Fore and midtibiae reddish, considerably paler than femora; pronotum usually with few if any striae................ 32

31\. Gena smooth without striation, pronotum depressed sublaterally, South American .... *flavicrus* Kimsey

Gena finely scratched or striate, pronotum evenly rounded, Mexican .... *townsendi* (Ashmead)

32\. Thoracic dorsum green, pronotum with transverse striae medially, forewings with unstained medial band .... *belizensis* Kimsey

Thoracic dorsum blue, pronotum without transverse striae medially, forewings evenly brown-stained 33

33\. Mesopleuron impunctate, or with few tiny punctures immediately below subalar fovea; F-I parallel-sided and 4× as long as broad .... *bennetti* Kimsey

Mesopleuron punctate immediately below subalar fovea, punctures subequal in size to those on anterior half; F-I dilated and 3.5× as long as broad 34

34\. Hindtibia and tarsus reddish, paler than femur .... *tenebrae* Kimsey

Hindtibia and tarsus dark brown, concolorous with femur..... .... *rufilateralis* Kimsey

Amisega species are characterized by: narrow metanotum, less than half as long as scutellum; malar space less than one-eighth eye height; underside of head with long narrow fovea on either side of midline of genal bridge (= suboral fovea); propodeum without lateral angles; mesopleuron without oblique mesopleural carina, and pronotum without medial groove or anterior and lateral carina.

Species distinctions in this group are difficult, and color patterns tend to be more useful than structural measurements. Unfortunately, unlike most chrysidids, male *Amisega* tend to be structurally conservative and have few color differences between species. Because of this difficulty with males, holotypes of most of the following new species are females.

Amisega belizensis Kimsey, new species

Holotype female. Body length 3.5 mm. Face with fine striatiform punctures, scapal basin densely cross-ridged; malar space 1.3 MOD; eye in lateral view widest at midline; postocellar area covered with fine transverse striae and punctures; F-I 4× as long as broad; F-II length 2.5× breadth; pronotum and scutum covered with striatiform punctures, with transverse striae on pronotum; scutum without notauli; scutellar punctures irregularly spaced 0.2–2.0 PD apart, faintly striatiform anteriorly; mesopleuron with punctures densely clumped on anterior half, posterior area smooth and impunctate; propodeal enclosures smooth and impunctate; T-I and III-IV nearly impunctate, except for a few widely scattered tiny punctures; T-II with small anteromedial patch of tiny punctures, otherwise impunctate. Head, pronotum, scutum, scutellum and metanotum coppery; rest of thorax and propodeum with faint blue-green tint; terga black, except T-I-II with a lateral bluish spot; antenna dark brown; legs, including coxae, red, except posterior half of hindfemur dark brown; wings brown-stained with unstained medial stripe across wing at stigma.

Male. Same as female, except wing color fainter, body with green tints, coxae and femora dark brown, and tibiae and tarsomeres red.

Holotype female—BELIZE: Middlesex, 125m, 15 April 165, E. C. Welling (OTTAWA). Paratypes: 1 female and 2 males, same data as type except 27 April 1965, 3 April 1965 and 15 March 1965.

Discussion. The female of *belizensis* can be readily distinguished by the pale legs, coppery head and thorax and banded wings. Males are more difficult to distinguish but their legs tend to be pale apically, the notauli are essentially absent and the mesopleural punctation is distinctive.

Amisega bennetti Kimsey, new species

Holotype female. Body length 3 mm. Face with fine contiguous punctures; scapal basin cross-ridged with scattered punctures; malar space 1.2 MOD; eye in lateral view widest at midline; F-I length 4×

breadth; F-II length 2× breadth; postocellar area finely transversely striate, with scattered punctures 1–3 PD apart; pronotum, scutum and scutellum covered with fine transverse striae and small shallow punctures 1–3 PD apart; scutum with notauli present posteriorly and absent anteriorly; mesopleuron smooth with moderate punctures along anterior half, 0.2–1.0 PD apart; propodeal enclosures smooth and impunctate; T-I with transverse band of small punctures along posterior margin; T-II with small punctures clumped anteromedially; T-III-IV with tiny punctures along posterior margin. Face with green highlights; vertex coppery; thorax with bluish green highlights; abdomen dark brown without metallic highlights; antenna dark brown, except F-I yellow; legs including coxae yellow.

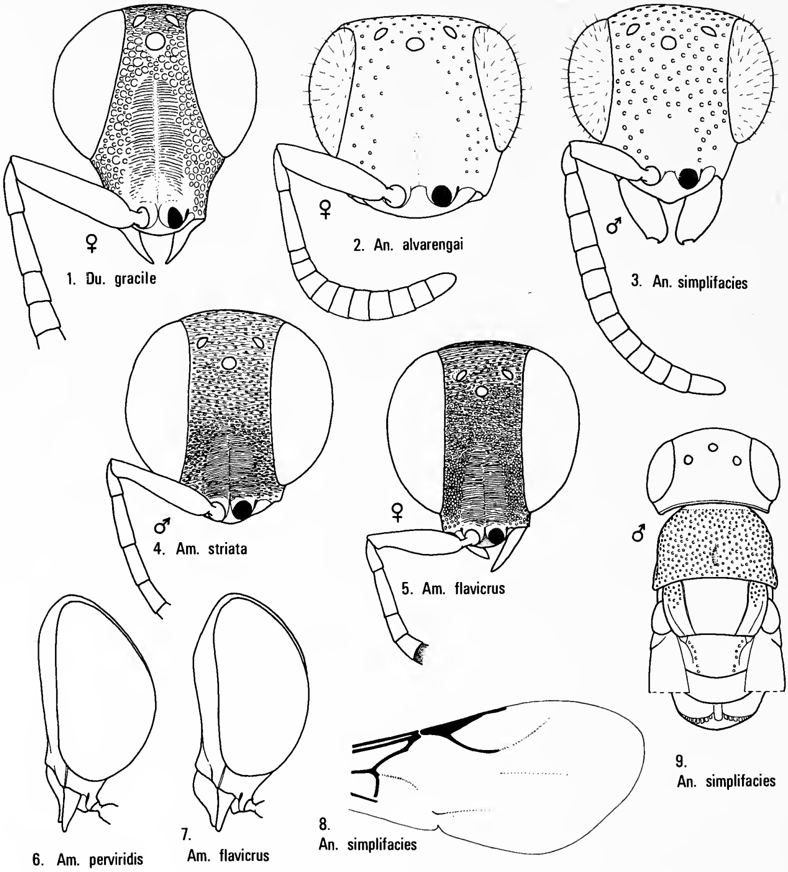
Male. Same as female, except body color greener; antenna entirely dark brown; coxae, femora and most of tibiae dark brown; tarsomeres paler and reddish, and scapal basin often smooth without transverse striae.

Holotype female—TRINIDAD, W. I., Curepe, Santa Margarita, 1–14 January 1974, E. D. Bennett (OTTAWA). Paratypes: 59 females and 302 males, same data as type except dates between January and December 1974 and 3 March 1961 (2 males), and 1 male: Piarco, 27 February 1961.

Discussion. *A. bennetti* and *flavicrus* are very similar and can be most readily separated by the color of the female antenna and legs. Otherwise *bennetti* can be distinguished by the evenly rounded pronotum, notauli indicated by a fine line; and the mesopleural punctation.

Amisega bicolor Kimsey, new species

Holotype female. Body length 3.5 mm. Scapal basin with smooth impunctate areas, without cross-ridging; frons to postocellar area appearing granular with contiguous small punctures and without striae; pronotum, scutum and scutellum same as vertex, without striae; malar space 1.5 MOD; eye in lateral view widest medially; F-I 4× as long as broad; F-II length twice breadth; mesopleuron with dense nearly contiguous punctures on anterior two-thirds, posterior part smooth and largely impunctate; dorsal propodeal enclosures finely rugose; T-I with few very scattered punctures; T-II with small anteromedial clump of punctures. Head, scape and thoracic dorsum



1. Du. gracile
2. An. alvarengai
3. An. simplifacies
4. Am. striata
5. Am. flavicrus
6. Am. perviridis
7. Am. flavicrus
8. An. simplifacies
9. An. simplifacies

Figs. 1–5. Front view of face. Figs. 6, 7. Lateral view of head. Fig. 8. Forewing, apical two-thirds. Fig. 9. Dorsal view of head and thorax, with wings removed. Am = *Amisega,* An = *Anadelphe,* Du = *Duckeia.*

brassy green; rest of thorax greener; pedicel and flagellum dark brown; legs, including coxae, yellow, except apex of hindfemur brown; terga black except I with anterior face reddish brown and posterolateral corners bluish.

Paratype females with cross-ridging in scapal basin and transverse striae on vertex.

Male. Same as female, except somewhat darker on T-I and II with more punctures.

Holotype female—MEXICO: Sinaloa, 20 mi. e. Concordia, 3000 ft., 12 August 1964, W. R. M. Mason (OTTAWA). Paratypes: 3 males and 3 females; Sinaloa: 5 mi w. El Palmito, 5000 ft., July 1964, W. R. M. Mason and L. Kelton (2 males, 3 females); Veracruz: Catemaco, 1100 ft., 16–18 June 1969 (1 male).

Discussion. Of the species with pale legs *bicolor* most closely resembles *striata,* based on the sculpture of the mesopleuron and propodeal enclosures. *A. bicolor* can be distinguished by the bicolored hindfemur, the entirely dark scape and bluer thoracic color.

Amisega chiapana Kimsey, new species

Holotype female. Body length 3 mm. Face finely cross-ridged in scapal basin, with transversely striatiform punctures on frons and vertex; malar space 2 MOD; eye in lateral view widest at midline; postocellar area with fine transverse striae and punctures; F-I length 3.5× breadth; F-II length twice breadth; pronotum, scutum and scutellum with punctures striatiform; scutum with notauli only indicated faintly anteriorly; mesopleuron with dense punctures on anterior two-thirds, posterior third polished and impunctate above scrobe, rugose below; propodeal enclosures finely striate; T-I-II with very scattered punctures. Head and thorax with light green tints laterally; antenna dark brown, except scape yellow; coxae, trochanters and base of femora yellow, rest of foreleg yellowish brown, rest of mid and hindleg brown; wings brown stained.

Male. Same as female, except head and thorax blue-green, legs and antenna entirely dark brown, and T-II usually with small anteromedial patch of punctures.

Holotype female: MEXICO: Chiapas, 20 mi. n. Bochil, 5700 ft., Yerba Buena, 24 June 1969 (OTTAWA). Paratypes: 2 males and 7 females; same data as type (2 males, 5 females); Yerba Buena, 5800 ft., 18 June 1969, Mason (2 females); Chiapas: se. side of Cerro Tres Picos, 28 May 1972, D. E. Breedlove (1 female).

Discussion. This species belongs to the group that has dark legs even in the females. *A. chiapana* most closely resembles *evansi* based on the finely sculptured propodeal enclosures, densely punctate mesopleuron and obsolescent notauli. It can be distinguished from *evansi* by the long malar space and pale female scape and legs basally.

Amisega flavicrus Kimsey, new species
(Figs. 5, 7)

Holotype female. Body length 3.5 mm. Face long and narrow (fig. 5), appearing granular, with fine contiguous punctures; scapal basin finely cross-ridged; malar space 1.3 MOD; eye in lateral view widest slightly above midline (fig. 7); F-I 4× as long as broad; F-II length 2× breadth; postocellar region transversely striate with small punctures 2–4 PD apart; pronotum more coarsely transversely striate, becoming smooth along posterior margin, punctures small and scattered 1–4 PD apart; scutum with some cross-striate between notauli and parapsides, notauli strong posteriorly and faint anteriorly, punctures 1–2 PD apart; scutellum smooth, punctures 2–5 PD apart; propodeal enclosures smooth and impunctate; mesopleuron smooth with punctures clumped along anterior half, nearly contiguous; T-I with transverse band of small punctures before posterior margin; T-II with large anteromedial zone of small punctures; T-III-IV with transverse band of small punctures before posterior margin; T-II with large anteromedial zone of small punctures; T-III-IV with transverse band of dense small punctures along posterior margin. Face green with brassy tints medially, thorax with greenish tints; terga blackish, except lateral triangular spot on T-I bluish; scape dorsobasally dark brown; remainder of scape, pedicel and F-I-III yellow, apical flagellomeres dark brown; legs, including coxae yellow; wings brown-tinted.

Male. Same as female except body color darker, and antenna and legs dark brown.

Holotype female—TRINIDAD: W. I. Curepe, CIBC lab. grounds, 14–28 May 1974, E. D. Bennett (OTTAWA). Paratypes: 75 males, 46 females; same data as type, except dates between January 1974 and January 1977 (57 males, 42 females); St. Augustine (2 males); Simla, 5 mi. n. Arima (3 males, 3 females); Morne Bleu (3 males); Curepe (2 males); Piarco (2 males), Arima Ward, Aripo Valley (1 male), Trinidad (6 males, 2 females).

Discussion. *A. flavicrus* females are distinctly colored and can be immediately recognized by the brassy green head and thoracic color, and yellow legs and scape to F-III. Both sexes have a long narrow face and the pronotum appears slightly depressed sublaterally. Males of *flavicrus* closely resemble those of *bennetti* but can be distinguished by the shape of the pronotum and the densely cross-striate face.

Amisega flavipes Kimsey, new species

Holotype female. Body length 3 mm. Scapal basin with dense transverse striae; vertex punctures touching to 2 PD apart; postocellar area without transverse striae except at posterior margin; malar space 1.5 MOD; F-I length 4X breadth; F-II length 2.3X breadth; pronotum coarsely transversely striate; scutum without notauli or transverse striae, scutellum without transverse striae; mesopleuron less than half punctate, posterior part smooth and impunctate; propodeal enclosures smooth; T-I with narrow transverse band of small punctures; T-II with anteromedial punctate area; T-III-IV with few minute punctures. Head and thorax, including propodeum blue; antenna dark brown, except scape paler beneath; legs including coxae yellow; terga blackish; wing membrane faintly brown-stained.

Male. Same as female except darker; scape entirely dark; legs dark brown, except fore and midtibiae and basal tarsomeres yellowish; T-II with purple tints.

Holotype female—BRAZIL: Bahia, Encruzilhada, November 1975, M. Alvarenga (GAINESVILLE). Paratypes—4 males and 8 females, same data as type, except some also collected by Seabra and Oliveira.

Discussion. *A. flavipes* is one of the 3 South American species with yellow legs and dark antenna in the female. It can be distinguished from *perviridis* and *semiflava* by the entirely yellow legs, black T-II, and the dorsum of the head without striation. Males can be recognized by the long malar space, purple T-II, dark legs and striate scapal basin.

Amisega perviridis Kimsey, new species
(Fig. 6)

Holotype female. Body length 4 mm. Face appearing granular, with fine contiguous punctures; scapal basin with small triangular zone of fine cross-ridging; malar space 1.2 MOD; eye in lateral view widest below midline, strongly tapering dorsally (fig. 6); F-I length 4× breadth; F-II length twice breadth; postocellar region covered with fine transverse striae, with scattered punctures 0.2–4 PD apart; pronotum covered with transverse striae; scutum and scutellum with sparser transverse striae, punctures 1–2 PD apart; notauli present posteriorly, obsolescent anteriorly; mesopleuron smooth with larger contiguous punctures along anterior half; propodeal enclosures smooth with scattered tiny punctures; T-I with narrow band of small punctures along posterior margin; T-II with dense small punctures anteromedially; T-III-IV with dense small punctures along posterior margin. Face brassy green with some coppery highlights around ocelli; thorax with green highlights becoming brassy dorsomedially; abdomen dark brown with blue highlights posterolaterally on T-I and medially on T-II; antenna dark brown; wings brown-tinted; legs including coxae yellow, except apical tarsomeres brown.

Male. Same as female except terga tend to be bluer.

Holotype female—TRINIDAD: W. I. Curepe, 1–14 January 1974, E. D. Bennett (OTTAWA). Paratypes: 2 females and 11 males, same data as type except dates between January 1974 and January 1975; 1 male: S. Grande, Turure Rd., April 1969, H. and A. Howden.

Discussion. This is another species from Trinidad. It can be distinguished from *bennetti* and *flavicrus* by the larger size, broader head and entirely dark female antenna. Other diagnostic features of *perviridis* are the short malar space, pale legs in both sexes, scutum without transverse striae and mesopleuron with punctures on anterior half or less.

Amisega rufilateralis Kimsey, new species

Holotype female. Body length 4 mm. Face with small dense punctures, smooth between, scapal basin densely cross-ridged; malar space 1.3 MOD long; eye in lateral view widest below midline; postocellar area punctate without transverse striae; F-I length 4× breadth; F-II length 2.5×; pronotum, scutum, and scutellum punctate without striation; mesopleuron with anterior half punctate, posterior part smooth and impunctate; propodeal enclosures smooth and impunctate; terga with dense tiny punctures. Vertex, pronotum, scutum, scutellum and metanotum greyish blue; face and propodeum bright blue; T-I reddish basally, T-II reddish laterally, rest of abdomen black; antenna dark brown; fore and midfemora and hindleg dark brown, fore and midtibiae and tarsi red; wing membrane brown-stained.

Male. Same as female, except F-I length 3.5× breadth; head and thorax concolorous.

Holotype female—BRAZIL: Guanabara, Repressa de Rio Grande, April 1966, M. Alvarenga (GAINESVILLE). Paratypes: 1 male and 12 females—Santa Catarina, Nova Teutonia, various dates from January 1961 to March 1965, F. Plaumann; 6 females—same data as type, except various dates from May 1966–June 1967.

Discussion. *A. rufilateralis* most closely resembles *aeniceps* based on the dark legs, smooth propodeal enclosures and dorsum without transverse striae. Diagnostic characteristics include T-I black medially and reddish laterally, the suboral fossae nearly reach the occiput, and particularly in females the propodeum is much bluer than the rest of the thoracic dorsum.

Amisega semiflava Kimsey, new species

Holotype female. Body length 3.5 mm. Scapal basin with fine dense transverse striae; frons and ocellar area without striation; postocellar area sparsely striate, becoming dense along posterior margin; malar space 1.2 MOD; eye in lateral view widest slightly below midline; F-I length 3.8× breadth; F-II length twice breadth; pronotal punctures striatiform; scutum and scutellum without transverse striae; scutal notauli well-developed; mesopleuron with anterior half punctate, posterior part polished and impunctate; propodeal enclosures smooth; terga with sparse fine punctures. Head and thoracic dorsum dark greyish green; antenna blackish; legs including coxae yellow, except apex of femora and tarsomeres dark brown; wings evenly brown-stained; terga black without metallic highlights.

Male. Unknown.

Holotype female—BRAZIL: Goias, Jatai, November 1972, F. M. Oliveira (GAINESVILLE). Paratypes—4 females, same data as type; 5 females—Mato Grosso, Itaum Douarados, March 1974, M. Alvarenga; 1 female—Mato Grasso, Sinop, February 1967, O. Roppa.

Discussion. This is the only South American *Amisega* species with dark antennae, strongly bicolored legs, non-metallic abdomen and sparse transverse striation on the thorax.

Amisega similis Kimsey, new species

Holotype male. Body length 3 mm. Scapal basin with dense fine transverse striae; rest of head densely punctate without striation; malar space 1.3 MOD long; eye in lateral view widest below midline; F-I length 3.5× breadth; F-II length 2.2× breadth; pronotum, scutum and scutellum without striation; notauli complete; mesopleural anterior half punctate, posterior part smooth and impunctate; propodeal enclosures smooth; terga with dense small punctures; head and thoracic dorsum blue; terga dorsally bright blue; antenna dark brown; fore and midfemora and hindlegs dark brown, fore and mid tibiae and tarsi pale yellowish brown; wing membrane brown-stained.

Female. Unknown.

Holotype male—BRAZIL. Guanabara, Represa Rio Grande, March 1972, F. M. Oliveira (GAINESVILLE). Paratypes—26 males, same data as type except various dates between 1968 and 1972; 1 male—Rio de Janeiro, Mangaratiba; 6 males—Rio de Janeiro, Guanabara; 1 male—Minas Gerais, Pedra Azul; 7 males—Pernambuco, Carvary; 5 males—Bahia, Encruzilhada.

Discussion. The most distinctive features of this species are the bright blue terga, and bicolored fore and midleg. Otherwise, *similis* closely resembles *aeniceps.*

Amisega striata Kimsey, new species
(Fig. 4)

Holotype female. Body length 4 mm. Face (fig. 4) short and broad, 1.1× as broad as long, with fine striatiform punctures; face and vertex finely cross-striate; scapal basin finely cross-ridged with striatiform punctures laterally; malar space 1 MOD long; eye in lateral view broadest at midline; F-I length 3× breadth; F-II length twice breadth; thoracic dorsum completely transversely striate with sparse striatiform punctures; mesopleuron sparsely striate below wing base, otherwise smooth with dense punctures along anterior half; propodeal enclosures striate; scutum with notauli obsolescent;

T-I with punctures along posterior margin; T-II with dense punctures on anterior two-thirds; T-III-IV with transverse band of dense punctures. Head and thorax with bluish green highlights, except ocellar triangle brassy; abdomen dark brown, except blue tints laterally on T-I-II; antenna dark brown, except ventral half of scape red; legs reddish brown becoming darker on mid and hindcoxa, and hindleg brown; wings brown-tinted.

Male. Same as female, except slightly darker.

Holotype male—COSTA RICA: Guanacaste, Junquillal Beach, 3 March 1976, R. M. Bohart (DAVIS). Paratypes: 1 male, same data as type; 1 male and 1 female—Santa Rosa Park, 5 November 1977 and 23 July 1977, D. H. Janzen.

Discussion. The most distinctive characteristic of *striata* is the extensive transverse striation of the head, thoracic dorsum and entire propodeum. In addition this species can be distinguished by the reddish brown legs, scape ventrally pale and thoracic dorsum brassy or with some brassy tints (in males).

Amisega tenebrae Kimsey, new species

Holotype female. Body length 3.5 mm. Scapal basin with dense transverse striae; rest of head punctate without striation; malar space 1.2 MOD long; F-I length 4× breadth; F-II length twice breadth; pronotum, scutum and scutellum punctures 1–3 PD apart and shallow, without striation; mesopleuron anterior half punctate, posterior part smooth and impunctate; scutal notauli complete; propodeal enclosures smooth; terga with sparse fine punctures, T-II punctures clumped anteromedially. Head and thoracic dorsum dark with faint bluish tints; antenna dark brown; legs dark brown, except fore and midtibiae and tarsi paler; wings evenly brown-stained; terga black, without highlights.

Male. Same as female, except head and thorax bluer, and malar space 1.5 MOD long.

Holotype female—BRAZIL: Teresopolis, 11 March 1966, H. Townes (GAINESVILLE). Paratypes—5 males and 3 females, same data as type; 6 males—Sao Paulo, S. J. Barreiros, Serra da Bocaina, January 1–13, 1969, Porter and Garcia; 1 male—Santa Catarina, Nova Teutonia, November 1971, F. Plaumann.

Discussion. This species closely resembles *rufilateralis* and the males of these 2 are nearly indistinguishable. Diagnostic features of *tenebrae* are: the dark legs, antennae and weakly metallic thoracic dorsum, black T-II, striate scapal basin and smooth propodeal enclosures.

Anadelphe Kimsey, new genus

Diagnosis. Malar space without vertical sulcus; occipital carina complete and well-developed; scapal basin flattened and smooth; flagellum short and fusiform in both sexes (figs. 2, 3); male mandibles broad and flattened with 2 small apical teeth (fig. 3); pronotum about as long as scutum, without medial groove or pit and without pit before lateral lobe; scutum with well-developed parapsides and deep notauli; mesopleuron with omaulus and without scrobal sulcus; metanotum 0.7× as long as scutellum, with elevated medial area without differential sculpturing or punctation (fig. 9); propodeum with long dorsal surface evenly rounded to steep posterior declivity, laterally rounded; tarsal claws with slender medial tooth; hindcoxa without dorsobasal carina; both sexes fully winged; forewing (fig. 8) RS extended by evenly curved dark streak, R1 0.5× as long as stigma or longer, medial vein arising before cu-a; terga rounded laterally.

Type: *Anadelphe simplifacies* Kimsey

Etymology: *An* = not, *Adelpha* = sister (Greek, feminine).

Discussion. *Anadelphe* appears to be most similar to *Adelphe* based on the unusual male mandibles, complete occipital carina, long ocular setulae, thickened clypeal apex, dentate tarsal claws, and propodeum with long dorsal surface. However, the absence of a pronotal carina and scrobal sulcus and no lateral propodeal angles immediately distinguish *Anadelphe* from *Adelphe.* In addition, *Anadelphe* differs from all the other American amisegines due to the long metanotum and the malar space with an obsolescent vertical sulcus.

Anadelphe alvarengai Kimsey, new species
(Fig. 2)

Holotype female. Body length 3 mm. Face (fig. 2) broad and highly polished; scapal basin flat, impunctate; brow with punctures shallow and small, 1–3 PD apart; malar space 2.5 MOD; subantennal distance 0.5 MOD; clypeus broad and projecting slightly medially; midocellus 2.7 MOD from ocular margin, hindocellus 0.8 diameters from ocular margin; F-I length 3.5× breadth; F-II 0.6× as long as broad; pronotum 1.2× as long as scutum, punctures large, shallow and faint; mesopleuron polished, with minute scattered punctures and smooth, broad and shallow depression along posterior margin; scutum, scutellum, metanotum, propodeum and abdominal segments highly polished and essentially impunctate. Head, metathorax and propodeum black; prothorax, scutum and scutellum orange; mesopleuron brownish orange anteriorly, posterior margin and ventral surface black; mandibles yellow medially, brown marginally; scape, pedicel and F-I-II yellow, apical flagellomeres dark brown; coxae and legs yellow; abdomen brown; wings lightly brown-tinted.

Male. Unknown.

Holotype female—BRAZIL: Mato Grosso, Itaum Dourados, March 1974, M. Alvarenga (OTTAWA).

Discussion. The orange coloration and smooth sparsely punctate integument will distinguish *alvarengai* from *simplifacies.* Other diagnostic features of *alvarengai* are the short, broad face and broadly rounded clypeus.

Anadelphe simplifacies Kimsey, new species
(Figs. 3, 8, 9)

Holotype male. Body length 2.5 mm. Face (fig. 3); scapal basin flat, impunctate; brow with punctures 0.5–1.0 PD apart; malar space 2.4 MOD; subantennal distance 1 MOD; clypeus projecting medially; midocellus 3 MOD from ocular margin; hindocellus 0.8–0.9 diameters from ocular margin; F-I length 1.9× breadth; F-II 1.6× as long as broad; pronotum (fig. 5) about as long as scutum medially, punctures 0.2–0.8 PD apart; scutum, scutellum and metanotum shiny, with sparse minute punctures; mesopleuron with large irregularly spaced punctures and shallow, broad, roughened depression along posterior margin, extending from scrobe to midcoxa; propodeum posteromedially rugose, laterally smooth and impunctate; abdominal segments shiny, flattened and impunctate. Head and most of thorax black, except scutum dark brown and scutellum lighter brown; mandibles yellowish brown; scape and pedicel yellow; flagellum dark brown; coxae dark brown; trochanters yellowish brown; femora brown, becoming yellow apically; tibiae and tarsi yellow; wings lightly brown-tinted; abdominal segments brown.

Female. Unknown.

Holotype male—ECUADOR: Pastaza, 22 km sw Puyo, 900 m, 14–16 July 1976, S. and J. Peck (OTTAWA).

Discussion. In *simplifacies* the face is longer and narrower than *alvarengai* and the clypeus is angulate medially.

Duckeia gracile Kimsey, new species
(Fig. 1)

Holotype female. Body length 3.5 mm. Face (fig. 1), long and narrow, 0.9× as long as broad; scapal basin long and densely cross-ridged; midocellus 1 MOD from ocular margin; malar space 3.3 MOD; subantennal distance 0.4 MOD; genal flange small and short; occipital carina absent dorsally; facial punctures coarse and contiguous; eyes strongly converging dorsally; F-I length 2.9× breadth; F-II 1.3× as long as broad; pronotum 0.9× as long as scutum, narrower than head; scutum with parapsides and notauli complete and well-developed, notauli strongly converging posteriorly; mesopleuron with small, simple scrobal pit and impunctate stripe along posterior margin; metanotum 0.4× as long as scutellum; thoracic dorsum with contiguous shallow punctures becoming smaller on scutum and scutellum, metanotal punctures contrastingly deeper and larger; forewing with brown spot across stigma and RS; propodeum with posterior surface coarsely rugose between carinae; abdominal punctures small, shallow and 0.5–1.0 PD apart. Body dark brown, except head with blue tints, antenna dark brown; legs, including coxae dark brown becoming red on tarsi, mesopleuron with ventral and posterior reddish stripe and T-II with faint bluish tint on lateral margin.

Male. Same as female.

Holotype female—BRAZIL: Represa Rio Grande, Guanabara, July 1972, M. Alvarenga (OTTAWA).

Discussion. The most distinctive features of this species are the slender compressed body, narrow face, the faint metallic color and the weak abdominal punctation. These characteristics will immediately distinguish *gracile* from *cyanea* Costa Lima.

Duckeia vagabunda Kimsey, new species

Holotype female. Body length 3.3 mm. Scapal basin long and densely cross-ridged; midocellus 2.5 MOD from ocular margin; malar space 4.3 MOD; subantennal distance 0.7 MOD; genal flange slightly shorter than eye height; occipital carina complete dorsally; facial punctures coarse and contiguous; F-I length 2.6× breadth, F-II 1.2× as long as broad; F-V length 0.9× breadth, pronotum 0.9× as long as scutum, about as broad as head posteriorly; scutum with parapsides clearly indicated and notauli faint; mesopleuron with small, simple scrobal pit and impunctate stripe along posterior margin; metanotum 0.4× as long as scutellum; thoracic dorsum with coarse contiguous punctures, becoming only slightly smaller on scutellum and metanotum, metanotal punctures deeper; forewing with brown spot across stigma and RS; propodeal dorsal enclosures smooth and polished medially and evenly rugose along margins, posterior surface smooth with scattered punctures; abdominal punctures coarse, contiguous and subequal to thoracic punctures. Body bright metallic blue, except antenna, legs and tegular dark brown, becoming paler on tarsi.

Male. Unknown.

Holotype female—MEXICO (WASHINGTON) reared from phasmatid egg on leaf of *Chamaeodora oblongata* from quarantined material arriving on airplane in Memphis, Tennessee, 27 March, 1962. Phasmatid egg probably that of *Prisopus berosus* Westwood according to label. Paratype female reared from phasmatid egg on palm leaf in quarantine material arriving in San Antonio, Texas, by airplane from Mexico.

Discussion. *Duckeia vagabunda* most closely resembles *cyanea,* having a more robust body than *gracile.* It can be distinguished from *gracile* by the greater distance between the midocellus and eye, longer malar space and bright blue coloration. *D. vagabunda* differs from *cyanea* in having the eye encircled by a faint carina versus a pronounced one in *cyanea,* the female flagellomeres not lobulate and F-V not less than 0.9× breadth. The paratype female closely resembles the holotype except that the legs and scape are reddish.

SUMMARY

One new genus, and new species, *Anadelphe (simplifacies* and *alvarengai)* are described. In addition, *Mesitiopterus* is synonymized under *Amisega,* and 10 new species of *Amisega* are described. Two new species of *Duckeia* are also described.

ACKNOWLEDGMENTS

I would like to thank Lubomir Masner, Henry Townes and Jim Carpenter for providing the specimens used in this study. The manuscript was reviewed by R. M. Bohart. This study was supported by NSF Grant No. BSR 84-07392.

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THE IDENTITY OF *ODYNERUS SCUDDERI* CAMERON AND *O? BRADLEYI* CAMERON (HYMENOPTERA: VESPIDAE: EUMENINAE)*

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Bohart (1965) treated the identity of 100 names of North American Eumeninae described by Peter Cameron from 1905 to 1912. This paper established the synonymy of all but four of these names, and so solved many problems in the nomenclature of nearctic Eumeninae. During a recent visit to the British Museum, I studied the type specimens of two of the unrecognized species, and in the present work establish their synonymy.

Euodynerus scudderi (Cameron, 1908) New Combination

Odynerus scudderi Cameron, 1908: 196. ♀; locality not stated (British Museum).
Odynerus discogaster Bequaert, 1939: 65. ♀; "Mt. Diablo, Contra Costa Co., 1,500 to 2,000 ft., CALIFORNIA" (Museum of Comparative Zoology). New Synonymy.

Bohart (1965) stated in regard to this species: "Type location unknown; pseudotype ♀, Chimney Gulch, Colorado, BMNH #18.541, does not agree with original description." In fact, it agrees with the original description perfectly, and I regard it as the true type. It bears a handwritten label "Chimney Gulch Col. 6/17/98". The writing is identical to that on material of other Cameron species collected by Oslar and specifically referred to in the same paper. Cameron's description did omit various details which he commonly included in other descriptions, such as the coloration of the legs, and the label data. But the details which he did report match the specimen, and are sufficiently precise to dispell doubt. In particular, the features of the clypeus are convincing. Cameron stated (1908: p. 197): "Clypeus distinctly longer than wide; in its centre is a black mark extending from top to bottom, the top square, from there it becomes gradually widened to the middle, then gradually narrowed to near the apex, which extends in a clearly separated angle; the

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*Manuscript received by the editor August 15, 1986.

sides of the mark are irregular, the apex is transverse." This is distinctive, as coloration goes. Further, he mentioned (p. 196): a "mark over the antennae, broader than long, transverse above, gradually roundly narrowed below, ending there in a nipple-like point", which is also distinguishing. Finally, he also mentioned (p. 197): "The head, thorax and base of the abdomen are densely covered with long, fuscous black hair." This is a specific character of *Euodynerus discogaster* (Bequaert, 1939), which now becomes a junior synonym. I have compared the holotype of this latter species with the holotype of *Euodynerus scudderi,* and *scudderi* differs primarily by the absence of the discal spots on metasomal tergum II. Among the specimens of *discogaster* in the MCZ is a female labelled "Webster Colorado July" which also lacks these spots and confirms that *discogaster* is variable in this regard.

Pterocheilus decorus Cresson, 1879

Pterochilus [!] *decorus* Cresson, 1879: xvii. ♀♂ (Bohart, 1940, states that the female is the holotype); "Nevada" (Academy of Natural Sciences).

Odynerus ? *bradleyi* Cameron, 1909: 81. "♀" (= ♂); "Durango, Colorado" (British Museum). Senior secondary homonym in *Pterocheilus* of *Pterocheilus bradleyi* Bohart, 1950. New Synonymy

Bohart did not find the type of this species. I chanced upon a specimen labelled in Cameron's hand "*Odynerus ? bradleyi* Cam." It lacks a BM type number label, but was probably not assigned one because "type" was not written on the determination label, contrary to Cameron's usual practice. The specimen is labelled with a printed label reading "Oslar. Durango Col.;" beneath this is a handwritten label reading "Durango Col 5/29/99;" a label bearing the number "5197;" the printed label "P. Cameron Coll. 1914-110;" and the aforementioned determination label. The handwritten labels are in the same hand as other specimens stated to be from Oslar. The type has the head glued in place, the forelegs and propleura broken off, the midlegs (the left coxa remains), and the right hind tibia and tarsus also broken off. One of the fore coxae and femur, the right midleg and the right hind tibia and tarsus are glued to the first label. The specimen is otherwise intact, and is easily recognizable as a species of *Pterocheilus.* The specimen matches the (for Cameron) extended description quite well, both in coloration and structure.

Distinctive details are the distribution of rufous color on the metasoma, the (Cameron, 1909: p. 81) "Clypeus not much longer than wide, the top dilated broadly in the middle, the apex with a shallow incision," the "Antennae longish, stout, dilated towards the apex," the pronotal "keel," and the metasomal shape (I "cup-shaped," II "as wide as long and narrowed at the base;" actually it is one and one third times as wide as long). However, Cameron stated that the specimen is a female, but it is a male. The description of the antennal apex leaves no doubt that Cameron was dealing with a male and erred in stating the sex. He stated: "the apical joints marked with black at the apex, the last rounded above, flat below, roundly narrowed at the apex." This is a common feature of males in the subgenus *Megapterocheilus,* to which this species belongs. *Pterocheilus bradleyi* Cameron, 1909 is a junior subjective synonym of *Pterocheilus decorus* Cresson, 1879.

Pterocheilus chesteri NEW NAME

Pterocheilus (*Megapterocheilus*) *bradleyi* Bohart, 1950: 195. ♂; "Nogales, Arizona" (Cornell University). Junior secondary homonym in *Pterocheilus* of *Odynerus ? bradleyi* Cameron, 1909

Unfortunately, the discovery of the identity of *O. bradleyi* Cameron creates a case of secondary homonymy in *Pterocheilus. P. bradleyi* Cameron, although a junior synonym, is an available name (Article 10(g) of the International Code of Zoological Nomenclature), and as such is a senior homonym of *P. bradleyi* Bohart, 1950. This latter species, described from Arizona in the same subgenus, must be rejected (Art. 59(a)), and replaced by a new name (Art. 60(c)), as it has no junior synomyms. I herewith propose the name *Pterocheilus chesteri* for *bradleyi* Bohart. The original name was proposed by Bohart as a patronym for J. Chester Bradley, and that intent is maintained by the replacement name.

ACKNOWLEDGMENTS

Work in the British Museum was supported by a Milton Fund grant to the author. I thank M. C. Day for assistance during my stay, and for valuable comments on the initial draft of this paper.

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HOMOPTERAN ATTENDANCE BY WASPS AND ANTS: THE STOCHASTIC NATURE OF INTERACTIONS

By Deborah K. Letourneau[1] and Jae C. Choe[2]

Associations of Hymenoptera with Homoptera have intrigued ecologists and evolutionary biologists as model systems of mutualism. The extensive body of literature, however, tends to be skewed to the interactions between ants and homopteran trophobionts in the Aphidae or Coccoidea (e.g., Kloft et al. 1965, Nixon 1951, Way 1963, Wilson 1971). In the following account we document a web of multispecies interactions within and between trophic levels, involving a species of wasp, several species of ants, and two species of Homoptera. This account is unique in the literature on Hymenoptera-Homoptera associations because it (1) addresses observable interference between hymenopteran attendants, (2) reports behavioral preference by homopterans for certain hymenopteran attendants, and (3) describes an interaction between a polistine wasp and an aetalionid planthopper. In addition, this study has general implications about the quality of diffuse and multiple associations between Homoptera and their honeydew foragers.

Materials and Methods

Ten aggregations of feeding *Aconophora ferruginea* Fowler (Homoptera: Membracidae) and four of *Aetalion reticulatum* (L.) (Homoptera: Aetalionidae) were located in the tropical wet forest along the Quebrada Camaronal at La Sirena, Parque Nacional de Corcovado, Osa Peninsula, Costa Rica. Both species of Homoptera are common in Costa Rica, ranging from Mexico and from Costa Rica to Brazil, respectively, and possessing wide ranges of host plants (Ballou 1935, 1936, Wood 1984). They are generally sessile, mating and depositing egg masses at the feeding site (Wood 1984).

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Manuscript received by the editor February 3, 1987.

Parachartergus fraternus (Gribodo) (Hymenoptera: Vespidae), a major diurnal attendant, occurs from Costa Rica to Argentina and commonly nests on trees and saplings (Fig. 1a) near streams or swamps (Richards 1978). Six species of formicine and one species of myrmicine ants were also recorded among the hymenopteran attendants.

Behavioral observations were made during 15–18 August 1984 for approximately 18 hours in daylight, six at dawn or dusk, and three at night. *Parachartergus fraternus* attendants were marked to determine if the same individuals returned to the same groups of Homoptera. An extended anal tube of aetalionids allowed inspection of honeydew delivery to individual attendants. We noted the size class of droplets, and recorded the number of droplets per feeding bout and length of feeding bout for three major attendants. Common attendant Hymenoptera and Homoptera were collected for identification, and voucher specimens were deposited at the Museum of Comparative Zoology, Harvard University.

RESULTS

Two aggregations of *A. ferruginea* and two of *A. reticulatum* were tended by *P. fraternus* during daylight hours (Fig. 1b, c). Of 14 homopteran aggregations, 13 were visited by two or more species of ants. These ant species included *Camponotus abdominalis* (F.), *C. novogranadensis* Mayr, *C. sexguttatus* (F.), *C. simillimus* (F. Sm.), two unidentified *Camponotus* spp., *Zacryptocerus porrasi* (Wheeler), and a few other unidentified occasional species. One male-female pair of *A. reticulatum* was not tended during our observation period. All homopteran aggregations except one were feeding on *Piper auritum* Kunth, a common plant of forest edges and disturbed sites in moist regions from Mexico to Columbia (Burger 1971). One aggregation of *A. reticulatum* was found on balsa, *Ochroma lagopus* Swartz var. *bicolor* (Rowlee) Standl. & Steyermark.

The most explicit forms of ownership behavior (*sensu* Brown 1976) were displayed by *P. fraternus,* which tended throughout the daylight hours. During our observation period, the same individual wasps returned to the same homopteran aggregations shortly after dawn and remained there until dusk except for several short (less than 10 minutes each) breaks. The wasps constantly antennated and

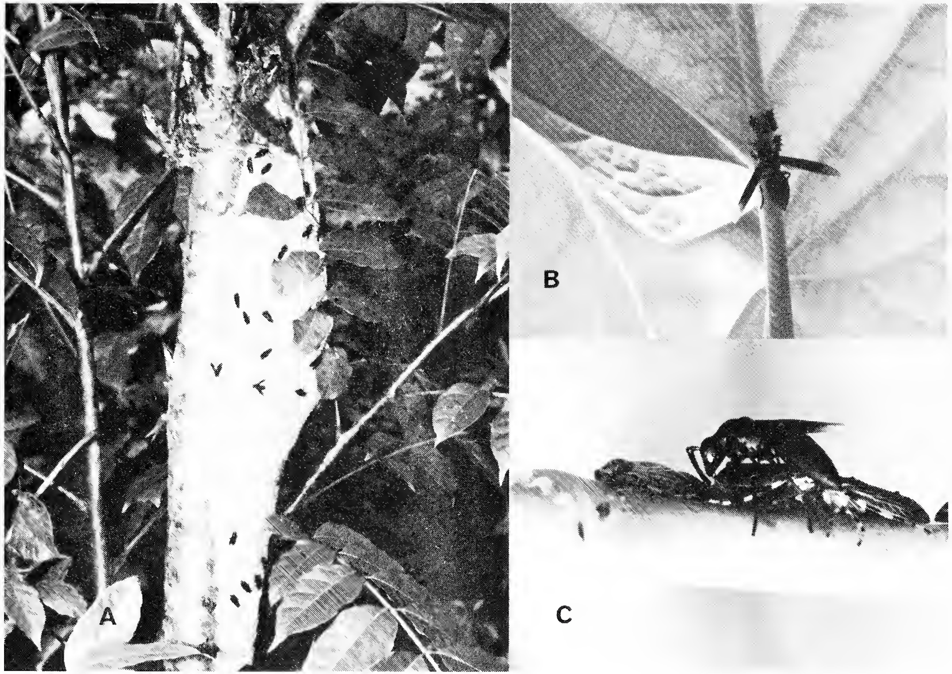

Fig. 1. *Parachartergus fraternus,* a polistine wasp (ca. 13 mm): A, on the nest; B, tending nymphs of a membracid, *Aconophora ferruginea,* on *Piper auritum;* C, tending adults and nymphs of an aetalionid, *Aetalion reticulatum,* on *P. auritum.* Photographs by Jae C. Choe.

actively herded the homopterans. Whenever an aetalionid moved away from the feeding group, the wasp quickly flew over the aetalionid and assumed a stiff posture with stilt legs and elevated wings (N = 12). The wasp sometimes buzzed its wings and the aetalionid soon returned to its own group. The same type of behavior was observed in the wasp when attending membracid nymphs.

Parachartergus fraternus responded to any approaching animals, including ants, conspecific wasps, anole lizards, and even humans. The typical display involved a combination of the following behaviors: positioning antennae low to the dorsum, extending wings laterally, buzzing wings, chasing, making stinging movements, or biting. These activities appeared to be successful in preventing most ants from soliciting honeydew from the homopterans. On one occasion, a wasp flew at an approaching myrmicine ant and actually knocked it off the branch. Workers of *C. sexguttatus* were observed frequently (on average once every 20 seconds during three six-minute periods) to descend the branch and petiole to a point approximately 5 cm from the wasp-tended homopteran aggregation, but the mere presence of *P. fraternus* seemed to deter the ants from approaching closer. Unlike *P. fraternus,* most attendant ant species did not actively interfere with other approaching ants. One exception was *C. abdominalis,* the major nocturnal attendant, which pursued and disrupted any approaching ant of a different species.

Ants tended in groups of two or three, whereas *P. fraternus* always tended alone. *P. fraternus* also tended much larger groups of *A. reticulatum* (19 and 25 individuals) than did ants (1 and 3 individuals). For smaller membracids, however, there was no such trend; ants managed to tend groups of four to 24 individuals, while *P. fraternus* tended 12 and 13 nymphs. In wasp-tended aggregations, when a wasp was momentarily absent, ants were often quick to move in and collect honeydew. Upon the return of the wasp, however, ants always retreated.

A specialized anal tube of *A. reticulatum* enabled us to assess honeydew delivery. In response to vigorous antennation on the dorsal tip of the abdomen by wasps or ants, aetalionids protruded the anal tube and secreted droplets of honeydew often at a high rate. We counted up to 34 consecutive droplets taken from an adult aetalionid during a single feeding bout by *P. fraternus.* Aetalionid nymphs also produced honeydew, but presented droplets on the dorsal surface about 2 mm from the tip of the abdomen. It appeared that nymphs did not have fully developed tubes.

Aetalion reticulatum appeared to discriminate between attendants. The mean number of droplets per feeding bout was significantly higher (Kruskal-Wallis test: $p < 0.001$) when *P. fraternus* was soliciting than when either *C. abdominalis,* the major nocturnal tender, or *Z. porrasi* were tending (Table 1). The size of droplets from the same adults was consistently larger (about twice in diameter) when *P. fraternus* was tending. Duration of feeding bouts, however, did not differ (Table 1). In the presence of *P. fraternus,* aetalionids commonly raised a pair of legs nearest an approaching ant, kicked at it, and prevented it from collecting honeydew. Thus *A. reticulatum* appeared to play an active role in selecting an attendant.

Discussion

Associations of Hymenoptera with Homoptera cover the entire range of interaction categories including predation (e.g., Evans 1968, Hook 1981), parasitism, mutualism, commensalism, and behavioral combinations such as mutualism-predation (Pontin 1958) and parasitism-predation (Gerling 1966). It is well known that wasps and bees, like ants, depend upon homopterans as sources of carbohydrates (Evans and West Eberhard 1970, Spradbery 1973); however, the behaviors associated with honeydew collection in wasps and bees have not been reviewed.

Our literature survey and field study revealed that bees and wasps exhibit nearly as great a range of interactions as do ant associates. Honeydew foraging of bees and wasps involves various types of behavior ranging from little or no contact with Homoptera to displays of active herding and guarding (Table 2). Unlike some ants (e.g., Maschwitz and Hänel 1985), however, no bees or wasps have been observed to move homopterans to favorable feeding sites. At least eight species of *Trigona* bees and ten species of polistine wasps are now known to tend and collect honeydew from various Homoptera. It is interesting to note that all hymenopteran species known to collect honeydew directly from Homoptera are meliponine bees and polistine wasps. Other social hymenopterans such as honey bees, bumble bees, and vespine wasps have been observed only to obtain

Table 1. Honeydew excretion rates of *Aetalion reticulatum* when solicited by three species of Hymenoptera.

Soliciting Hymenoptera (size, mm)	N	Drops per bout (mean ± SD)	Length of bout (mean ± SD, seconds)
Formicidae			
Z. porrasi (3.5)	20	2.7 ± 2.0	11.3 ± 10.0
C. abdominalis (6.0)	7	3.4 ± 1.0	10.6 ± 4.5
Vespidae			
P. fraternus (12.9)	22	8.6 ± 6.5	13.1 ± 8.9

honeydew by gleaning foliage near feeding homopterans. Furthermore, all studies, except for *Polistes fuscatus* (Barrows 1979), have been reported from tropical areas. Distinct ownership behavior has been recorded from only a few species.

Our observations on two homopteran species and their complex of hymenopteran attendants, together with those of other workers, add several facts regarding the nature of mutualism between these two groups. First, the association between Homoptera and their hymenopteran attendants is highly stochastic and often involves a multispecies complex. Most studies have focussed on a single hymenopteran species (e.g., Fritz 1982, Messina 1981), but several workers (e.g., Addicott 1979, Bradley and Hinks 1968, Bristow 1984, O'Neill and Robinson 1977) have now investigated community aspects of the relationship. An individual Homoptera may host several species of Hymenoptera during its lifetime. For instance, *A. reticulatum* has been observed to be tended by *Trigona amalthea* and *T. spinipes* along with a variety of ant species in Brazil (Brown 1976, Castro 1975, Cockerell 1920). Brown (1976) studied hymenopteran attendance of *A. reticulatum* on the Osa Peninsula, not far from our study site, and found a completely different complex of attendant species with diel shifts. An attendant hymenopteran species may also associate with more than one species of Homoptera. *Trigona amalthea* is known to tend *A. reticulatum* and at least two species of membracids (Cockerell 1920, Salt 1929, Schuster 1981). Our study also reports that *P. fraternus* readily associates with both *A. reticulatum* and *A. ferruginea.* Elements of chance due to nest distribution and nutritional need of hymenopteran attendants, and

Table 2. Activities of bees and wasps as honeydew foragers.

Taxon	Reference
Gleans honeydew from foliage near feeding homopterans	
Apidae	
Apinae (Apini)	
Apis mellifera	Bloc et al. 1984, Kunkel & Kloft 1977, Prabucki 1972, Santas 1983
Bombinae	
Bombus bifarius	Wagner & Cameron 1985
Vespidae	
Vespinae	
Vespa orientalis	Ikan & Ishay 1966
Vespula spp.	Duncan 1939, Evans & West Eberhard 1970
Obtains honeydew directly from feeding homopterans	
Apidae	
Apinae (Meliponini)	
Trigona amalthea	Cockerell 1920, Salt 1929, Schuster 1981
Trigona cagafogo	Müller 1873, 1874
Trigona corvina	Jiron P. & Salas D. 1975
Trigona cupira	Silvestri 1902
Trigona hyalinata branneri	Laroca & Sakakibara 1976
*Trigona spinipes**	Castro 1975
*Trigona tataira**	Cortopassi-Laurino 1977
Trigona sp.	Wood 1984
Vespidae	
Polistinae	
*Polistes fuscatus**	Barrows 1979
Parachartergus apicalis	Williams 1928, Wood 1984
*Parachartergus fraternus**	This study
*Parachartergus richardsi**	Schremmer 1978
Mischocyttarus drewseni	Jeanne 1972
Stelopolybia testacea	Jeanne 1972
Pseudopolybia compressa	Brown 1976, Wood 1984
Pseudopolybia vespiceps	Jeanne 1972
Polybia sp.	Jiron P. & Salas D. 1975
Brachygastra sp.*	Belt 1874

*Distinct ownership behavior has been observed.

habitat heterogeneity may play a large role in determining the partnership. Recently, Law and Koptur (1986) provided an elegant theoretical argument supporting the evolution of non-specificity in mutualistic interactions.

Second hymenopteran attendants differ in tenacity of attendance. Components of these differences include fidelity and constancy of attendance, foraging strategy, and temporal activity pattern. *Parachartergus fraternus* showed high fidelity during our observation period, i.e., the same individuals tended the same homopteran groups. Similar behavior is known for *Polistes fuscatus* (Barrows 1979). In general, wasps tend to forage as individuals (Barrows 1979, Schremmer 1978, and this study), whereas social bees, like ants, more often recruit (Cortopassi-Laurino 1977, Schuster 1981). Both wasps and bees remain with homopterans for long periods interrupted only by short forays to the nest. Honeydew foraging activities of wasps and bees are always diurnal (Schremmer 1978 and this study).

Third, hymenopteran attendants also differ in quality. It is now well established that hymenopteran attendance enhances the fitness of homopterans (Bristow 1984, Fritz 1982). However, the quality of hymenopteran services varies widely in terms of the effectiveness of sanitation, enhancement of growth rate, and defense. At least in a few studies with ants and aphids (Banks and Nixon 1958, El-Ziady 1960), rapid rate of honeydew excretion indicates an increased rate of assimilation of essential nutrients, higher growth rate, and higher fecundity in homopterans. In our study, sanitation was maintained by most attendants, but wasp attendance could potentially increase the fitness of homopterans through providing better defense and enhancing growth rates. Jiron P. and Salas D. (1975), on the other hand, report no evidence that the presence of bees and wasps deter scale predators but observe benefits due to site sanitation. *Bombus bifarius* may not enhance aphid growth rates, but its leaf-gleaning activities can disrupt potential enemies (Wagner and Cameron 1985).

Fourth, homopterans may show preference for certain attendants. Benefits to homopterans from hymenopteran attendants may not be equal and certain Homoptera-Hymenoptera associations may be favored (Addicott 1979, Bristow 1984, Messina 1981). In this study, we documented differential responses of *A. reticulatum* to various hymenopteran attendants. In the presence of *P. fraternus,* aetalionids behaved defensively and provided little, if any, honeydew to soliciting ants. Furthermore, under wasp solicitation, aetalionids produced significantly larger quantities of honeydew. This behavioral plasticity may be adaptive under conditions of variable tender quality. It may also play an important role in mediating competitive interactions within mutualistic systems.

SUMMARY

A web of multispecies interactions involving a planthopper, *Aetalion reticulatum,* and a membracid, *Aconophora ferruginea,* and their hymenopteran attendants were studied in Costa Rica. A wasp, *Parachartergus fraternus,* tended both species of Homoptera diurnally and prevented other Hymenoptera from obtaining honeydew. *Camponotus abdominalis,* a major nocturnal attendant, also showed a similar degree of "ownership" behavior. Other ant species, however, appeared to be opportunistic. Although associations were highly stochastic with regard to partnership, *A. reticulatum* showed a clear preference for *P. fraternus* over ant attendants. It provided significantly more honeydew to *P. fraternus* and in the presence of *P. fraternus* it behaved antagonistically toward any ants. The literature on associations of Homoptera with wasps and bees is also reviewed.

ACKNOWLEDGMENTS

We thank the Servicio de Parques Nacionales of Costa Rica and the Organization for Tropical Studies (OTS) for making our study in Parque Nacional de Corcovado possible. We are grateful to R. R. Snelling for identifying the Hymenoptera and to T. K. Wood for identifying the Homoptera. P. H. Adler, C. B. Bristow, J. Carpenter, B. Hölldobler, S. Koptur, D. L. Perlman, and E. O. Wilson have provided important suggestions for improving earlier drafts. JCC was supported by the Richmond Fund of Harvard University.

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A KEY TO THE SPECIES OF *SPINTHARINA* WITH DESCRIPTIONS OF NEW SPECIES AND INDICATION OF SPECIES GROUPS (HYMENOPTERA, CHRYSIDIDAE)*

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Spintharina Semenov (type species: *vagans* Radoszkowski occurs in the southern Palearctic and Ethiopian Regions. This group is characterized by the absence of teeth on tergum III, a long triangular forewing marginal cell, and an apically blunt or emarginate lateral propodeal projection. Fragmentary evidence points to Masaridae as hosts. I have been able to study types or authentically determined specimens of 23 of the 26 species. Status of the other 3 is in doubt. Complete synonymy and distribution will be given in a generic revision of Chrysididae now in preparation by L. S. Kimsey and R. M. Bohart. I would like to thank Dr. Kimsey for turning over to me her basic research on the genus, and for reviewing this paper.

Technical terms used in the key and descriptions are: F-I etc., flagellomeres; T-I etc., terga; S-I etc., sterna; MOD, midocellus diameter.

Type material has been studied at or borrowed from most of the important European and South African Museums. Acknowledgements will be made in the aforementioned revision.

Key to *Spintharina*

1. Hindtibia on outer surface with a whitish basal band (fig. 4), malar space slightly more or less than 1.0 MOD, T-III basolaterally with a moderate convexity at most, male F-I-II brilliant white in front (fig. 3) (males unknown in *poecilopus, cyanophris, and apiculata*), (*cyanophris* group); S. Africa. . 2

   Hindtibia on outer surface dark basad, malar space and T-III basolaterally various, male F-I-II usually dark 7

**Manuscript received by the editor February 16, 1987.*

2. Body dorsum mostly green, a little purplish on propodeum and T-III postpit .... *arnoldi* (Brauns)
   Body not mostly green dorsally 3
3. Mesopleuron green overlaid with coppery .... *poecilopus* (Mocsáry)
   Mesopleuron not coppery..............................4
4. Lower mesopleuron extensively polished, T-III apex broad and a little indented medially (male only known).. *albata* (Edney)
   Lower mesopleuron mostly sculptured-punctate, T-III apex somewhat pointed medially 5
5. Hindtibia white on basal 1/3 of outer surface (fig. 4)... *bispinosa* (Mocsáry)
   Hindtibia white on basal 1/4 of outer surface 6
6. Scutellum, metanotum, and pleuron reddish to coppery .... *apiculata* (Mocsáry)
   Scutellum, metanotum and pleuron purple with a little green .... *cyanophris* (Mocsáry)
7. T-III with a conspicuous translucent distal strip nearly all around (figs. 8, 10), male F-I-II together about as long as III (fig. 10) (*vagans* group)..............................8
   T-III without a translucent strip, or such strip broken medially, or extreme edge only translucent; male F-I-II not unusually short 12
8. T-III basolaterally with an angled swelling or large lobe (fig. 8) 9
   T-III basolaterally with at most a low, broadly rounded swelling 10
9. Scutal midsection with a strong longitudinal furrow, malar space shorter than F-IV, TFC angulate, basolateral lobe of T-III quite prominent; Ethiopia, Mideast .... *invreai* Zimmermann
   Scutal midsection not furrowed, malar space as long as F-IV, TFC crescentic, basolateral lobe of T-III a low angular lobe; s. Palearctic Region............. *vagans* (Radoszkowsky)
10. Scutum with a pretegular hook (fig. 7), translucent rim of T-III pale brownish, Israel .... *houskai* (Balthasar)
    Scutum without a pretegular hook, translucent rim of T-III practically white.................................11

11. Body nearly all bluish purple (fig. 10), United Arab Emirates .... *dubai* Bohart
Body bright green, terga extensively coppery (fig. 9), Senegal .... *senegalae* Bohart
12. T-III basolaterally with a somewhat angled swelling (fig. 5), T-III apex rather smooth but concolorous reddish or coppery with rest of terga (*versicolor* group) 13
T-III basolaterally nearly straight or somewhat convex but not angled, apex various 15
13. Malar space shorter than subantennal space; male F-I slightly longer than pedicel, a little longer than II but shorter than III; T-III basolaterally with a promiment, partly rounded lobe (fig. 5); United Arab Emirates .... *sugdeni* Bohart
Malar space longer than subantennal space; male F-I 1.5× as long as pedicel, longer than II or III; T-III basolaterally with a flattened, obtusely angled lobe 14
14. Pits of T-III in a narrow groove, and rounded (S. Palearctic Region) .... *versicolor* (Spinola)
Pits of T-III more impressed, elongate .... *agadirensis* Buysson
15. Malar space 1.7–2.3 MOD, at least as long as subantennal space (*innesi* group) 16
Malar space 0.9–1.2 MOD (fig. 1) (*pleuralis* group) 20
16. Lower mesopleuron rounded under, not denticulate 17
Lower mesopleuron somewhat expanded, weakly to strongly denticulate 18
17. Medial vein curved sharply as it approaches cu-a, terga bright coppery, TFC distinct; Mideast ... *appendiculata* (Buysson)
Medial vein gently curved as it approaches cu-a, terga green with coppery tint, TFC obsolescent; s. USSR .... *tenellula* (Semenov)
18. Male face with fine crossridging in middle third, not densely silver setose; male F-I apex, F-II-III contrastingly light tan, flagellomeres somewhat nodose within (fig. 2); female unknown; S. Africa .... *edneyi* Bohart
Male or female face not obviously crossridged, densely silver setose in male; flagellum in male not bicolored, flagellomeres nodose or simple 19
19. Punctures below midocellus elongate, somewhat striatiform;

flagellomeres of male not nodose; T-III indented apicomedially; Egypt .... *cornigera* Zimmermann

Punctures below midocellus not elongate, flagellomeres of male nodose within, T-III not indented apicomedially; Spain, Morocco, Sinai .... *innesi* (Buysson)

20\. Terga mostly coppery red, face with at least some bright coppery 21

Terga green to purple, face various 22

21\. T-III pit row indistinct, not indented, postpit area all coppery and punctured as in rest of terga (fig. 6), face and pleuron all bright coppery; S. Africa .... *postpunctata* Bohart

T-III pit row distinct and well indented, postpit area partly micropunctate and shiny, face partly green, pleuron green; S. Africa .... *pleuralis* (Mocsáry)

22\. Head, notum, and pleuron coppery to red; S. Africa .... *polychroma* (Mocsáry)

Head, notum, and pleuron mostly green (fig. 1); S. Africa..... .... *kimseyae* Bohart

Notes on species not included in the key

S. bleuthgeni (Linsenmaier) 1959: 102. Holotype male; Jordan: Jerico (LUZERN). Similar to *versicolor* according to Linsenmaier. Flagellum nodose.

a *S. integerrima* (Klug) 1845: pl. 45, fig. 14. "Arabia" (BERLIN?). Similar to *versicolor* according to Mocsáry 1889.

S. obscuriventris (Linsenmaier) 1968: 57. Holotype female; Greece (LUZERN). Similar to *versicolor* according to Linsenmaier.

Spintharina dubai Bohart, new species

Holotype male. Length 5.5 mm. Stout; bright purple with faint green tinges, tarsi and postpit rim of T-III whitish, wings nearly clear; scapal basin densely silver setose except narrow median line; punctation moderately coarse and close, weak on clypeus, practically absent on T-III postpit; F-I as broad as long, F-I and II together a little longer than III (fig. 10); malar space 1.5 MOD, subantennal space 1.0 MOD; TFC sharp, slightly irregular but nearly straight; midocellar area weakly defined, a little depressed; mesopleuron sharply tridentate below polished scrobal sulcus; propodeal projection stout, emarginate truncate (as in fig. 1), T-II and III with a weak median longitudinal carina; T-III convex basolaterally, pit row distinctly impressed, pits somewhat elongate (fig. 10), apical rim convex; S-II spots round, broadly separated.

Female. As in male but F-I 1.6× as long as broad, 1.2× as long as II or III.

Male holotype and 9 male, 5 female paratypes, Dubai, United Arab Emirates, IV-18-84 (some paratypes are months I, II, V, and VII), E. A. Sugden (U. C. Davis).

Discussion. The continuous whitish distal margin of T-III and the short male F-I-II place *dubai* in the *vagans* group.

Spintharina senegalae Bohart, new species

Holotype female. Length 5.5 mm. Bright green, terga extensively coppery to red, apical rim of T-III whitish translucent, tarsi light brown, legs otherwise green, wings nearly clear; scapal basin silvery pubescent in lateral third, medially punctate and crossridged (fig. 9); punctation otherwise moderate and close but weak on clypeus and absent on T-III postpit; F-I 1.5× as long as broad, slightly longer than pedicel, F-II or F-III; malar space 1.7 MOD, subantennal space 1.3 MOD; TFC sharp; weakly parenthesis-like; midocellar area slightly depressed; mesopleuron with 3 angles or teeth below polished scrobal sulcus; propodeal projection truncate and apex a little emarginate; T-III convex basolaterally, pit row distinctly impressed, pits slightly elongate, apical rim convex; S-II spots rounded, separated by nearly 2 MOD.

Female holotype. Savoigne, Senegal, III-9-76, G. Couturier (U. C. Davis).

Discussion. The continuous whitish translucent margin of T-III places *senegalae* in the *vagans* group. The green and coppery-red terga separate it from *dubai.*

Spintharina sugdeni Bohart, new species

Holotype male. Length 6 mm. Stout; head, thorax and sterna bright green, terga coppery with a greenish tint, tarsi pale brownish, legs otherwise green, wings nearly clear; scapal basin all silver pilose except a narrow median line of punctation and crossridging; punctation moderate and rather close but small on clypeus and absent on T-III postpit, forefemur well punctate above a ventral ridge; F-I

1.4× as long as broad, a little longer than pedicel or F-II, slightly shorter than F-III (fig. 5); malar space 1.5 MOD, subantennal space 1.7 MOD; TFC sharp and broadly M-shaped; midocellar area depressed and weakly delimited; mesopleuron tridentate below areolate scrobal sulcus; propodeal projection stout, truncate; T-III with an angular basolateral projection (fig. 5), pit row weakly impressed, pits long oval; apical rim convex; S-II spots nearly confluent.

Female. As in male. F-I about 1.5× as long as broad, slightly longer than pedicel, F-II or III; F-II very slightly shorter than F-III.

Male holotype. Zabeel, Dubai, United Arab Emirates, I-27-79, E. A. Sugden (U. C. Davis). Paratypes, 18 males, 4 females, Zabeel, Dubai, United Arab Emirates, I-IV, 1984-5, E. A. Sugden; 1 female, Amir, United Arab Emirates, V-2-84, E. A. Sugden.

Discussion. The prominent basolateral swelling and concolorous T-III place *sugdeni* in the *versicolor* group, where it is distinct in having the subantennal space longer than the malar space. The species is named for Evan Sugden, who collected a large number of Chrysididae in Dubai.

Spintharina edneyi Bohart, new name

Chrysis (Gonochrysis) rubescens Edney 1952: 446. Holotype male, "Springbok, Namaqualand," South African (South African Museum, Capetown). Nec Radoskowski 1880.

I have seen the type which is a *Spintharina* in the *innesi* group. In addition to the relatively long malar space the flagellum is somewhat nodose and bicolored (fig. 2). The scapal basin is plainly microridged in the middle third. T-III is broad with a slight apicomedial indentation. The new name is given in honor of E. B. Edney, who published extensively on South African Chrysididae.

Spintharina postpunctata Bohart, new species

Holotype female. Length 5.5 mm. Bright reddish coppery with tinges of green on scutellum and metanotum, sterna green and coppery, wings lightly stained; scapal basin lightly silver setose on outer fourth, middle half epunctate and microridged; other punctation moderate, slightly separated, continued evenly to apex of T-III; F-I 2.5× as long as broad, nearly twice as long as pedicel, F-II or

III; malar space 1.0 MOD; subantennal space 1.4 MOD; TFC irregular, midocellar area depressed, limited below; mesopleuron tridentate below areolate scrobal sulcus; propodeal projection with a slanting apical truncation (fig. 6); T-II and III weakly ridged at middle; T-III with a low basolateral convexity, pit row hardly indented, pits nearly obsolete, postpit area well punctured (fig. 6), apical rim convex; S-II spots weakly defined, well separated.

Female holotype. Jackkalwater, "Bushmanland," Namaqualand, South Africa, Lightfoot Coll. (Transvaal Museum, Pretoria).

Discussion. The short malar space, unbanded tibiae, and discrete microridging of the scapal basin place *postpunctata* in the *pleuralis* group. As in *polychroma,* the face is all coppery, but the nearly obsolete pit row, well punctate postpit area (fig. 6), and all coppery terga are distinguishing.

Spintharina kimseyae Bohart, new species

Holotype female. Length 6 mm. Head and thorax green, terga purple, sterna brown and purple, legs purple to green, wings faintly stained; pubescence pale, inconspicuous; punctation moderately coarse, less so on head, outer fourth of scapal basin finely punctate, middle half microridged (fig. 1); F-I 2.9× as long as broad, nearly twice as long as pedicel, F-I or II; malar space 1.1 MOD; subantennal space 1.7 MOD; TFC broadly M-shaped, not strong; midocellar area weakly depressed, hardly limited; mesopleuron tridentate below coarsely punctate scrobal sulcus; propodeal projection emarginate truncate (fig. 1). T-III straight basolaterally, pit row well indented, pits large and nearly round, apical rim slightly angled but rounded at tip (fig. 1); S-II spots slightly separated, not clearly defined.

Female holotype. Worcester, Karoo Gardens, Cape Province, South Africa, IX-29-75, R. M. Bohart (U. C. Davis).

Discussion. The short malar space, unbanded tibiae, and microridged middle half of the scapal basin place *kimseyae* in the *pleuralis* group. The T-III roundly pointed shape is much like that of *pleuralis* and *polychroma,* both of which have the thorax bicolored copper and green instead of green and a little purple as in *kimseyae.* The species is named for Lynn Kimsey, who has contributed a great deal to our knowledge of Chrysididae.

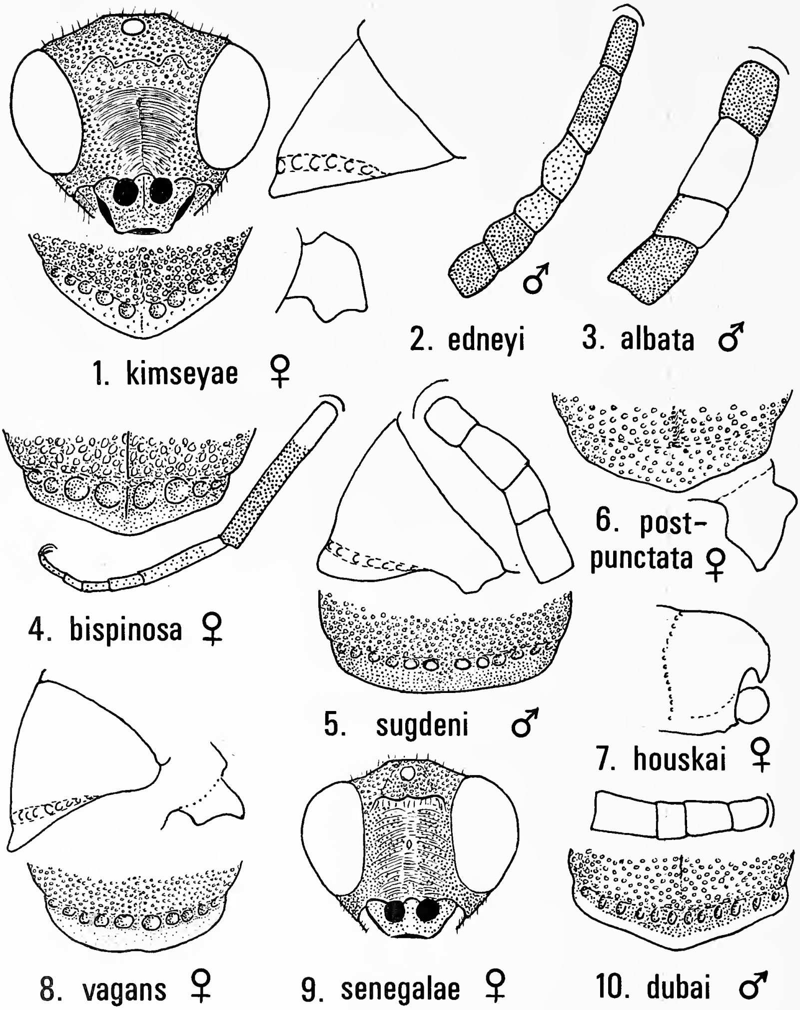

Fig. 1, face, T-III lateral and dorsal, right propodeal projection. Figs. 2, 3, pedicel and basal flagellomeres. Fig. 4, T-III; hindtibia and hindtarsus. Figs. 5, 8, T-III lateral and dorsal; pedicel and basal flagellomeres. Fig. 6, T-III and right propodeal projection. Fig. 7, scutum (right side) and tegula. Fig. 9, face. Fig. 10, pedicel and basal flagellomeres; T-III apex.

SUMMARY

A key is given to 23 species of *Spintharina.* New species described are *dubai* and *sugdeni* from United Arab Emirates; *senegalae* from Senegal; and *postpunctata* and *kimseyae* from South Africa. A replacement name is *edneyi* for the homonymous *rubescens.*

PREY SELECTION IN AN ORB-WEAVING SPIDER: *MICRATHENA GRACILIS* (ARANEAE: ARANEIDAE)*

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Introduction

A number of studies have examined the prey captured by web building spiders, and many have compared the captured prey with the insects available in the environment (Bilsing 1920; Turnbull 1960, 1962; Cherrett 1964; Kajak 1965; Olive 1980; Nentwig 1980, 1983; Brown 1981; Shelly 1983, 1984; Robinson & Robinson 1970, 1973; Riechert & Tracy 1975; Uetz et al. 1978; Chacon & Eberhard 1980; Uetz & Biere 1980; Riechert & Cady 1984). The most common comparisons are between prey found in webs and the "potential prey" captured by traps that in some way mimic spider webs (sticky traps, windowpane traps, etc.). Although there is disagreement about what kind of trapping method most accurately assesses the prey actually available to spiders (see Uetz & Biere 1980; Chacon & Eberhard 1980; Shelly 1984), all these studies suggest, to a greater or lesser extent, that the range of prey taken by spiders demonstrates some degree of selectivity. Recent research has shown that specialization is the result of web placement, web structure, and behavioral choices in the attack process (Chacon & Eberhard 1977; Uetz & Biere 1980; Riechert & Luczak 1982; Nentwig 1983; Shelly 1983, 1984; Riechert & Cady 1984; Craig 1986; Stowe 1986).

An important question that many of these studies have addressed concerns the role of the spiders' web in the selection of prey, and why some prey insects are trapped more or less efficiently than others. Most workers agree that the process by which insects fall prey to spiders in their webs is neither random nor passive because insects vary in their ability to avoid webs, or escape from them once caught (see Nentwig 1982; Craig 1986); and web design and function favor capture of specific prey types and sizes (see Riechert & Luczak 1982; Rypstra 1982; Stowe 1986). The capture of insects by spiders on the

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**Manuscript received by the editor October 26, 1986.*

web is also a non-random process; i.e., spiders have the ability to choose whether or not to attack, ignore or reject prey caught in their webs. Behavioral choices made by spiders at this level of contact are made on the basis of prey size, activity, and palatability (Riechert & Luczak 1982; Shelly 1983, 1984). Here, we examine the prey capture process in a common orb-weaving spider, and demonstrate selectivity at several levels.

STUDY SPECIES

Micrathena gracilis is a common orb weaver (Araneidae) occurring in the Eastern deciduous forest region of North America (Levi 1985). *Micrathena* occurs solely in large open spaces in the forest understory, where it is exposed to a diversity of flying insect prey. *M. gracilis* builds a small (20 cm diameter) orb within a relatively large frame (often 1.5–2 meters across). This suggests that these spiders have a large energetic expense in their webs, but should have a low encounter probability for all but the most abundant of prey. In addition, *Micrathena* is slow moving and almost clumsy, and usually takes > 3 sec. to reach a prey item in its web. Since most insects can escape entanglement in that time (Nentwig 1982), prey capture efficiency should also be low. This species is thus uniquely suited to provide a conservative test of the null hypothesis of no prey selectivity, because its characteristics suggest that opportunistic predation and extreme generalization of diet are an appropriate strategy.

In an earlier study (Uetz & Biere 1980), the prey caught in several types of web-mimicking traps (windowpane, sticky screen, artificial sticky web) and in a sweep net were compared with prey captured by spiders. It was clear from these data that *M. gracilis* were not taking prey in the proportions encountered. The spiders appear to capture larger flies and hymenopterans at far greater frequencies than they are potentially available. Artificial sticky webs, similar in size and with thread density identical to *M. gracilis,* were hung in the forest next to live spiders. For several days, the insects that flew into and escaped from the natural and artificial webs were noted from an observation post nearby. Both webs retained a different size array of insects than they encountered, and from this array, spiders selected only the largest insects (Uetz & Biere 1980). These preliminary studies suggested that *M. gracilis,* contrary to predictions based on its habits, might be a prey size specialist, and so this study was conducted.

METHODS

The study sites were located in Mount Airy Forest and Felter's Tanglewood, two deciduous ravine forest city parks in Cincinnati, Ohio. Both woods were characterized by a high, patchy canopy and a variable understory of shrubs, saplings and wide open spaces between vegetation. The dominant tree species were *Acer saccharum, Quercus alba,* and *Fagus grandifolia.* The two study sites were very similar in their physiognomy and were located within 3 km of one another. Two sites were chosen in order to minimize any vegetational disturbances that might occur during the course of the study due to the placement of artificial sticky web traps in the understory vegetation.

Because of potential bias in sampling insects found in spiders' webs, prey preference in orb weavers is best studied by examining the fate of insects that encounter the web. Observation of *Micrathena* in the field allows a comparison of the prey captured by the spider with potential prey items made available to the spider by its web within the forest understory. Because the spider was present, these observations allow a test of the null hypothesis of no selectivity: that *Micrathena* actively attacks all types and size classes of insects sticking to its web in proportion to the rate at which they are encountered.

Adult female *Micrathena* were observed for a total of 77 web hours (No. of webs × hours observed) between 1 August and 10 September 1981. After locating the web(s), the observer sat on a stool 1 to 1.5 m from the web(s). This distance allowed close observations of even the smallest insects striking the web, but was far enough away not to disturb the spider. Observations took place during the normal diurnal activity period for this species, between 0800 hrs and 1800 hrs, and lasted from 1 to 2 hours at a time. Up to three webs could be observed at once if they were clumped within 1 to 2 m of one another.

When an insect struck the web, its length (estimated by holding a mm scale close to the web) and taxon were recorded. The insect's "fate" in the web was then followed. (It should be noted that the "fate" of insects already present in the web at the beginning of the observation period was not recorded. This was done in order to prevent over-estimating the number of small insects that actually came in contact with webs (i.e. larger insects may have contacted the web and escaped—while the smaller ones were trapped and remained in the web—and the observer has no way of knowing the former unless he or she was present). An insect that struck any part of the orb was

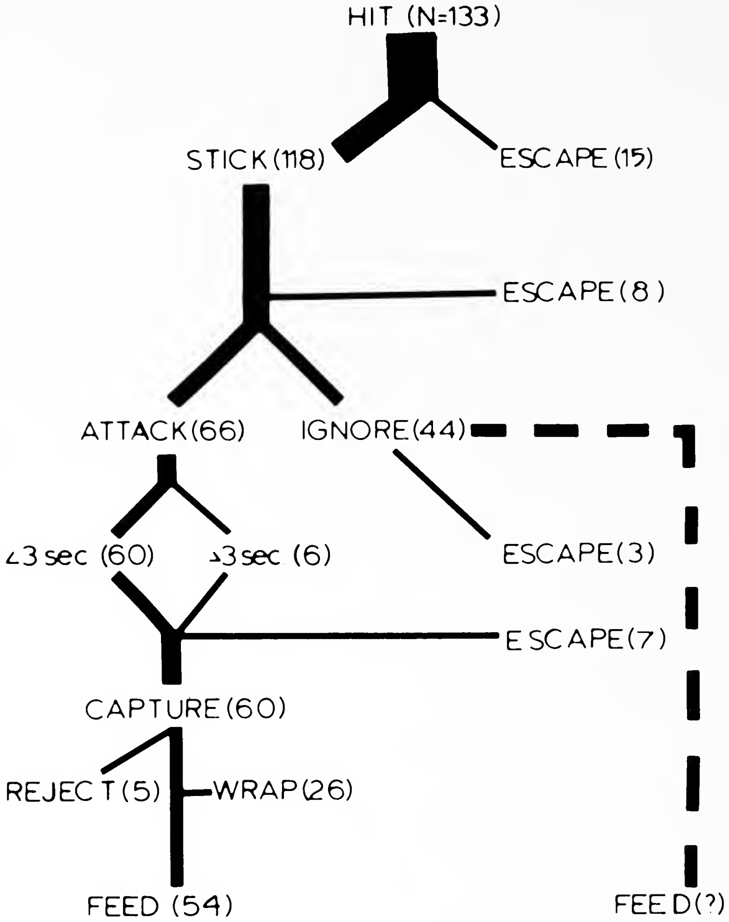

Figure 1. The predation sequence of *Micrathena gracilis.*

recorded as a HIT. An insect that was retained by the web longer than 3 seconds was called a STICK (after Rypstra 1982). Any insect that left the web at any time under its own power was termed an ESCAPE. An escape could occur at a number of different points along the predation sequence (see Fig. 1). An ATTACK occurred if the spider came in contact with the insect, usually with its two front legs. An IGNORE was recorded when the spider made no contact with the insect even

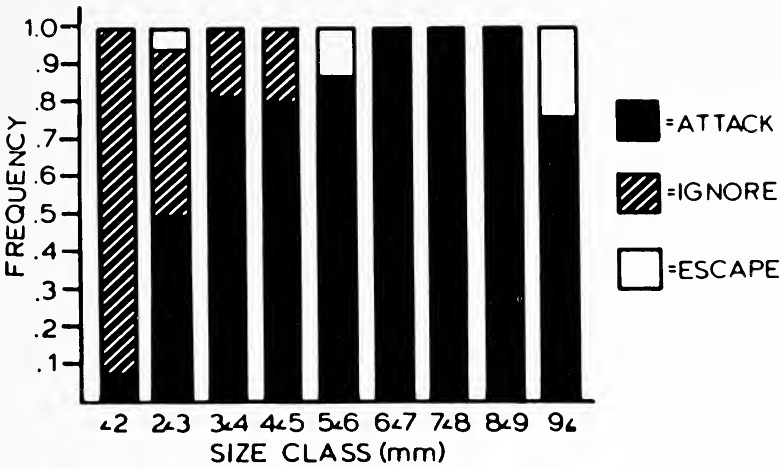

Figure 2. Size frequency distribution of insects attacked or ignored by spiders, showing the increased frequency of attacks on larger sized insects. Escapes shown occur after the 3 second "stick" criteria.

though it may have oriented toward and plucked at the insect in the web. A CAPTURE was recorded when the spider actually had control of the insect in its chelicerae. If the spider voluntarily discarded the insect, a REJECT was recorded. If the spider wrapped the prey item in silk after capture, a WRAP was recorded. Finally, if it fed on the insect during the observation period, a FEED was entered.

A comparison was also made of the insects captured by the web and those captured by a web-mimicking artificial sticky web trap (ASW) modified from a design reported by Uetz & Biere (1980). ASW trap frames were constructed out of 3/8 inch by 3/4 inch aluminum window screen frames (Custom Aluminum Products, Cincinnati, Ohio), with an area slightly larger than *M. gracilis* webs (38 cm × 38 cm). Clear, monofilament nylon thread woven onto a wooden loom surrounding the frame was held in the grooves of the window screen frame with spline in order to permanently secure the thread to the frame. This clear thread was 0.2 mm in diameter and could be woven into any desired mesh size. The mesh sizes used closely approximated those of *M. gracilis* (1 to 2 mm between threads). Parallel threads representing radii were spaced 6 mm apart and perpendicular to these other threads (woven parallel 1–2 mm apart). The threads of each ASW were covered with equal amounts of adhesive (Stick'em Special TM Sea Bright Enterprises) the night before they were placed in the field. The traps were transported to and from the field in reinforced cardboard boxes with dividers to keep webs from touching one another.

In the field, frames were suspended on sturdy string with centers at 1.50 m high in microhabitats similar to these exploited by *M. gracilis.* Traps were placed in the field seven times, on nonrainy days between 23 July 1980 and 14 September 1980 (four times in Mt. Airy Forest and three times in Felter's Tanglewood). They were in place by 0730 hrs (while spiders were actually building their webs) and removed by 1900 hours (when spiders began taking down their webs). Care was taken in moving throughout the study sites so as not to destroy the vegetation of the microhabitats; two study sites were chosen in order to keep this problem to a minimum. Temperature and humidity were recorded on a Hydrothermograph placed in the center of the study site. Wind speed and direction were recorded only for the first two dates because wind was found to be negligible within the understory (also see Biere & Uetz 1980).

Traps were taken to the laboratory, where the insects were removed (by individually placing a trap in a large porcelain pan containing pure kerosene). This dissolved the adhesive and facilitated the removal of even the smallest insects. After the insects were removed and placed in labeled vials, the screen was cleaned by blowing the kerosene off with an air hose, rinsing it under hot water, air-hosing the water off, wiping the frame dry, and then placing the screen on absorbent paper for at least four days. No odor of kerosene could be detected at this point and further applications of adhesive stayed on with no apparent problems, so we felt confident in the re-use of traps. Insects were identified to order and their length was recorded with a micrometer to the nearest 0.5 mm.

The visibility of ASW's is a potential problem with their use, but we minimized this effect by using clear, nylon thread and a large frame size. Besides functioning in the same way as real webs, ASW traps have advantages over other sampling techniques that add to their usefulness in the field. Primarily, they allow an air-flow that is not present in window-pane traps, which probably affects the accuracy of the latter (Robinson and Robinson 1970).

The design of our ASW's differs from that of previous studies in construction, area, mesh structure, and thread thickness. In comparison to Chacon and Eberhard (1980), ours more closely resembled the structure of actual spider webs, due to the presence of "radii", and thread thickness of 0.22 mm, (theirs was nearly 1.0 mm thick). This reduced the visibility of traps, an especially important consideration when studying diurnal orbweavers. Even though the "radii" of our traps were sticky, we believe that their presence is important since insects are often only capable of detecting and avoiding webs, after it appears that they are going to strike it (Turnbull 1960; Buskirk 1975; pers. obs.). If an insect is able to detect individual threads and alter its course to avoid a collision (or fly mistakenly into another sticky thread), it will probably do so because the thread is there and not because it may or may not be sticky. The elimination of "radii" from ASW traps could alter the flight behavior of small insects that are capable of flying through wider meshes in a way that is different than if they were present. Because the function of these devices is to intercept flying insects in nearly the same manner as spider webs, Chacon and Eberhard (1980) may be too harsh in their criticism of ASW's as mimics of spider webs. Even in illuminated areas, insects were only occasionally seen to avoid both spider webs and ASW's, and the capture rate for ASW traps was as high as or higher than that of the webs under observation. We would expect capture rates of ASW's to be lower than those of spider webs if the visibility of the traps affected their intended function. Consequently, while not being exact mimics of spider webs, ASW traps are reasonably effective sampling devices for flying insects in a forest understory. While some authors have discouraged their use (see Chacon and Eberhard 1980) and ASW's may not be suited for use in all environments, we feel that they can effectively sample the potential prey of many orb-weaving spiders better than conventional sampling methods (see Uetz and Biere 1981 for field comparisons).

A comparison of web catches with ASW's will reveal if the web of the spider contributes to dietary selectivity. Data from observations, and from web traps placed nearby while observations were being made, were analyzed using an index of dietary specialization—the

Table 1. Web selectivity (E_w) values for prey types and sizes caught in webs of *Micrathena gracilis*

	Caught in spider web		Caught in sticky trap		
	No.	R_i	No.	P_i	E_w
Taxon					
Diptera	89	.669	268	.355	+.307
Hymenoptera	20	.150	338	.448	−.498
Coleoptera	5	.038	48	.064	−.255
Homoptera	4	.030	43	.057	−.310
Thysanoptera	–	.000	21	.028	−1.00
Psocoptera	–	.000	11	.015	−1.00
Hemiptera	–	.000	8	.011	−1.00
Lepidoptera	–	.000	1	.001	−1.00
Other (Unident.)	–	.000	17	.023	−1.00
Size mm					
0–2	56	.475	600	.795	−.252
2–4	32	.271	138	.183	+.194
4–6	16	.136	13	.017	+.778
6–8	4	.034	2	.003	+.838
8+	10	.085	2	.003	+.932

"Electivity" index of Ivlev (1961): $E = r_i - p_i / r_i + p_i$ where $r_i =$ proportion of item *i* taken, and $p_i =$ proportion of item *i* available. Values for this index range from +1.0 (highly preferred) to −1.0 (least preferred). For this comparison, the catches of the artificial webs were assumed to estimate the proportions of prey available in each size class or taxon considered.

RESULTS

Of the 133 insects observed to strike webs, 118 stuck to the web for at least 3 sec. (for an initial web capture efficiency of 88.7%). Of these 118 insects, 66 were actively attacked by the spider, 44 were ignored, and 8 escaped before a "decision" was made. Of these 66 insects actively attacked, 54 were captured, 5 were rejected, and 7 escaped due to mishandling. A total of 38 insects escaped at some point in the predatory sequence (Fig. 1), leading to an overall web capture efficiency of 71.4% (HIT-ESCAPE/HIT × 100).

Comparison of traps and webs indicate that the webs of *Micrathena gracilis* are selective, and show electivity for Diptera sized >2 mm (Table 1). However, the majority of insects hitting and then sticking to the web was quite small (<3 mm): 53% (70 of 133 hits) and 58% (67 of 116 sticks) respectively. Therefore, well over half of the insects which encountered the web (and were thus available as potential prey items) were small insects containing very little biomass/insect.

Larger insects contain far more biomass per individual, but they are much rarer. Since the electivity index measures the degree to which prey are preferred in comparison to their availability, the results of the comparison between the web and the trap suggest that the web selectively retains larger prey. This conclusion is supported by the observation that escapes occurred in nearly the same proportion for all size classes except for the smallest and the very largest (Fig. 2). Escapes by very small insects (1–3 mm) can be attributed to almost instantaneous escape after contact with the web. It is possible that these insects were not flying very fast but were strong enough to pull free of the web before the chance of attack. On the other hand, 75% of the insects > 9 mm escaped before being attacked, with 50% of these insects escaping within 3 seconds of hitting the web. This is probably due to their faster flight velocities and strength (see Nentwig 1980).

As a consequence of web selectivity, *Micrathena* is presented with a preselected array of potential prey items to "decide" whether to attack. Within this array, the spiders were observed to attack a greater proportion of larger insects than smaller ones (Fig. 2). A comparison of prey taken by the spiders with those taken by the web shows evidence of greater selectivity (Table 2). The Ivlev index values are highest for Diptera in the middle range of size classes (4–8 mm). The frequency of insects attacked or ignored vs. insects sticking in each size class shows that *Micrathena* is not attacking (or ignoring)

Table 2. Spider selectivity (E_s) values for prey types and sizes caught by *Micrathena gracilis*

	Captured by spider		Caught in web		
	No.	R_i	No.	P_i	E_s
Taxon					
Diptera	41	.759	89	.669	+.670
Hymenoptera	10	.185	20	.150	−.567
Coleoptera	2	.037	5	.038	−.013
Homoptera	1	.019	4	.030	−.224
Size (mm)					
0–2	20	.370	56	.475	−.124
2–4	16	.296	32	.271	+.044
4–6	13	.241	16	.136	+.279
6–8	2	.037	4	.034	+.042
8+	3	.056	10	.085	−.206

insects in each size class with the same frequency in which they are encountered. A Kolmogorov-Smirnov test of the difference in the frequency distributions across size classes of those insects sticking to the web and those being attacked by the spider indicates a significant difference ($p < .001$), supporting a rejection of the null hypothesis of no selectivity. This spider is ignoring the smaller, more abundant insects sticking to the web and is preferentially attacking the larger yet rare insects.

DISCUSSION

The constraints on spider "decision-making" in the prey capture process involve a balance between the cost of handling of the prey item and the return in biomass from the investment of energy in its capture. Turnbull (1973) suggests that the size range of prey attacked by spiders is set at the lower end of the range by a minimum amount of biomass needed to "justify" the energy expended, and at the upper end of the range by limits to handling probability of escape, and danger to the spider. The profitability of prey capture by spiders will thus determine how much a spider will specialize on particular prey types. If among the prey available there are species which are easier to capture and/or subdue, or in some way are more likely to provide a high reward for the energy expended, they should be preferred over others (which should be ignored or rejected unless the hunger level dictates otherwise) (Charnov 1976). Riechert (in Riechert & Luczak 1982) has shown that *Agelenopsis* rejects a total of 20.8%, and ignores 11.3%, of all potential prey, based primarily on the profitability factors mentioned above. She also found that the majority of these "decisions" were made early in the prey capture sequence, and suggests that selection should favor discrimination among prey before much energy is expended in the capture process.

Micrathena appears to concentrate its efforts on larger size classes where the available biomass is the greatest, not the small size classes where the abundance of prey is the greatest. This species forages in an optimal manner in the long term sense (Dawkins 1986), by electing to attack the size classes and taxa that provide the spider with the most energetic reward, despite low availability. Even though the spider would appear to forage in a sub-optimal manner, by ignoring a disproportionately higher number of small prey, it is not necessarily omitting a large amount of biomass (<15%) from its diet by doing so (Nentwig 1985). It is probable that the spider consumes these insects at night when it takes down its web (if the insects do not escape during the day). The spider may therefore reap this collective caloric benefit without actively attacking each small insect striking its web during the day.

By following the predatory sequence of *Micrathena gracilis* (Fig. 2), it is clear that throughout the sequence, the spider is presented with many more small insects than large insects. After the web has restrained an insect, the spider will either attack it or ignore it. It has been shown that the spider attacks insects > 3 mm with a significantly higher frequency than it does those < 3 mm, which are ignored most of the time. Similar results were seen in *Micrathena schreibersi,* a neotropical congener (Shelly 1984). The term "ignore" implies that the spider actually makes a choice of what it attacks, which is what is implied in this study, and has been used by other arachnologists (e.g. Olive 1980; Riechert and Luczak 1982; Shelly 1984). During the course of observations, spiders did appear to make a choice of whether or not to attack certain insects, most probably based on some sort of vibrational stimuli. For example, the spider was often seen orienting toward the impact area of a small insect with the web, plucking the radii in that area, and even advancing a few millimeters toward the insect, but not attacking it. The impact of the insect may have been enough of a vibrational stimulus to initiate the attack sequence, but the lack of vibration after impact indicated either a very small prey item or no prey item. Suter (1978) found that the impact stimulus was important in initiating the attack behavior of *Cyclosa turbinata,* another forest-dwelling orb-weaver. This particular species may be capable of detecting the mass of an insect by its impact vibration, which could be, according to Suter, a mechanism for discerning the insect's relative food value. This same mechanism could be operating in *Micrathena.*

Riechert and Luczak (1981) suggest that three parameters regarding profitability should be important in the spider's decision to consume (attack) or ignore the prey item: prey type, prey size, and level of hunger. Observations of other species indicate that orbweavers are able to discriminate between prey and alter their attack behavior accordingly (Eberhard 1967; Robinson 1969; Robinson, Mirick, and Turner 1969; Robinson and Olazarri 1971; Robinson and Mirick 1971; Robinson & Robinson 1973, 1976) allowing them to secure prey in such a way as to prevent quick escapes and/or minimize the risk of injury. Most of the potential prey of *Micrathena* is small Hymenoptera and Diptera (as seen in availability estimates in Table 1), and they pose little threat to the spiders. *Micrathena* exhibits the more primitive "bite-wrap" behavior pattern (Robinson et al. 1969), which suggests that it should be more efficient in attacking fast-escaping but relatively harmless prey. Prey size is probably a more important criterion in prey selectivity for such a species than is prey type. The hunger level of the spider may also play an important role in what the spider may choose to attack, but it is a difficult parameter to control in observational field studies such as this. Spiders are often subjected to severe food shortages (Olive 1982) and may switch from being a specialist to a generalist, i.e. accept a less preferred prey item due to the paucity of preferred prey types (Emlen 1966; Schoener 1969, 1971; Pulliam 1974; Lacher et al. 1982).

The degree of selectivity shown by *Micrathena gracilis* is surely not as precise as many prey specialists (see Stowe 1986). However, given that any specialization should be risky for a spider with its attributes, this prey selectivity must pay off in providing this species with an apparently adequate diet.

SUMMARY

The prey of a common deciduous forest orb-weaver, *Micrathena gracilis* (Walckenaer), was compared with potential prey sampled by artificial sticky web traps. Comparison of traps and webs indicated that webs of *Micrathena* are selective, showing selectivity for Diptera sized greater than 3 mm, even though the majority of prey hitting webs and in traps are much smaller. Spiders also showed selectivity in attacking larger dipteran prey, and ignoring the majority of tiny insects (< 3 mm) stuck in their webs. Prey specialization seen in *Micrathena* appears based primarily on insect size, and is likely related to the profitability (energetic reward) of larger Diptera as prey.

ACKNOWLEDGEMENTS

This research represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences at the University of Cincinnati.

We thank the Cincinnati Park Board for use of their parks. We are grateful to G. Stratton, C. Meininger, T. Bultman, W. Hopple, J. Fisher, D. Francis, N. Folino, P. Bianconi, and J. Stout for diverse assistance in field and lab. We also appreciate the help of T. C. Kane, A. Butz, and M. Hodge for reviewing earlier drafts of this manuscript. Thanks also to M. Killeen for typing.

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SYNONYMY OF *LEONOMYRMA* ARNOLDI 1968 WITH *CHALEPOXENUS* MENOZZI 1922 (HYMENOPTERA: FORMICIDAE)*

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Arnoldi (1968) erected the genus *Leonomyrma* for a single new species, *L. spinosa,* which he had collected in July, 1949, near Peremetriaja, East-Kasachstan (USSR), at the lower course of Ural River. Up until present, only the type series of 4 ♀♀ and 14 ♂♂ have been known; no ☿☿ were found. In the course of a study in morphology and behavior of several species of the ant genus *Chalepoxenus,* I came across the description of *Leonomyrma.* A direct comparison of its holotype (♀) and an allotype (♂) with material of two *Chalepoxenus* species, *C. muellerianus* (Finzi) (= *C. gribodoi* Menozzi) and *C. kutteri* Cagniant, clearly revealed the synonymy of the two genera.

Genus *Chalepoxenus*

Chalepoxenus Menozzi, 1922: 257, worker, female. Type species by original designation: *C. gribodoi.*

Leptothorax (Temnothorax) muellerianus Finzi, 1921: 118, synonymized with *Chalepoxenus* by Müller 1923: 98.

C. gribodoi Menozzi, 1922: 257, synonymized with *C. muellerianus* (Finzi) by Kutter (1973).

Leonomyrma Arnoldi, 1968: 1809, female, male. Type species: *L. spinosa,* monobasic. NEW SYNONYMY.

Since the original description of *Leonomyrma* was published in Russian, I provide an English translation of its main contents:

> "*Leonomyrma* K. Arnoldi gen. n. (Leptothoracini)"
>
> "Type of the genus: *Leonomyrma spinosa* K. Arnoldi sp. n. Female: Head elongate rectangular. Antennae 12-jointed,

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*Manuscript received by the editor August 14, 1986.

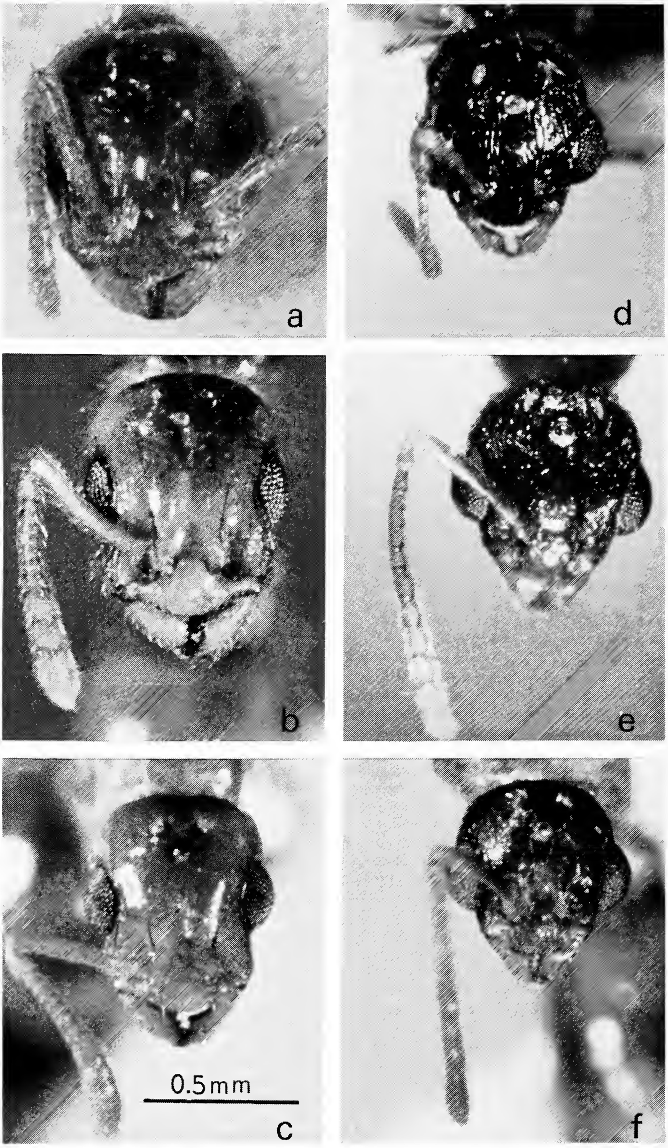
> mandibles triangular with dentate masticatory border. Frontal carinae long and straight, not forming scrobes for hiding the antennal scapes. Epinotum with two long spines. Petiolar nodes rounded above, low, petiole with a conspicuous ventral tooth, postpetiole with a long spine. The femora somewhat swollen. Erect hairs of the body long, fine, pubescence only present in legs and scapes. Wings with reduced venation, with a long, closed cubital cell.
>
> "Male: Antennae 13-jointed, the long, slender scape overreaching the occipital margin, club 4-segmented, not shorter than the remainder of the funiculus. Eyes very large, convex. Masticatory border of mandibles dentate. Thorax narrow, with Mayrian furrows and strong epinotal spines. Hairs and wings as in the female."

The description of the new species, *L. spinosa,* contains some measurements of the holotype ♀:

> "Head length 0.85 mm, width 0.70, scape length 0.60, length of eye 0.30, thorax length 1.15, width 0.60, height 0.70, length of petiole 0.30, width 0.29, height without ventral tooth 0.36, postpetiole length 0.30, width 0.47 mm.
>
> "Female: Head elongate, 1.5 times longer than wide, with nearly straight lateral margins, with distinct anterior and more rounded posterior corners. Eyes much larger than the genae. Clypeus moderately vaulted, slightly concave in the middle of the anterior margin, with an indistinct central carina. Frontal triangle impressed, smooth, indistinctly confined. Antennal club 3-segmented, only slightly shorter than the remainder of the funiculus. Last segment (like in the male) about the length of the two preceding ones together. Scape not fully reaching the occipital margin. Segment 3 to 7 of funiculus wide, not longer than wide. The long frontal carinae reaching behind the hind margin of the eyes. Thorax slender, elongate, somewhat flat above, anterior part of mesonotum narrowing, not covering the pronotal shoulders. Epinotal spines strong, longer than half their basal distance. Petiole short, massive, in profile with descending anterior and rounded upper surface, with a big tooth below. Postpetiole with a fingerlike spine. Dorsal side of

Table 1. Indices of *Leonomyrma spinosa* (from Arnoldi, 1968)

	head	length	length	thorax		petiole		postpetiole	width
Indices	length/width	head/scape	head/eye	1/w	1/h	1/w	1/h	w/1	postpetiole/petiole
4 ♀♀	1.21	1.46	2.90	1.93	1.66	1.13	0.93	1.45	1.68
6 ♂♂	1.25	1.28	2.37	2.03	1.41	1.36	1.12	1.62	1.27


a
d
b
e
0.5 mm
c
f

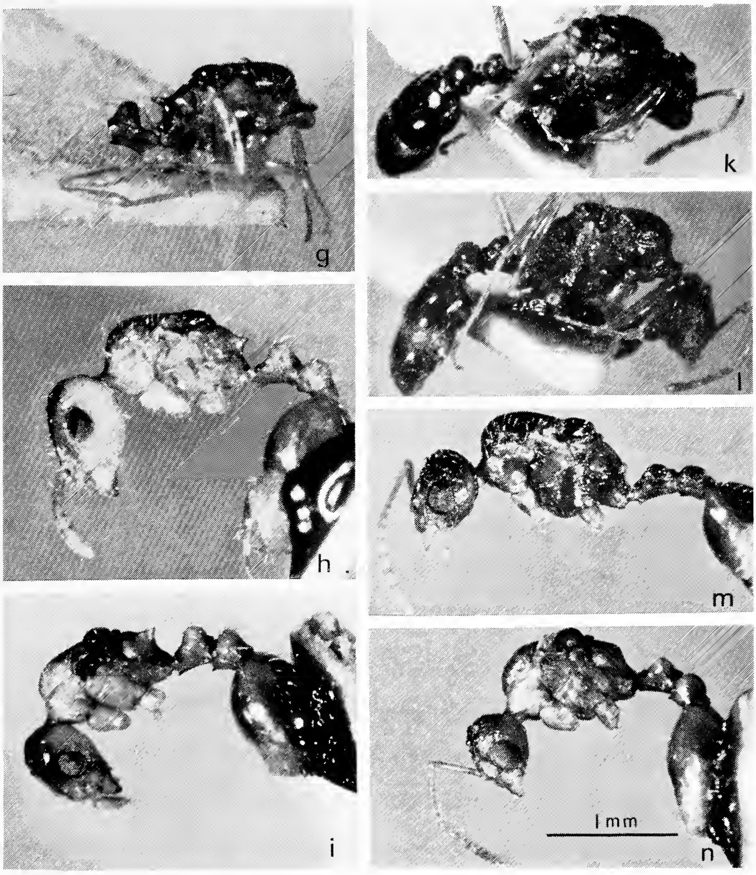


Fig. 1. (Facing page and above.) Heads and lateral views of *Chalepoxenus spinosus* (nov. comb.) (a, g—♀; d, k, l—♂; in k an epinotal spine, and in l the postpetiolar spine are clearly visible), *C. muellerianus* (b, h—♀; e, m—♂), and *C. kutteri* (c, i—♀; f, n—♂). Pictures were taken with a Wild Photomakroskop M 400.

> alitrunk with very long, not dense hairs, which are more developed in the petioles and the gaster. Tibiae and scapes with sparse (not in all specimens preserved) outstanding hairs and a fine pubescence which is mostly lacking in other body parts. Body shining, head and thorax with long, sparse, longitudinal wrinkles, one particularly long wrinkle along the inner margin of the eye. Petioles smooth, gaster very smooth and shining. Light brown, gaster and top of the head brown, 3.75–3.95 mm.
>
> "Male: Head elongate, 1.25 times longer than wide, with slightly vaulted sides and very large, very convex eyes. Antennal clubs with very long segments, all funicular segments much longer than wide. Clypeus elongate, reaching behind the genae, its anterior border blunted in the middle, vaulted, smooth like the triangular frontal area. Frontal carinae straight, parallel, visible until the anterior ocellus, all ocelli very large. Thorax narrow above, anterior part of mesonotum narrowing. Alitrunk shining, with sparse longitudinal wrinkles, petioles smooth, with ventral teeth as in the ♀, but smaller. Hypopygium and squamulae long, leaf-shaped. Brown, legs and antennae straw-yellow. 3.3–3.7 mm."

A comparison is made with other leptothoracine genera, and the author stresses that *Leonomyrma* exhibits some characters of social parasitic ants. Thus, the ventral projections of the petioles appear similar to those in *Formicoxenus,* the long frontal carinae resemble those of *Chalepoxenus,* the structure of the male antenna and the wing venation are said to match those of *Myrmoxenus,* to which *Leonomyrma* is closely related. It differs, however, from *Myrmoxenus* by the dentate mandibles of males and the queens, the strong epinotal spines, the rounded nodes, and the long and fine postpetiolar spine. From *Formicoxenus* it is distinguished by the number of antennal segments, shape of head, etc.; *from* Chalepoxenus *by lacking the long scrobes along the frontal carinae,* much stronger epinotal spines, and the long hairs; and from *Epimyrma* also by the long hairs, number of antennal segments, and so on.

Thus, the most important difference between *Leonomyrma* and *Chalepoxenus* refers to the antennal scrobes, since size and shape of epinotal spines and the density and length of hairs usually are characters varying widely within one genus. In the original description of

Chalepoxenus, however, Menozzi (1922) explicitly writes: "frontal carinae long, sub-parallel, and laterally confining an *antennal scrobe,* which is *little marked* and much shorter than the antennal scape" (translated from Italian). Direct comparison (Fig. 1) reveals that there is literally no difference between the antennal scrobes of *Leonomyrma* and *Chalepoxenus.*

In table 2 *L. spinosa* is compared with two *Chalepoxenus* species. I choose for reference *C. muellerianus* and *C. kutteri,* because they represent the two most different species in the genus. *C. siciliensis* and *C. insubricus* closely resemble *C. muellerianus, C. gribodoi* was already synonymized with the latter (Kutter 1973), and *C. tramieri* is close to *C. kutteri* (Cagniant 1983).

The comparison shows that there are some morphological differences between *L. spinosa* and *Chalepoxenus* species, but not more than between the latter two. *L. spinosa* is sharing some characters (postpetiolar spines in ♂ and ♀, long and acute epinotal spines in ♀, long body hairs) with *C. kutteri,* others (steeply ascending petiolar node, erect tibial hairs) with *C. muellerianus.* No crucial differences could be found which would justify the maintenance of a separate genus for *L. spinosa,* whereas its species rank in the genus *Chalepoxenus* appears sufficiently substantiated.

Since *C. muellerianus* is an active slavemaker (Ehrhardt 1980), and also *C. siciliensis, C. insubricus,* and *C. kutteri* (Buschinger et al., in prep.), we may predict that *L. spinosa,* too, will exhibit this particular life habit. The original material consists of alate sexuals, only, which were apparently caught during swarming. The lack of workers in the sample, therefore, is not surprising*.

Summary

The monotypical genus *Leonomyrma,* described by Arnoldi 1968 from 4 ♀♀ and 14 ♂♂ of *L. spinosa* from East-Kasachstan, USSR, is

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**Chalepoxenus brunneus* Cagniant 1985, described from males and females from one colony, is a workerless and thus not a slave-raiding species. We (A. Buschinger, J. Heinze, H. Cagniant, X. Espadaler) collected 11 colonies at its type locality, Tizi-n-Test, Great Atlas of Morocco, on May 6, 1987. None of them contained *Chalepoxenus* workers, and their brood also consisted of male and female pupae only. Thus, *C. spinosus* also might be truly workerless. [Added in proof, May, 1987].

Table 2. Comparison of *Leonomyrma spinosa* Arnoldi with *Chalepoxenus muellerianus* Menozzi and *C. kutteri* Cagniant.

Characters ♂	*L. spinosa*	*C. kutteri*	*C. muellerianus*
Frontal area	not clearly marked	not clearly marked	not clearly marked
Frontal carinae	parallel, slightly divergent	slightly divergent	slightly divergent
Mandibles	dentate, 4–5 teeth	dentate, 4–5 teeth	dentate, 5 teeth
Mayrian furrows*	indistinct	indistinct	indistinct
Mesonotum	anterior part narrowing	wider, nearly as wide as long	wider, nearly as wide as long
Epinotal spines	long, fine	lacking, or blunt projection	blunt projection
Wing venation	—	identical in all 3 sp.	—
Petiole	truncated but long, with strong ventral tooth	truncated, short, with short ventral tooth	truncated, short, with very small ventral projection
Postpetiole	wide, large, with ventral spine	smaller, with short, very acute ventral spine	smaller, without ventral projection
Body hairs	long, not sparse	mostly lacking, very sparse on head, thorax	shorter, not sparse
Tibial hairs	some erect	decumbent	erect
Sculpture	head wrinkled, thorax longitudinally wrinkled, epinotum wrinkled, postpetiole shining	head wrinkled, thorax, epinotum, petioles, gaster smooth, shining	entire body coarsely wrinkled, except gaster

*Notauli

Table 2, continued.

Characters ♀	*L. spinosa*	*C. kutteri*	*C. muellerianus*
Frontal area	not clearly marked	not clearly marked	clearly marked
Frontal carinae	divergent	slightly divergent	divergent
Epinotal spines	long, fine, acute	long, fine, acute	shorter, more triangular in lateral view
Petiole	rounded, node very steeply ascending, ventral tooth present	rounded, with ventral tooth, shortly truncated, node less steeply ascending	rounded, with ventral blunt tooth, node steeply ascending
Postpetiole	with long ventral spine	with ± long v. spine	without spine, or with short tooth
Body hairs	sparse, long	sparse, long	sparse, shorter
Tibial hairs	decumbent	decumbent	erect

synonymized with the genus *Chalepoxenus* Menozzi 1922. A morphological comparison of the *Leonomyrma* holotype ♀ and an allotype ♂ with material of *Chalepoxenus muellerianus* and *C. kutteri* revealed a close similarity in most relevant characters. It may be predicted that *Chalepoxenus spinosus* (nov. comb.) will be a slavemaking ant like the other species of the genus.

ACKNOWLEDGEMENTS

I am indebted to Dr. A. V. Antropov and the Zoological Museum, Moscow, for having provided the type material of Leonomyrma spinosa. The Deutsche Forschungsgeneinschaft has generously supported our studies in *Chalepoxenus*.

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NATURAL HISTORY OF A SUBSOCIAL TORTOISE BEETLE, *ACROMIS SPARSA* BOHEMAN (CHRYSOMELIDAE, CASSIDINAE) IN PANAMA

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Introduction

Insects are said to be "subsocial" if either or both parents directly involve themselves in the care of their own offspring after hatching (Michener 1969, Eickwort 1981). The literature suggests that parental care occurs in a few neotropical chrysomelid beetles. Surprisingly, there have been few reports on the natural history of these species. Below I describe aspects of the behavior, ecology, and morphology of *Acromis sparsa* Boheman, a "tortoise-beetle" common throughout the Republic of Panama.

The life histories of subsocial insects are known to differ greatly. In some species parents provision offspring with food, while in others parents buffer offspring against extremes of the physical environment or shield offspring from predators and parasites (Wilson 1971, pp 121–135; Eberhard 1975). Females are the providing sex in most subsocial insects.

Parental care has been reported in only nine of several hundred families of coleopterous insects (Hinton 1944). The trophic habits of these groups are diverse, embracing the eating of flesh (Tenebrionidae, Hydrophilidae), carrion (Silphidae), dung (Staphylinidae, Scarabeidae), decomposing wood (Passalidae), fungi (Scolytidae and Platypodidae) and green leaves (Chrysomelidae). Of the three chrysomelid species listed by Hinton (1944) as displaying subsocial habits, all are members of the subfamily, Cassidinae.

The Cassidinae ("tortoise beetles" or "gold bugs") is a large subfamily comprised of more than 3,000 species distributed world-wide and reaching greatest diversity in tropical latitudes (Arnett 1968, p. 941). Larvae of many species are slow-moving, leaf-feeders whose

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Manuscript received by the editor February 26, 1987.

concealment and defense is enhanced by the accumulation of fecal matter and exuviae on a caudal fork held over the body and used against predators (Shelford 1916, p 175; Eisner et al. 1967). The adults of many Cassidinae are conspicuous, diurnally-active insects especially abundant on young or rapidly growing vegetation.

References to subsocial habits in the Cassidinae are few and all come from the Neotropics. Ohaus (1899–1900) observed adult female *Omaspides (Omoplata) pallidipennis* Boheman clinging to the backs of larvae on the undersurfaces of *Passiflora* leaves in Peru (Abb. 205 in von Lengerken, 1954; also Fig. 118, p 62, O'Toole and Preston-Mafham 1985). Ohaus (1909) noted that another cassidine, *Pseudomesomphalia (Neomphalia) thallassina* Boheman, shielded tightly aggregated larvae with its elytra. Fiebrig (1910, Abb. 1a) observed female *Acromis spinifex (= Selenis spinifex* L.) guarding stalked egg masses in Paraguay (redrawings of this figure, Fig. 156/1 in Linsenmaier 1972, p 156 and Abb 206 in von Lengerken 1954, erroneously have a male guarding the egg mass). Fiebrig's observations did not indicate how long mothers guarded their offspring or from whom they were being guarded.

The genus *Acromis* Chevrolat (*Selenis* Hope) (Tribe: Stolaini, Hincks 1952) is comprised of four species whose ranges appear to meet or overlap in Amazonia. *A. sparsa* has been collected from Mexico south through Central America into Brazil and Bolivia (Blackwelder 1982, p 743). Extensive collecting by H. Stockwell and others in Panama has turned up only *A. sparsa. A. nebulosa* Boheman has been collected in Brazil, Peru and Bolivia; *A. spinifex* L. in Guadeloupe and other locales in South America (Paraguay) and *A. venosa* Erichson (illus. no. 186/16, Linsenmaier 1972, p 186) in Peru and Bolivia. I have found no reports on parental care in either *A. venosa* or *A. nebulosa;* however, the similarities in adult morphology throughout the genus suggest similar habits.

METHODS

Observations and specimens were collected at low to middle elevations (0–500 m) in central Panama where *A. sparsa* is abundant in disturbed areas and is rarely, if ever, observed under closed forest canopy or in forest light-gaps. *A. sparsa* is not seen, for example, on Barro Colorado Island, nor has it been recovered from the light traps run there by H. Wolda for 13 years. However, *A. sparsa* is an abundant insect in second growth on the mainland at Frijoles, 4–5 km away and is found in disturbed habitats across the Isthmus of Panama including areas of quite different mean annual rainfall (1.8 m on the Pacific side versus 3.2 m on the Caribbean side). This beetle has become common along the El Llano-Carti Road (approximately 45 km east of Panama City), an area converted from forest to second-growth within the past 15 years.

Quantitative observations of *A. sparsa* were made in mid-isthmus at three sites within 15 km of one another, primarily between August and November of 1978. The "mixed" site is a roadside transect through grass and young forest along the Pipeline Road, 3–6 kms NW of Gamboa (79° 42′ W, 9° 07′ N). The "field" site is an expanse of tall grass, occasional shrubs and vines at the beginning of the Pipeline Road, 2 km NW of Gamboa. The "forest" site is shaded 1 km transect along the Old Gamboa Road, 7 km SE of Gamboa.

FOOD-PLANT

The life history of *A. sparsa* is closely tied to a single host-plant, *Merremia umbellata* L. (Convolvulaceae). The range of *M. umbellata* includes S. Florida, W. Indies, Mexico, Central and South America and much of the Old World Tropics (Austin 1975). I have never observed *A. sparsa* feeding on other plant species although I have occasionally found larvae and pupae "stranded" on vegetation touching their food plant. *Merremia umbellata* is a common roadside vine which grows rapidly in the early wet season using support from grasses, dead shrubs, etc. to reach sunlight. Older plants have a substantial underground tuber which sends out a network of aboveground runners, each of which gives rise to numerous vertically climbing shoots. During the first four to six weeks of the wet season *M. umbellata* grows rapidly and may form a closed canopy over second-growth vegetation. Growth slows during the late wet and dry season and fewer leaves are supported. Flowering occurs in January of most years.

Merremia umbellata has many casual and host specific herbivores including at least six species of Cassidinae. This is the richest assemblage of Cassidinae on a single plant species that I have observed in Panama. Of these species, only *A. sparsa* is subsocial, three are solitary in all stages and two have eggs in clutches—one of these has gregarious larvae. *A. sparsa* is probably the most important herbivore on *M. umbellata* because of its abundance throughout the wet season and its exploitation of apical foliage.

SEASONALITY

Acromis sparsa populations were not systematically censused so I can only present a subjective account of activity through the year. Reproduction ceases during the dry season, January through April of most years. The few adults observed during this period were usually associated with host plants rooted in permanently moist habitats. The onset of the rains in early or mid May brings increased growth by the host plant and the reappearance of *A. sparsa* males and females on new growth. Females immediately begin to oviposit. A second round of mating and oviposition begins in late June and early July. Several more synchronized reproductive bouts follow at approximately two month intervals before dry season conditions set in. Although abundance appeared greatest in the mid wet season there were few times when adults could not be found in quantity just by inspecting the host plant. There were exceptions such as when females were guarding pupae or periods following the emergence and first feeding of tenerals. Adults and the larval groups they were attending also suddenly became rare during extended rainless periods within the wet seasons of some years.

THE EGG STAGE.

Location and composition of the egg mass

Eggs were deposited in masses (Fig. 1a) attached to the undersurfaces of leaves. Each egg is anchored to the midrib by a flexible, lacquer-like thread which fuses with other threads producing a short (3–5 mm) pedicel holding the egg mass out toward the leaf apex. Eggs are smooth and ovate (0.5 × 1.5 mm), and are stuck firmly to one another during oviposition in two to three orderly layers forming the final 10–15 mm of the egg mass. The stiffened egg mass provides a roosting platform for the guarding mother during egg development.

Although oviposition is often under the first or second unfolded leaf, egg masses are often encountered under the third, fourth or fifth leaf since several new leaves normally unfold during the 12 days it takes eggs to develop (Table 1). The distal portion of many leaves

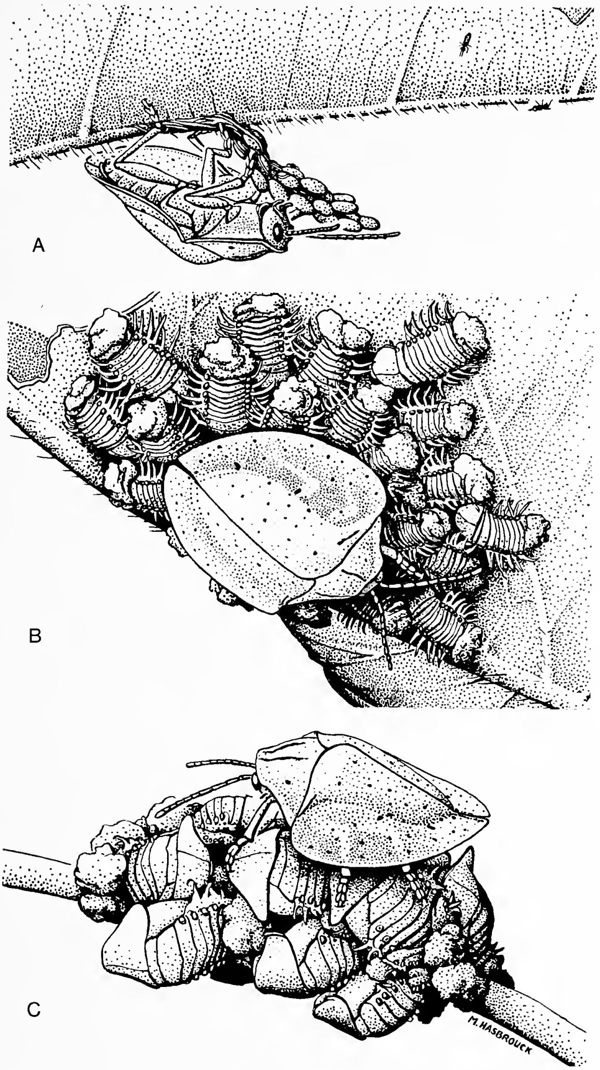

Fig. 1. Guarding postures of female *Acromis sparsa.* A, on an egg mass with parasites nearby; B, on medium-aged larvae aggregated on the undersurface of a *Merremia* leaf; and C, on a pupal mass located low on a *Merremia* stem.

with egg masses tended to droop slightly. Leaf hairs and the mid rib near the egg mass on these leaves were chewed by the female prior to oviposition. The significance of this behavior is unclear. A drooping leaf increases concealment of the female on her clutch. It also better shields them from insolation. Bruising of the leaf tissue may mechanically prepare the site for the first feeding of her larvae or prevent the induction of plant defensive chemicals to the area of first larval feeding.

The median number of eggs per egg mass is 40 ($n = 126$, range $=$ 13 to 49). The frequency distribution is skewed to the left (Fig. 2). The number of eggs per egg mass did not differ significantly between the three study sites (Kruskal Wallis one-way analysis of variance, $H = 1.99$, $df = 2$, $p = 0.37$). The number of eggs in an egg mass and the width of the guarding female's elytra were positively correlated (Spearman $r = 0.75$, $n = 46$, $p < 0.01$). Although the number of eggs per egg mass is correlated with female size, other factors such as mother's age or ovipositional history may also influence clutch size.

Table 1. The distribution of (A) large, solitary males, (B) solitary females, (C) copulating pairs, (D) females on eggs, (E) females with larvae, and (F) the number of leaves on *M. umbellata* vines recorded by leaf number from the first unfolded leaf at the apex. Median values are indicated by asterisks.

Leaf Number	A	B	C	D	E	F
1	9	1		4		
2	9	12	1	3		
3	17	6	4	11		
4	*15	3	* 2	*11	2	
5	9	* 2	1	10	2	2
6	6	4	3	4	2	4
7	1	4	1	5	4	1
8	3	6		3	1	3
9	2		1	2	* 5	3
10	1			3	2	1
11	3	1			1	7
12	2	1			1	* 2
13	1		1	1	1	2
14	2	2		1	1	2
15		1				4
16		1			1	2
>16	3	1	14		1	11
Totals	83	45	14	58	24	44

Females were able to rapidly replace a missing egg mass. Egg masses were removed from eighteen guarding females during the last week of May 1984. Nine of these females were discovered nearby on new egg masses the following week. The difference in the average number of eggs in original and replacement egg masses, 37.4 and 35.5 respectively, was not significant (Mann-Whitney U test, $U = 38$, $p > 0.05$).

Egg parasitoids and hatching success

Mothers frequently moved in a jerky manner on or near their egg mass when parasitic Hymenoptera (unidentified Eulophidae) were present. Wasps normally landed on the undersurface of a leaf 2–4 cm away and oriented toward the eggmass (Fig. 1a). From this position they darted directly to the eggmass to oviposit. Movements by the wasps on the leaf appeared to stimulate *A. sparsa* females to rapidly move back and forth and around the eggmass for short periods of time. Wasps were also observed resting on the elytra of brooding females, females without offspring and occasionally on males. Carroll (1978) mentioned similar phoresy by a eulophid wasp on a Brazilian cassidine beetle, *Stolas sp.*.

To assess the importance of egg parasitoids, a total of 103 abandoned egg masses were collected from three habitats between late August and early November 1978 and examined egg by egg for the small exit hole of an emerging wasp or the larger serrated opening of an *A. sparsa* larva. These eggs, numbering 3893, produced 1004 wasps (26%) and 2342 larvae (60%). Five hundred and forty-seven eggs (14%) failed to develop. Significant differences existed between habitats in the number of wasps and the number of undeveloped eggs per egg mass (Table 2). The median number of wasps emerging from egg masses was greatest at the "field" site, least at the "forest" site and intermediate at the "mixed" site. The median number of undeveloped eggs was also much higher at the "field" site than either of the other two sites. Thus, *A. sparsa* females were most successful in producing larvae at the "forest" site, intermediately successful at the "mixed" site and least successful at the "field" site. It is unclear why some eggs fail to hatch. That undeveloped eggs are more common where egg parasitoids are more abundant suggests that multiple ovipositions by parasitoids might be responsible. Physical conditions, especially maximum daytime temperature and humidity, also differ between shaded and open sites.

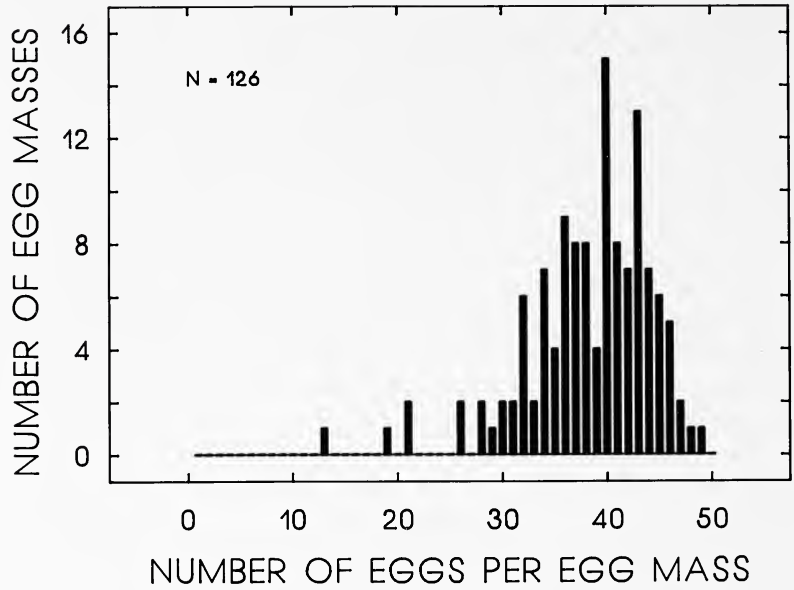

Fig. 2. Variation in the number of eggs per egg mass.

One or more wasps emerged from 79 of 103 (77%) *A. sparsa* egg masses (26% of all eggs). None of the egg masses, however, was completely parasitized—85% was the highest value obtained. In contrast, Carroll (1978) found 86 percent of egg clutches (n = 117, 31.5 eggs per clutch) of *Stolas sp.,* a Brazilian cassidine that does not have maternal guarding, were completely parasitized by wasps; 14 percent were totally unparasitized. Thus, guarding may make it less likely that all eggs in an egg mass are parasitized.

Eberhard (1975) noted that maternal guarding by the pentatomid, *Antiteuchus tripterus* Ruckes, was highly effective against generalist predators and phoretic egg parasitoids. However, when he removed mothers from their clutches, the number of eggs parasitized actually decreased because parasitoids apparently used olfactory or visual cues associated with the mother to locate egg masses. This may also occur with *A. sparsa* and deserves investigation.

Opportunistic predators of eggs

The importance of maternal guarding during the egg stage was investigated by locating eighteen egg masses with mothers at the

Table 2. The median number of eggs per egg mass producing wasp parasitoids, beetle larvae or failing to develop classified by collection site. The Kruskal Wallis one-way analysis of variance statistic, "H", tests for significant between-site differences ("*" = p 0.001).

Site	Wasps (%)	Larvae (%)	Undevel. (%)	Eggs N
Field	14 (35)	13 (32)	11 (28)	40 29
Mixed	10 (26)	25 (64)	2 (5)	39 42
Forest	2 (5)	30 (75)	2 (5)	40 32
H	11.7*	25.3*	21.2*	1.99 ns

"forest" site during the mid wet season 1984. The sample was divided into nine matched pairs consisting of an egg mass from which the mother was removed and the nearest neighboring egg mass from which the mother was removed and immediately replaced. Each egg mass was revisited 6 times at intervals of 24 hours. The unguarded egg mass was missing or destroyed before the guarded eggmass in each pair. Five of nine motherless egg masses were preyed upon within 24 hours, eight of nine within three days and all nine within five days. Myrmecine ants consumed two of the unguarded egg masses. Eight of nine "control" egg masses and mothers were intact and in perfect condition at the end of the five days. One "control" egg mass was sandwiched between two wet leaves during a rain and subsequently abandoned by the guarding female. This egg mass was also overrun by myrmecine ants.

Relocating and discriminating between egg masses

Females were removed from egg masses and dropped so that they landed within 1–2 m of a point on the ground directly beneath their egg mass. In most cases these females returned to their egg mass within 30–60 minutes. When females were moved more than 2 meters from the egg mass they rarely returned. Females that lost their own egg mass as a result of being displaced readily adopted and protected the first unguarded eggmass they came upon, even if it was not their own. However, when 12 marked mothers from six pairs of neighboring egg masses (located on different shoots of the same plant) were removed and dropped on the ground midway between their egg masses, 11 returned to their own egg mass. The exceptional mother adopted a nearby untended group of *A. sparsa* larvae, perhaps because her egg mass was being preyed upon by ants. Two females from one of the pairs were observed guarding the same egg mass for roughly 15 minutes. One of the females lost interest, walked away and later encountered her own eggs on another shoot of the same plant. Thus it appears that *A. sparsa* females can home from limited distances and can discriminate between their own egg mass and those of their neighbors, behavioral capabilities strikingly similar to those described by Tallamy and Denno (1981) for the subsocial tingid, *Gargaphia solani* Heidemann.

LARVAL PERIOD

Grazing pattern

Larvae begin to graze on the under surface of their natal leaf immediately after eclosing from the egg. Young larvae consume the lower epidermis and part of the mesophyll leaving the upper epidermis intact. Later instars consume the entire leaf, save the central midrib. First instar larvae advance slowly in an organized front on their natal leaf, grazing a path along one side toward the tip and then back toward the petiole along the other side of the leaf. Two to three days are spent on the first leaf where two molts are completed. Larvae then move down the pedicel to the stem where they have the option to move toward younger leaves at the tip or toward older leaves further down the plant. Nine of ten larval groups observed at this juncture moved toward the vine apex (2-sided, Binomial probability = 0.04). Later, after apical leaves are eaten, the family descends along the stem to feed on older leaves.

Acromis sparsa mothers normally stay behind their moving larvae and do not appear to influence their movements. When larvae stop feeding they form a tight knot of bodies encircling the stem or a flat rosette of bodies under a leaf (Fig. 1b). Mothers often stand on the backs of their larvae but move to the edge or off of the group to challenge any approaching arthropod. Larvae spend most of their time on the undersurfaces of leaves and at night remain tightly aggregated and defended by their mothers. In contrast, Ohaus (1909) noted that female *Omaspides* shielded their aggregated larvae during the day, possibly from the effects of the sun, and that larvae wandered apart at night to feed.

Predation on larvae

Guarding has the appearance of being highly effective at thwarting predators. However, there are at least two circumstances in which predators seem to have an advantage. When *A. sparsa* larvae move between feeding sites they normally move 2–6 cm ahead of their mother. In so doing they are unguarded and on several occasions I observed chalcid wasps (probably *Spilochalcis* sp.) flying in tight circles around and briefly landing on these moving groups of larvae. This may be especially common as groups composed of older larvae move the 1–2 m down the vine to a pupation site. Mothers did not shield or otherwise defend their offspring under those circumstances and may not have sensed the danger. Larvae also became vulnerable to predators if their aggregation became divided into two groups, only one of which could be competently guarded. Predacious bugs, especially *Stiretrus spp.* (Pentatomidae, Asopinae), were adept at creating and exploiting this situation. Females could charge and "bulldoze" a *Stiretrus* adult from an area with larvae. However, repeated approaches by the bug were eventually rewarded by the temporary isolation of some larvae, some remaining on the under surface of the leaf while the others had moved to the top, etc. These were quickly speared and sucked dry. Predacious bugs tended to remain with a family group for several days, often until offspring were gone. Orphaned larval groups were only rarely encountered. Individuals within these groups were usually tightly aggregated suggesting that the presence of the mother is not crucial to maintenance of the aggregation. Poorly aggregated, orphan groups were also occasionally found. Individuals in these groups were usually few in number implicating predators or parasitoids as the disruptive factor. Aggregated larvae did not disperse nor did mothers react when I presented injured or crushed members of their group indicating the absence of an effective volatile alarm substance.

Larval mortality in defended groups

Natural levels of larval mortality were examined at the "field" and "forest" sites during August and September 1978. Due to the differences in egg mortality described above only 8 of 19 females and brood reached the larval stage at the "field" site; all of 22 at the "forest" site. Additionally, the initial number of larvae per mother differed significantly between sites; 29 larvae per group at the forested habitat versus 14 in the old field site (Mann Whitney U Test, $z = 4.14$, $p < 0.001$). The rate of larval disappearance, roughly 1.2 larvae per day (Fig. 3), did not differ between sites (Mann Whitney U Test, $z = 0.133$, $p = 0.45$). Larvae from only one of eight groups

(8 individuals, 3%) reached pupation at the "field" site while larvae from 15 of 22 broods (96 individuals, 11%) reached pupation at the "forest" site ($p < 0.01$, Fisher's Exact test).

Larval mortality in undefended groups

The effect of maternal guarding on larval survival was investigated during August 1980 by removing mothers from some larval groups and comparing their survival to that of nearby guarded groups at similar stages of development. Initially, six nearest-neighbor pairs, groups with and without mothers, were found, marked and revisited daily. The unguarded group disappeared first in each of the six pairs. All unguarded larvae were gone within three days. One week later the procedure was repeated with another six pairs. The motherless group disappeared first in four pairs. Both groups of a fifth pair disappeared between visits and neither group of a sixth pair had disappeared at the end of the sixth day. Generalist predators, chiefly myrmecine ants and polybiine wasps, preyed upon some motherless larval groups within an hour after removing the mother. On one occasion a *Polybia sp.* wasp discovered a group within 5–10 minutes of removing the mother. The wasp returned at 2–4 minute intervals to remove larvae until the group was completely gone.

PUPATION.

After consuming their last leaf, penultimate instar larvae moved 1–2 m down their host plant to pupate, followed by their mother. The location of a pupal aggregation is often revealed by a stem which has been girdled by larvae as they descended to pupate. At the pupation site, often only 0.5 m or so above the ground, larvae form a tight cluster of bodies completely encircling the stem (Fig. 1c). The mother normally stands motionless for long periods of time on the backs of her pharate larvae or pupae. Movement in the vicinity of the aggregation often stimulated her to begin walking briskly and repeatedly around and over the group. No interactions were observed between mothers on pupae and predators.

Twenty-seven pupal masses were collected during September and October of 1978 from the "forest" and "field" sites and allowed to develop in the laboratory. Ten to 17 days passed in the lab before adults began to eclose. Teneral adults eclosed from 68 percent of the pupae, parasitoids from 14.3 percent and the remaining 17 percent

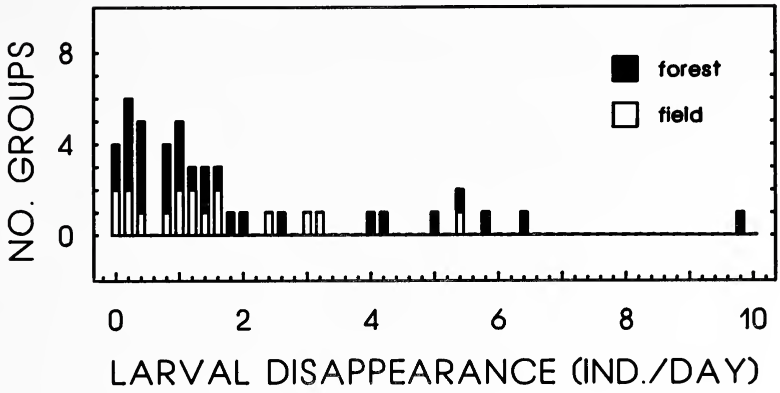

Fig. 3. Comparison of the disappearance rates (number of individuals disappeared per day of observation) for larval groups at the "forest" (solid bar) and "field" sites.

failed to develop (Table 3). Thirteen pupal masses (48%) produced at least some parasitoids. Numerically, tachinid flies eclosing from nine groups were roughly twice as important as chalcid wasps. The number of parasitoids reared could under estimate their importance since some pupal masses were collected soon after they had formed. However, I suspect that most parasitoids infect larvae and are carried to the pupation site. At least one other larval parasitoid that is worth noting is carried to the pupation site, although it was not reared from the 1978 sample. Several pupal groups collected in the early wet season of 1986 contained larvae of the entomophagous moth, *Schacodontia sp.* (Pyralidae), an important predator on the gregarious larvae of the cassidine beetle, *Polychalma multicava* Latreille (pers. obs).

Sixty-five larvae (17%) in 14 pupal masses of the 1978 sample failed to develop—a loss roughly the same as that to parasitoids. Again, it is unclear why development in these individuals does not proceed. In this case there is the possibility that some individuals do not feed sufficiently as larvae before moving en masse with their siblings to the pupation site. If there is significant variation in feeding within groups, then there could be conflict about the timing of the descent to the pupation site. Of course, larvae may wither at the pupation site because of parasites, fungi, etc.

Table 3. The number of pupae and pupal groups reared in the lab producing parasitoids, teneral adults and not developing.

	Pupae		Pupal Groups	
	N	%	N	%
Parasitoids				
Chalcidae	18	4.8	5	18.5
Tachinidae	36	9.5	9	33.3
Adults	258	68.4	27	100.0
Undev. pupae	65	17.2	13	48.1
Totals	377	100.0	27	100.0

ADULTS

Females terminated their care when adult beetles began to eclose. Freshly eclosed adults are a pale tan color and a week or more passes before elytra harden. Tenerals remain loosely aggregated for several days feeding heavily on leaves of the natal plant or nearby shoots before dispersing. No mating activity of predispersal adults was observed. The number of days between eclosion and oviposition for both teneral females and guarding mothers remains undetermined. Marked females kept on potted plants lived over most of one wet season and produced a succession of clutches.

Sex Ratio

The ratio of the sexes at eclosion was examined by recording the number of male and female tenerals emerging from twenty pupal masses collected in May 1986. Males were more numerous in ten, females in seven and the sexes equally represented in three. Males comprised 50.5 percent of all individuals (n = 378). Thus, there is no difference in the representation of the sexes above what is expected by chance. If males were competing strongly among themselves for sister matings prior to dispersal and if sex ratio were heritable, then mothers might be expected to lay more female than male eggs (Hamilton 1967).

Sexual dimorphism

Acromis sparsa is easily distinguished from other Cassidinae in Panama by its sparsely pigmented, translucent and broad elytra which extend roughly half of the body's width to each side of the abdomen (Fig. 4). Additionally, striking differences exist in the shape of some individuals. I examined morphological differences between the sexes by taking six measurements, three from the elytra,

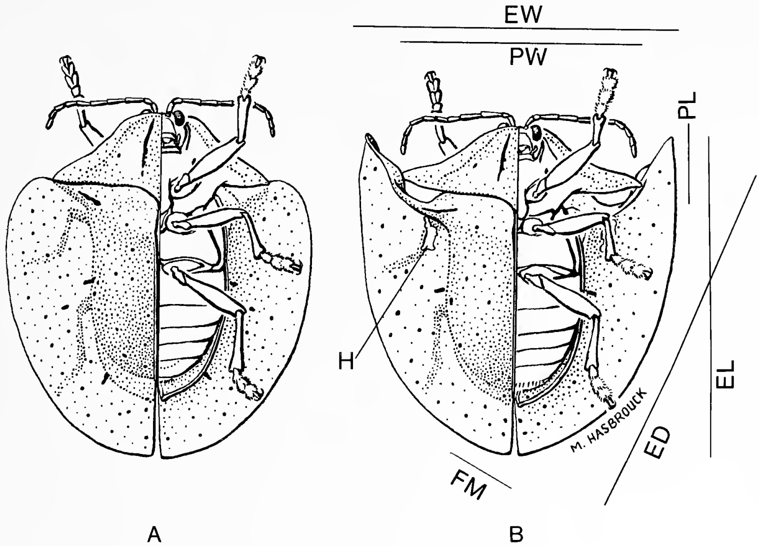

Fig. 4. Dorsal (left) and ventral (right) views of (A) a large female and (B), a large male *Acromis sparsa.* Note the hole "H" in the elytra of the male. The six measurements taken from pinned specimens were: "PW" = pronotum width, "PL" = pronotum length, '"EL" = elytra length, "EW" = elytra width, "ED" = elytra diagonal and "FM" = femora length.

two from the pronotum and one from the hind femora, from 30 pinned females and 71 males spanning much of the size distribution in each sex. Regressions were calculated for all pairwise combinations of these six measurements in each sex—30 regressions in all. The simple linear regression coefficients ranged from 0.922 to 0.983 indicating good fit to linear models throughout. Male and female regression lines were parallel in six of the fifteen possible comparisons and three had equal intercepts (Table 4).

Graphed against femur length, there were no differences between the sexes in the slope of regression lines for pronotum length, elytra width or elytra length. Only elytra width had a significantly different intercept. For any given body size, the elytra of females were slightly wider than those of males. Elytra diagonal length and pronotum width increase much more quickly in males than females relative to femor length (Fig. 5). However, there is little if any sexual difference in these characters in the small end of the size distribution.

Table 4. The lower left portion of the matrix contains the probabilities that male and female regression lines in each comparison have the same slope. The upper right portion contains probabilities that male and female regression lines have the same intercept. Intercepts have been computed only for those cases where slopes are homogenous. PW = pronotum width, PL = pronotum length, EW = elytra width, EL = elytra length, ED = elytra diagonal, FM = femora length.

	Morphological Character				
	PW	PL	EW	EL	FM
PL	<0.001	—	0.252	0.008	0.628
EW	<0.001	0.866	—	<0.001	0.027
EL	<0.001	0.146	0.169	—	0.061
FM	<0.001	0.417	0.534	0.226	—
ED	0.004	0.002	<0.001	<0.001	<0.001

Some aspects of beetle shape changed abruptly with incresing size in some individuals and were impossible to quantify. For instance, the elytra surface near the humeral angle which is an evenly curved surface in small and intermediate males is a complexity twisted surface in large males. Additionally, an oblong perforation as large as 2.5 × 1.5 mm was present in approximately the same location in the elytra of many males (Fig. 4). The abdomen lies just central to the holes and apparently is never penetrated. Only males whose elytra length exceeded 8 mm were perforated (Fig. 6). The elytra of recently eclosed, large males (elytra length 8 mm) often lacked any perforation or occasionally had a single narrow slit in one side. Recently opened holes in young individuals sometimes had the appearance of having been punched inward from the dorsal side. The holes of older males were jagged in outline and widened into elipses. The shape of a few holes resembled a cross indicating that a planar object had been inserted and then twisted by 90 degrees. Sectioned elytra from young males showed clearly that the thickness of the elytra varies considerably and is thinnest in the area where holes normally occur.

Interactions at the oviposition site

Individual males, large enough to be easily distinguished from females, tended to reside on leaves toward the apex of *M. umbellata* shoots where ovipositing and guarding females were also common (Table 1). Activity increased noticeably between 1000 and 1200 hrs.

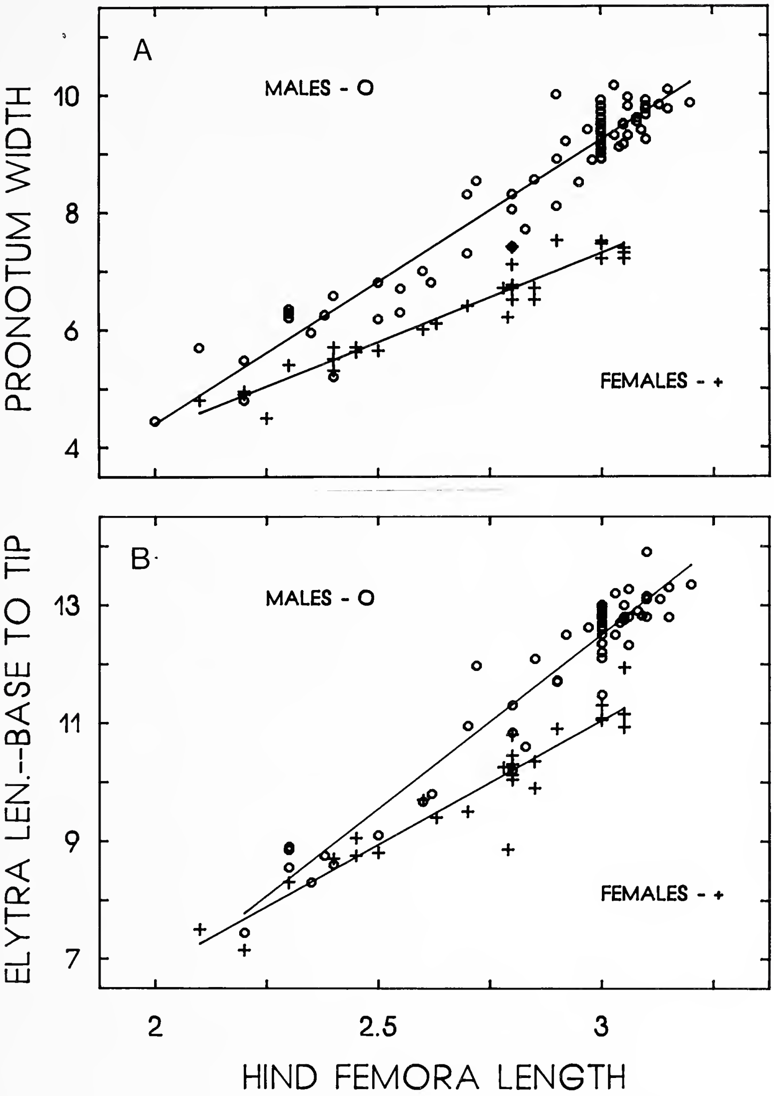

Fig. 5. Sexual differences in the relationship of pronotum width (A) and elytra diagonal length (B) to femur length.

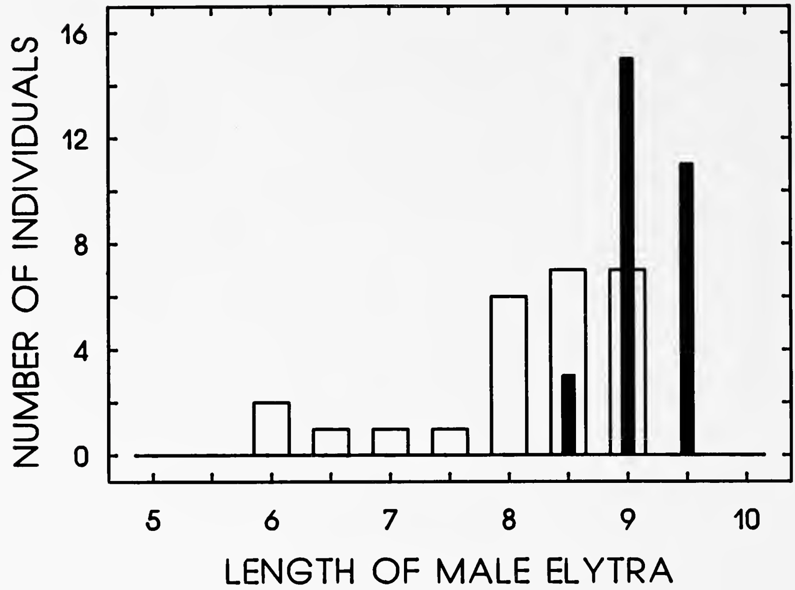

Fig. 6. The size-frequency distribution of males with (solid bars) and without elytral holes in one sample.

of most days as males ascended the vine from roosts under low and intemediate height leaves.

I first became aware of the intensity of competition at these sites when I observed a male-male chase which ended with one male flipping the other from a tip leaf. A few minutes later, I observed two males near the tip of a nearby plant with elytra locked firmly together. After several minutes the two separated and spent some minutes antennating one another. This was followed by maneuvering in which one male attempted to run around the other which pivoted in place. Eventually one male was chased down the petiole where it lost its grip and fell from the plant. The male that remained walked to the female on the first unfolded tip leaf and immediately copulated. Within three to four minutes, the male that had fallen from the plant had climbed back and approached to within two inches of the pair. Antennating began again and the mounted male withdrew his aedeagus but remained on top of the female to confront the intruding male. After two minutes the mated pair separated and the two males again clasped elytra and tugged against the other. Eventually, one of the males ran off and the female retreated to a nearby leaf.

Male–male encounters were easily staged by bringing two vine tips with resident males into contact or by transferring a male with a blade of grass. On several occasions the transferred male antennated the resident for 10 to 20 minutes and then walked off the leaf. Other encounters ended with one male rapidly chasing or flipping the other from the leaf. Using staged encounters of this sort it should be possible to directly investigate the importance of size in determining the outcome of male-male competition. Indirect evidence suggests that larger males are often the winners. Of twenty-one unmanipulated plants each with more than one male present, the largest male was nearer the vine tip in sixteen cases (2-sided, binomial probability = 0.03).

Males were occasionally observed locked firmly together for considerable periods of time, always on the host-plant and usually on or just below the youngest leaves of the plant. One male would be normally standing on the substrate supporting a second male held rigidly in the air, feet free, body perpendicular to the substrate (Fig. 7). The lower male was often simultaneously courting or copulating with a female. The lifted male was held by the elytra tip caught between the posterior edge of the pronotum and the leading edge of the elytra of the lower male. The pronotum of the lifted male was inserted into the elytral hole of the lower male. Thus, it appears that elytra holes may be made by opponents as they are flipped up and their pointed elytra pulled down onto the elytra of the lower male. Elytral holes may thus facilitate holding an opponent in a locked position for a period of time during which it is helpless to interfere with mating or attempting to mate with a female.

Discussion

Female *A. sparsa* guard their offspring on apical foliage against predators and parasitoids from oviposition through pupation. Unlike the larvae of many Cassidinae without parental care, *A. sparsa* larvae are seemingly defenseless without their mother. Predation comes swiftly and inevitably as ants and wasps quickly discover and harvest undefended larvae. Mortality in defended groups takes the form of a slow attrition of offspring over the entire development

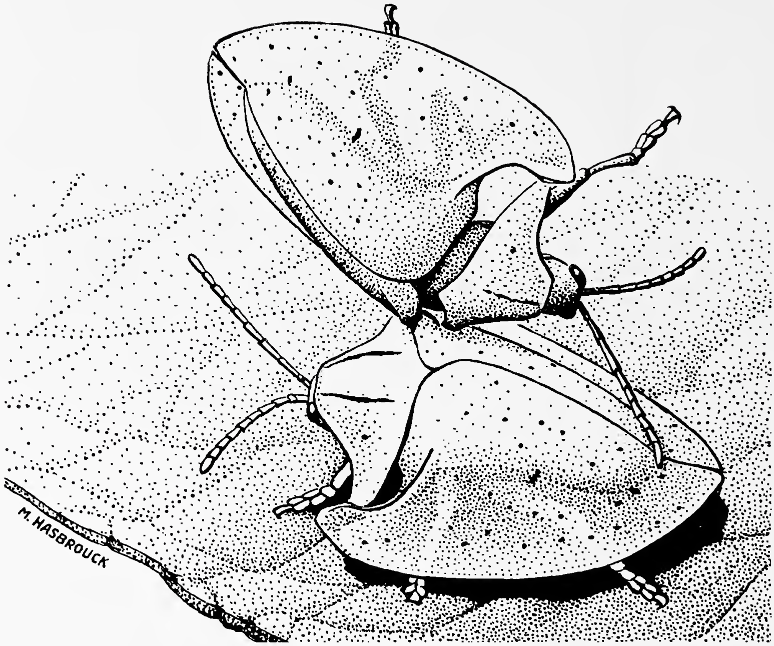

Fig. 7. A competitive encounter in which one male has been lifted from the leaf surface by another male which has gotten a hold on his elytra.

period and is often less than complete. Guarding females are efficient at repelling ants and wasps, but egg parasitoids, larval parasitoids such as chalcid wasps and tachinid flies, pentatomid bugs and an entomophagous moth were able to gain access to guarded offspring. These opportunities arose as groups moved between feeding sites or as individuals temporarily became separated from the rest of the group guarded by the mother.

Maternal care in this species seems to have a clear and unambiguous selective value: as in many other subsocial insects, it lowers mortality due to predation (Tallamy and Wood 1986). Why, then, has subsociality evolved in *A. sparsa* but not in many other cassids some of whom share the same host plant? It may be significant that of the six species of Cassidinae on *M. umbellata,* only larvae of *A. sparsa* heavily exploit the terminal foliage. The other 5 species can be found anywhere on the plant, but their larvae tend to occur low on shade leaves. One hypothesis is that predators are more numerous on apical foliage and maternal care is more effective defense under these circumstances than the defensive attributes of solitary species (eg. egg and larval crypticity, spines, fecal shields, etc.). Apical foliage may harbor higher numbers of predators because it is more open, more easily searched by polybiine wasps and other flying predators, and is nearer the active nectaries of other plants which concentrate such visitors (Hespenheide 1985).

While the possibilities of larval survival may decrease toward the apex of the plant, nutritional rewards could increase. There is a growing body of evidence that insects feeding on young foliage grow more quickly and achieve larger pupal weights and adult size (Schroeder 1986, Damman 1986 and references therein). Larval developmental time should have a direct bearing on the number of groups of offspring a female can guard in a season.

Most Cassidinae are sexually monomorphic or are very nearly so. Eberhard (1980) concluded after reviewing numerous examples that most beetles use their horns to physically displace their conspecific, sexual rivals at the location of important resources. The sexual dimorphism in *A. sparsa,* laterally elongated pronotum and elytra in large males, has probably evolved as a result of similar selection pressures. The chasing, flipping and immobilization of rivals which I observed suggest the existence of strong intrasexual competition although any size related advantages of these morphologies in *A. sparsa* have yet to be demonstrated.

Why does strong competition between males exist in *A. sparsa* and not in many other Cassidinae? Females spend much of their time guarding offspring to the near exclusion of other activities. Although females with brood were occasionally courted by males, most did not attract nearby males. A large proportion of the female population leaves the mating pool during the time offspring are being guarded. Males, on the other hand, do not guard and are presumably sexually competent the entire time. As females begin to look for oviposition sites, which in themselves may be limiting, the operational sex ratio should be heavily biased in favor of males.

While females become a rare item for males during brooding, their eventual reappearance should at least be fairly predictable: they nearly all go to the second or third open leaf on vine tips to oviposit. Larger males capitalize on this predictability by holding these sites and awaiting the arrival of females. Smaller males appear to have some opportunities for mating with females still searching for quality oviposition sites. The vigorous competition which I observed between large males was apparently for the last mating before oviposition. This suggests the existence of sperm precedence and an advantage to the last mating male (Smith 1984). Locking an opponent above the back may be one of several ways individuals of this species insure that theirs was the last mating before oviposition.

SUMMARY

Females of the neotropical tortoise beetle, *Acromis sparsa,* invested 40 or more days per generation in post ovipositional care of offspring. Broad elytra were used to shield eggs, larvae and pupae from invertebrate enemies. No egg masses or larval groups from which mothers were removed escaped opportunistic predators for longer than a few days. Defended groups suffered a slow attrition of offspring to parasitoids. Thirty-two to 75 percent of eggs, 3 to 11 percent of larvae and 68 percent of pupae survived to the next developmental stage in defended groups. The considerable variation in survival was generated by large differences in the importance of egg parasitoids among sites.

Courtship, mating, oviposition and early larval feeding occurred on apical foliage of the second-growth vine, *Merremia umbellata* (Convolvulaceae). Males attempted to chase, immobilize or dislodge competing males at these sites—often before females had arrived to oviposit. Of several characters measured, only those involved in combat, pronotum width and the extension of the humeral angle of the elytra, increased more rapidly in males than females with increasing body size. The elytra of most large males had small oblong holes, opened while young and subsequently enlarged by the entry by the pronota of opponents during combat. Holes appeared to help lock an opponent above the back where it was helpless to interfere or supercede in mating.

ACKNOWLEDGMENTS

I thank the Smithsonian Tropical Research Institute for providing financial and logistical support. The paper benefited from the critical reviews of A. Aiello, W. Eberhard, W. Nentwig, N. Smith and H. Wolda. H. Stockwell and D. Englemann provided identifications of the important species and encouragement throughout. E.

Munroe kindly identified *Schacodontia.* I am also indebted to M. Hasbrouck for the drawings and to C. Windsor for the maternal care of our offspring while I was in the field.

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SYMBIOSIS BETWEEN SOCIAL SPIDERS AND YEAST: THE ROLE IN PREY ATTRACTION

By William James Tietjen[1], L. Rao Ayyagari[1]
and George W. Uetz[2]

Introduction

A number of predatory animals use deception, including odors, signals, and bait-like body appendages or objects to lure prey (Alcock, 1984). Several spider species are known to emit chemical odors that mimic the sex attractants of certain noctuid or saturniid moths as a means of luring males to be captured (Tietjen and Rovner, 1982). Here we provide evidence that the social spider species, *Mallos gregalis,* uses a scented "bait" to attract prey. Our results indicate that this odor is produced by yeasts growing on the carcasses of previously fed-upon flies which these spiders incorporated into their webs.

Mallos gregalis is a social spider from Mexico which lives in huge colonies that may cover whole tree branches with webbing. Up to 20,000 individuals of both sexes and various stadia may occupy these extended colonies. Predation, feeding and nest construction are communal, with little or no cannibalism occurring among group members (Burgess, 1978; Tietjen, 1986).

Early records of *M. gregalis* indicated that the Indians of Michoacan used the spider colonies as natural fly traps. These reports also suggested that the nests attracted flies and prompted the importation of *M. gregalis* to France in the early part of this century as a potential biocontrol agent (Diguet, 1909a; 1909b). Recent field observations on *M. gregalis* have noted that swarms of muscoid flies sometimes surround the nest, although no attractants (such as animal carcasses) could be found in the immediate area (Burgess, 1979; Uetz pers. obs.). These observations, and the apparent specialization of *Mallos* on dipteran prey have raised questions about the attractiveness of *M. gregalis* nests to flies (Jackson, 1977; 1980).

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Manuscript received by the editor March 25, 1987.

Unlike most other social spiders, *M. gregalis* do not remove prey remains from their web, but rather incorporate these debris into the nest matrix (Tietjen, 1986). It seemed possible that this apparent untidiness might attract more prey, so we examined colonies in the field and laboratory for evidence of prey attraction.

Both field-collected nests and webs constructed by spiders in the laboratory had a sweet, yeast-like odor. A change from this usual sweet scent to an odor of ammonia often precedes population crashes or mass emigration, suggesting changes in web's microflora. The presence of microbiota in *Mallos* nests is likely, given their habit of incorporating prey remains into the web and the high-humidity conditions within the web (Tietjen, 1986). *Mallos* also do not completely consume their prey, which undoubtedly provides a rich medium for microbial growth (Burgess, 1978; Uetz, 1983). If these social spider webs actually do attract prey, this may be an important factor in maintaining group cohesion and/or allowing a relatively high population density in a marginal (seasonal subhumid or xeric) habitat.

METHODS

Field analyses

Mallos gregalis nests were collected from several sites including Guadalajara, Guanajuato, Mexico City and Tuxpan (Mexico), among the branches of Mexican Blue Oak (*Quercus oblongifolia*). A subsection of a typical colony (20 × 8 × 10 cm) was torn apart and the flies contained therein counted and identified. Inside the webbing, carcasses of 129 insects were found: 115 muscoid Diptera (Calliphoridae, *Calliphora sp.,* 76 individuals; Sarcophagidae, *Sarcophaga sp.,* 18 individuals; Muscidae, sp. unknown, 21 individuals), 9 Hymenoptera, 4 Coleoptera, and 1 Hemiptera. The large quantities of fly carcasses suggested the presence of an animal carcass or garbage pile nearby and more than a dozen flies hovered about the colonies when they were collected, but a systematic search of the surrounding area indicated there were no other potential fly attractants nearby.

Culture methods for microbiota

Adult *M. domestica* were reared in the laboratory and fed to colonies of *M. gregalis.* The fly carcasses (with a minimal amount of attached silk) were removed at random from the nests and assayed to determine the types of microflora associated with the flies. Flies were homogenated in 5.0 ml of triptose soy broth (TSB) and then transferred to 50 ml flasks and incubated at 22° C in a shaker bath for 24 hr. The broth was then transferred to agar plates and incubated for 48 hr at 35°C. Among the three types of agar media, triptose soy agar (TSA) supported mainly bacterial growth while Peptone-Yeast extract-Glucose (PYG), and Saboraud supported mainly fungal growth. Prey from the field-collected nests were similarly treated and plated on Nutrient agar and Saboraud.

Several other potential sources of microbiota were similarly assayed: non-fed-upon flies, adult female *M. gregalis,* web silk alone, stock fly food (powdered milk and sucrose, 3:1), soiled fly food removed from the fly rearing cages, and flies that other species of spiders had fed upon. Members of the following families were tested, as available: Agelendidae, Lycosidae, Linyphiidae, Salticidae, and Theridiidae. These tests were run using Saboraud agar. Web silk alone was obtained by establishing a colony in a Petri dish (N = 20 adult female *M. gregalis*), not feeding the spiders while they deposited silk, and then collecting the nest material a week later.

Behavioral assays

Groups of 15 flies were presented with paired stimuli to assess attraction to nest odors and/or associated microbiota. Flies were removed from access to food for 2–3 hr prior to testing. They were then introduced into a plexiglas test arena painted flat black on the interior (321 × 32w × 20h cm) and, following an acclimation period of 20 min, were presented with paired odor sources (the control and a single experimental odor). Odor sources were contained in Petri dishes (9.3 cm dia) covered with clean white cotton cloth. The position of the control and experimental odors (yeast cultures from fed-upon flies, mixed microbiota from non-fed-upon flies, clean silk or *Mallos* nest material with prey) was randomized for each run. Empty petri dishes were used as controls when nest silk was presented as the experimental stimulus, sterile media was used as a control when cultures were presented as experimental stimuli. Following introduction of the stimuli, flies were allowed an additional 5-min for acclimation followed by the 5-min recording period. The number of contacts with the upper cotton surface of the Petri dishes was scored as an index of attraction (N = 20 for all series).

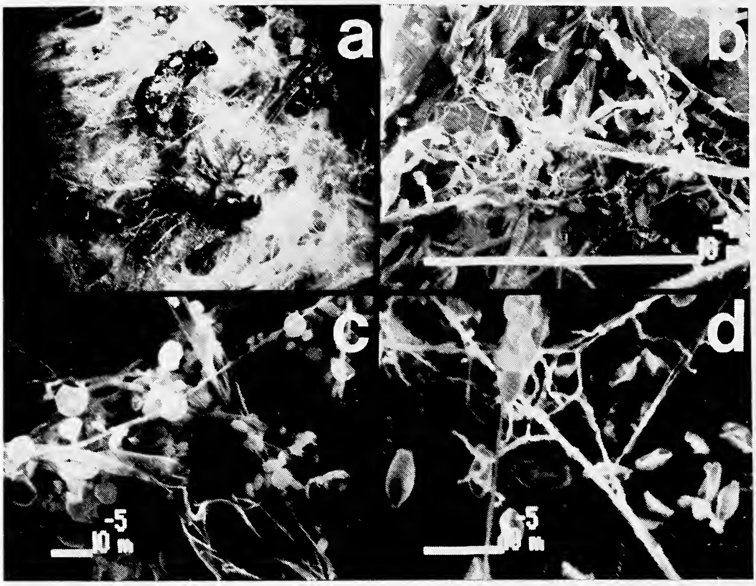

Fig. 1. a. Interior of *Mallos* colony, showing fly carcasses; b. SEM photo of microbiota community found on the interior abdomen of a fly from a *Mallos* colony; c. SEM photo of yeasts; d. SEM photos of individual collapsed yeast cells.

RESULTS

If spiders are not fed while building their nests in the laboratory, the webs do not acquire the sweet odor until prey (*Musca domestica*) are provided. Removal of fly carcasses is associated with a loss of this odor, suggesting that microbiota associated with the flies or feeding process of the spiders might be responsible for the scent of *Mallos* nests. Microscopic examination of fly carcasses reveals the presence of numerous hyphae, sporulating bodies, and budding yeasts (Fig 1).

Flies that had been killed and fed upon by *M. gregalis* had an altered microbiota when compared to most of the controls (Table 1). The odor of the yeast cultures (PYG plates) was very similar to that of healthy *M. gregalis* nests, and subculturing suggested the presence of three morphologically-distinct types of yeasts.

Table 1. Relative growth (average of triplicates) and odor of microflora on differential media. Determination of colony type was based on colony morphology and growth was scored within individual plates ("+" indicates relative number of colonies; "-" no colony growth and/or no odor; "S" a sweet odor, similar to that of the *Mallos gregalis* nest; "R" a rancid odor; and "nt" indicates not tested).

SOURCE	SABORAUD			
	Yeast	Mold	Bacteria	Odor
Flies fed upon by *M. gregalis*	+	+	-	S
Non-fed-upon flies	+	++	+	R
Female *M. gregalis*	-	+++	++	R
Clean silk from *M. gregalis* nests	-	++	+	R
Fly food (unsoiled)	-	++	+	R
Fly food (soiled from fly cage)	-	+++	++	R
Flies fed upon by other species of spiders	-	+++	++	R
SOURCE	PYG			
Flies fed upon by *M. gregalis*	+++	+	-	S
Non-fed-upon flies	++	++	-	S
Female *M. gregalis*	-	+++	++	R
Clean silk from *M. gregalis* nests	-	++	+	R
Fly food (unsoiled)	-	++	+	R
Fly food (soiled from fly cage)	-	+++	+	R
Flies fed upon by other species of spiders	nt	nt	nt	nt
SOURCE	TSA			
Flies fed upon by *M. gregalis*	+++	+	+	S
Non-fed-upon flies	+	+	+++	R
Female *M. gregalis*	nt	nt	nt	nt
Clean silk from *M. gregalis* nests	nt	nt	nt	nt
Fly food (unsoiled)	nt	nt	nt	nt
Fly food (soiled from fly cage)	nt	nt	nt	nt
Flies fed upon by other species of spiders	nt	nt	nt	nt

Non-fed-upon flies cultured on TSA agar had a rancid odor due to the large number of bacterial and non-yeast fungal colonies. However, non-fed-upon fly homogenates on differential media (PYG and Saboraud) indicate that the yeasts are normally present on the flies before feeding by *M. gregalis*. Other potential sources of microbiota (fly food, adult female *M. gregalis*, and silk) did not contain the yeasts.

We have examined the microbiota associated with the field-collected nests of *M. gregalis* and obtained identical results, indicating that the odor and its source is similar in field and laboratory populations. This suggests that feeding by *M. gregalis* alters conditions within fly carcasses so that the usual competitive growth advantage of bacteria is shifted toward the yeasts and/or bacterial growth is inhibited. Homogenates of flies fed upon by other spider species did not show evidence of such a growth advantage for the yeasts (Saboraud media).

Nest material with fly carcasses was attractive to flies while silk alone showed no such attraction (Fig. 2). Cultures of yeasts derived from the fed-upon flies were similarly attractive to flies while cultures from non-fed-upon flies showed no attraction. In addition, both the nest material with prey and yeast stimulus attracted more flies than either the non-fed-upon microflora or clean silk alone (Chi Square and Wilcoxon tests; $p < 0.01$). The higher attractiveness found in controls for nest material and fed-upon flies as compared to non-fed-upon flies and clean silk could be accounted by the generally higher activity of the flies in the presence of the yeasts.

DISCUSSION

The present research suggests that *M. gregalis* attract their prey by using odors based on a symbiotic relationship between spiders and yeasts. Although other social arthropods, such as the fungus-growing ants, beetles and termites make use of yeasts and/or fungus, the function is one of "farming" a crop for food (Wilson 1971). To our knowledge, this is the first example of any organism using microflora as a means of attracting prey through an odor. Under natural conditions, visual cues of the fly carcasses on the web may provide additional attraction (Jackson 1980).

Most discussions on evolution of sociality in spiders emphasize the maternal route in which the young remain with the mother for an extended period of time. Among the Eresidae and Theridiidae, for example, a progression from one level of aggregation (parents and offspring) to another (several generations present on the web) is well documented (Buskirk, 1981). Recent arguments suggest that for *M. gregalis,* unrelated individuals may have gained a foraging advantage by collective nest construction (Fritz, 1984; Tietjen, 1986).

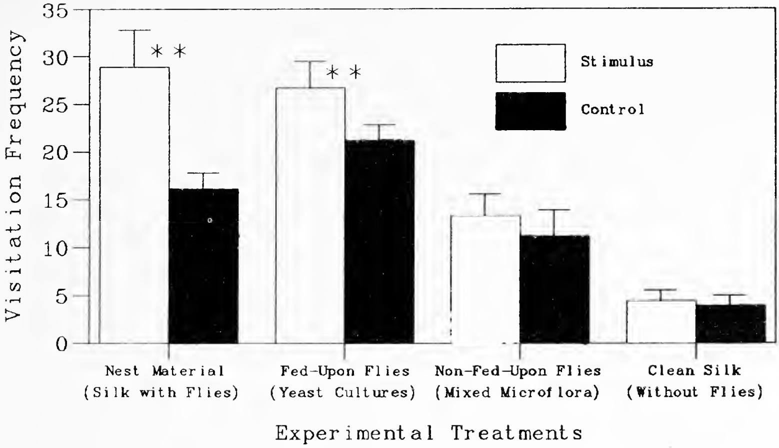

Fig. 2. Mean visitation of grouped flies to paired experimental odors. For tests using *Mallos gregalis* silk (with and without flies), the silk provided the experimental odor while empty covered dishes were controls. Those tests using microorganisms as an odor source used sterile agar as the control. Asterisks indicate a significant difference in visitation frequencies within a test (Chi Square and Wilcoxon Tests; $p < .01$).

Those individuals with increased tolerance of neighbors would have a greater concentration of fly carcasses (and their associated yeasts) to attract prey. Further increases in interspider tolerance and eventual construction of a communal nest would provide additional concentration of prey attractants. The use of microbiota is not without disadvantages, however, since a large prey input may not be adequately fed upon by the spiders resulting in a shift to bacterial growth and an ammonia-based odor. Under such conditions the colony must abandon the nest and start construction anew.

ACKNOWLEDGMENTS

This work was supported, in part, by a research grant from the National Science Foundation (BNS 79-10186 to W. J. T.). Specimens were collected during field expeditions funded by the National Geographic Society and the American Philosophical Society (grants to G. W. U.). We thank C. A. Meininger and M. J. Benton for assistance in the field, D. Fritz and M. Hodge for assistance in rearing spider colonies, M. Kaufman for SEM photography and preparation.

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AN ANALYSIS OF GEOGRAPHIC VARIATION IN THE *POGONOMYRMEX OCCIDENTALIS* COMPLEX (HYMENOPTERA: FORMICIDAE)[1]

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Introduction

While examining samples of *Pogonomyrmex* from southeastern Oregon, I encountered difficulty in segragating the two species reported as occurring in the area, *P. owyheei* Cole and *P. salinus* Olsen (Cole, 1968). Analysis of material from Oregon, Nevada and Utah suggested that the taxonomy of these two forms needed reevaluation. Smith (1953) considered them a single species, but this view was subsequently rejected by Cole (1968).

Cole (1963, 1968) described the *occidentalis* complex as composed of *P. owyheei* and *salinus,* together with *P. anzensis* Cole, *brevispinosus* Cole, *occidentalis* (Cresson), *subdentatus* Mayr and *subnitidus* Emery. MacKay (1980) described *P. montanus* from southern California, bringing the complex to a total of 8 species.

Within the *occidentalis* complex, the species *P. owyheei, salinus, occidentalis, subdentatus* and *montanus* form a distinct, plausibly monophyletic group, united by the cephalic sculpturing, configuration of the antennal scape base, and thoracic sculpturing. This group is referred to here as the *occidentalis* subcomplex. Because they do not possess this combination of characters, and because monophyly of the *occidentalis* complex as a whole is uncertain, *P. anzensis, brevispinosus* and *subnitidus* were excluded from this group and the present study.

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[1] Extracted from a thesis submitted to the University of Kansas in partial fulfillment of the degree of Master of Arts. Present address: Department of Entomology, University of California, Davis, CA 95616. Contribution number 1953 from the Department of Entomology, University of Kansas.

**Manuscript received by the editor February 8, 1987.*

MATERIALS AND METHODS

Lending museums and individuals are referred to by the following abbreviations:

AMNH	American Museum of Natural History, New York, New York.
LACM	Los Angeles County Museum of Natural History, Los Angeles, California.
MDPC	Mark B. DuBois, Washington, Illinois.
ORST	Oregon State University, Corvallis, Oregon.
UKS	University of Kansas, Lawrence, Kansas.
SSPC	Steven O. Shattuck, University of California, Davis, California.
UALB	University of Alberta, Edmonton, Alberta, Canada.
UCB	University of California, Berkeley, California.
UCD	University of California, Davis, California.
UCOL	University of Colorado Museum, Boulder, Colorado.
UIDM	University of Idaho, Moscow, Idaho.
UNSM	University of Nebraska State Museum, Lincoln, Nebraska.
USNM	United States National Museum, Washington, D.C.
UTST	Utah State University, Logan, Utah.
UWYL	University of Wyoming, Laramie, Wyoming.
WAST	Washington State University, Pullman, Washington.

ANALYSIS OF SPECIMENS

Every attempt was made to record character data on worker specimens from the entire range of each species and to represent all areas with roughly equal numbers of individuals. In some cases this meant ignoring specimens from densely collected areas, when other areas lacked sufficient samples for analysis. If a single nest was represented by many individuals, three individuals were selected at random and their characteristics recorded. Queens and males were not analyzed because they are poorly represented in collections. Specimens were examined with a dissecting microscope at 75× magnification. Measurements were made with an ocular micrometer and recorded to the nearest 0.01 mm. The collection sites for specimens studied are listed in Shattuck (1985).

THE *P. OCCIDENTALIS* SUBCOMPLEX

This group is characterized by the presence of punctures in the interrugal spaces of the head; spines or denticles on the propodeum; postpetiole with a rounded venter; occipital corners with regular, uniform rugae; and frontal lobes only slightly expanded laterally, with a thickened border. The 5 nominal species were examined to find characters that varied geographically within and/or between forms. While many such characters where found, only six varied consistently enough to be of value. Each character was divided into character states (except Scape Index, which was quantified). Since these characters were continuous, division into states was somewhat arbitrary. However, the large variation of each character and the limited number of states recognized in each allowed ready placement of most specimens. Before states were assigned, specimens were compared with "standard" specimens established for each character state. Specimens were initially identified using the concepts of Cole (1968). Many specimens had been previously determined by Cole (primarily from Cole's personal collection, now at LACM), and data were recorded using his identifications. Specimens not readily determined were recorded, but not utilized in the initial analysis. The characters are listed below by their abbreviations, followed by an explanation of the character and a list of the recognized states.

WORKER CHARACTERS AND CHARACTER STATES

Gaster: Base of the first gastric (fourth abdominal) tergum, near the insertion of the postpetiole, viewed dorsally.

1) Very shiny, with no sculpturing.
2) Very shiny, with faint reticulate sculpturing.
3) Shiny, with reticulate sculpturing.
4) Dull, with moderate reticulate sculpturing.
5) Dull, with heavy reticulate sculpturing.

PetDor: Dorsum of petiolar node viewed dorsally.

1) Entire surface covered with fine punctations, transverse rugae absent.
2) Anterior surface with fine punctations; 1 to 2 weak, transverse rugae superimposed over punctation on posterior quarter.

3) Anterior surface with fine punctations; 2 to 3 weak to moderate, transverse rugae superimposed over punctation on posterior quarter.
4) Anterior surface with fine punctations; 4 to 5 moderate, transverse rugae superimposed over punctation on posterior half.
5) Rugae (usually 6 to 7) superimposed over punctation on entire surface.

PpDor: Dorsum of postpetiolar node viewed dorsally.

1) Entire surface covered with fine punctations, transverse rugae absent.
2) Anterior surface with fine punctations; 1 to 2 light, transverse rugae superimposed over punctation on posterior quarter.
3) Anterior surface with fine punctations; 3 to 4 light, transverse rugae superimposed over punctation on posterior third.
4) Anterior surface with fine punctations; 5 to 6 moderate, transverse rugae superimposed over punctation on posterior half.
5) Rugae (usually 7 to 9) superimposed over punctation on more than half of surface.

PetVent: Lateral profile of anterior, ventral surface of petiolar peduncle with the petiole, postpetiole and gaster raised dorsally.

1) Tooth absent, entire profile smooth (Figs. 1 and 2).
2) Tooth absent, profile uneven (Figs. 3 and 4).
3) Tooth present but small or indistinct (Figs. 5 and 6).
4) Tooth distinct and moderately developed (Figs. 7 and 8).
5) Tooth well developed and broad (Figs. 9 and 10).
6) Tooth well developed, elongate and narrow (Figs. 11 and 12).

Scape: Base of the antennal scape in lateral view with the antennae parallel to and resting against the dorsal surface of the head.

1) Rounded; flange absent (Figs. 13 and 14).
2) Rounded; flange absent dorsally, but indicated laterally (Figs. 15 and 16).
3) Rounded; flange present, distinctly broader dorsally than ventrally (Figs. 17 and 18).
4) Angular; flange present, slightly broader dorsally than ventrally (Figs. 19 and 20).
5) Angular; flange present, uniform in thickness (Figs. 21 and 22).

SI: Scape Index (SL × 100) / (HW) where:

SL is the scape length (maximum length of the scape exclusive of the radicle).

HW is the head width (maximum width of the head in full face (dorsal) view, exclusive of the eyes).

Analysis of Character States

In this section the species concepts of Cole (1968) are maintained. Each character is considered separately by species, or pair of species where applicable. In the next section each species is considered individually and specific taxonomic changes proposed. Data are pooled and analyzed by county within each species or group of species. Figures 23 through 36 represent the character distribution data graphically. Each bar graph represents pooled data for one county, with the vertical axis representing frequency and the horizontal axis representing the character states (state 1 on the left, state 5 or 6 on the right). The number of specimens represented is indicated and each graph is located at the approximate center of the area pooled.

GASTER

Pogonomyrmex occidentalis possesses Gaster states 1, 2 and 3 (Table 1) distributed randomly, with all states occurring in all areas of the range in roughly equal proportions (Fig. 23).

Cole (1968) stated that in *P. salinus* the "base of dorsum of first gastric segment [is] frequently densely and coarsely punctate and opaque, sometimes only very finely punctate or densely shagreened and subopaque or shining," while for *P. owyheei* it is "as in *occidentalis*," which has "light to moderate shagreening which does not dull the shining surface". These characterizations were confirmed in the present study. The gaster of *P. salinus* may possess any of the states, with state 1 the least common and state 5 the most common (Table 1). In *P. owyheei,* most specimens possess states 1, 2 or 3, with states 4 and 5 represented in lower frequencies (Table 1). Thus while this character is of some value in distinguishing these two forms, there is frequent overlap with 80% of the *P. owyheei* and 44% of the *P. salinus* specimens showing Gaster states 2 or 3.

Table 1. Table of Character State Frequencies*

Character / State	Taxa				
Gaster	*P. mon*	*P. occ*	*P. owy*	*P. sal*	*P. sub*
1	0	36	10	3	24
2	50	62	54	22	51
3	50	2	26	22	24
4	0	0	2	12	0
5	0	0	8	42	0
PetDor					
1	0	12	19	2	6
2	0	37	26	8	0
3	0	37	32	6	26
4	0	11	9	16	8
5	100	4	14	69	59
PetVent					
1	0	21	43	29	2
2	50	44	33	27	6
3	50	17	19	20	9
4	0	12	2	13	9
5	0	3	3	11	28
6	0	2	0	2	46
PpDor					
1	0	74	52	13	16
2	0	22	28	11	10
3	0	2	13	38	43
4	0	1	2	14	12
5	100	0	5	25	18
Scape					
1	0	0	21	76	11
2	0	0	10	13	6
3	0	12	32	5	19
4	50	35	10	3	13
5	50	53	27	3	52
Sample Size:	4	343	261	148	128

*All values are percentages. Taxa abbreviations are: *P. mon* = *P. montanus, P. occ* = *P. occidentalis, P. owy* = *P. owyheei, P. sal* = *P. salinus, P. sub* = *P. subdentatus.*

The geographic distribution of this character supports Cole's (1968) northern limit for *P. salinus* as southern Oregon (Lake, Harney and Malheur counties), but indicates *P. owyheei* as occurring throughout Nevada and Utah (Fig. 24) rather than northern Nevada and Utah northward.

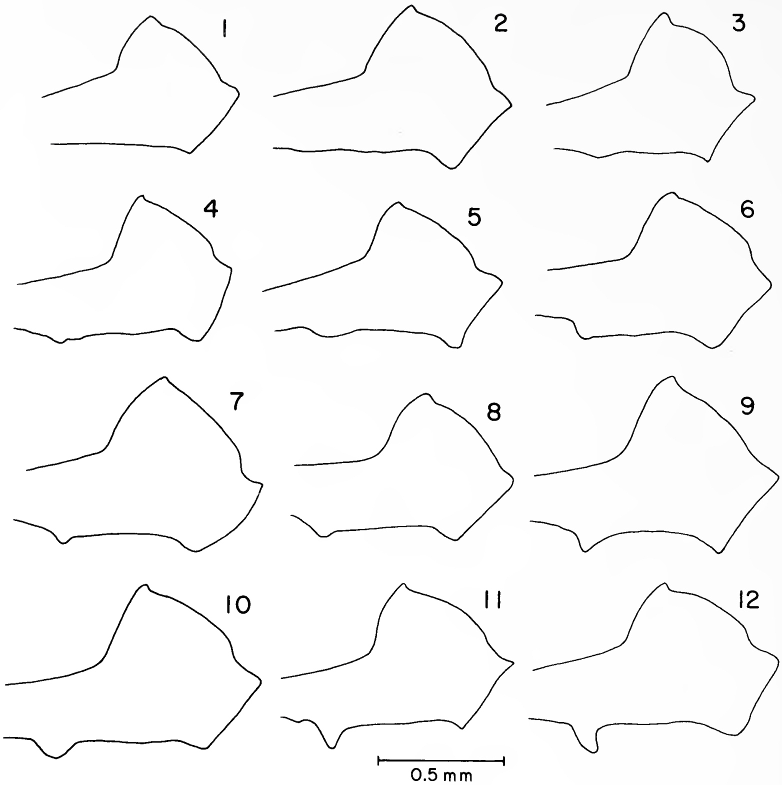
P. montanus has Gaster states 2 and 3 in equal proportions (Table 1), but shows no geographic pattern. *P. subdentatus* possesses states 1, 2 and 3, with state 3 the most common (Table 1); the states are distributed randomly throughout the range of the species.

DORSUM OF PETIOLE AND POSTPETIOLE (PETDOR AND PPDOR)

All character states of PetDor are represented in *P. occidentalis* (Table 1). The character PpDor is represented by states 1, 2, 3 and 4 (Table 1). Both of these characters show random geographic distribution; all states occur in all areas of the range of *P. occidentalis* (Figs. 25 and 26).

Cole (1968) described the dorsum of the petiolar and postpetiolar nodes of *P. salinus* as "generally covered with numerous, strong, wavy, closely spaced, subparallel, usually transverse rugae" (PetDor states 4 and 5; PpDor states 4 and 5). In *P. owyheei* he described these structures as "not covered with numerous, strong, wavy, closely spaced, subparallel, transverse rugae, the nodes with or without irregular rugae, rugulae or striae" (PetDor states 1, 2 and 3; PpDor states 1 and 2). In this study all states of PetDor and PpDor were found to occur in both *P. salinus* and *P. owyheei* (Table 1) in frequencies which agree loosely with Cole's (1968) descriptions of these species. *P. salinus* possesses primarily PetDor states 4 and 5 (85%), but substantial numbers have states 1 and 2 (10%). Similarly, PpDor states 4 and 5 occur in 39% of the specimens, but states 1 and 2 occur in 24%. In *P. owyheei,* PetDor states 1, 2 and 3 account for 77% of the specimens, but states 4 and 5 occur in 23%. PpDor states 1 and 2 are represented in 80% of the specimens, while states 4 and 5 are only found in 7%. The broad overlap in the states of these characters makes them of limited value in discriminating these forms.

The geographic distribution of the states of these characters shows a pattern similar to that of the Scape states: decreasing frequencies of states 1 and 2 and increasing frequencies of states 4 and 5 from north to south, with a broad area of overlap from central Oregon into northern Nevada (Figs. 27 and 28). PpDor state 1 is found as far south as Washington County, Utah (100%), while state 5 occurs only as far north as Harney and Lake counties, Oregon



Figs. 1–12, states for ventral surface of petiolar peduncle (PetVent). Fig. 1, state 1 (*P. salinus,* 17 mi S. Eureka, Eureka Co., Nevada). Fig. 2, state 1 (*P. salinus,* Lovelock, Pershing Co., Nevada). Fig. 3, state 2 (*P. salinus,* Aurora, Mineral Co., Nevada). Fig. 4, state 2 (*P. salinus,* Reno, Nevada). Fig. 5, state 3 (*P. salinus,* 6 mi E Wells, Elko Co., Nevada). Fig. 6, state 3 (*P. subdentatus,* Gonzales, Monterey Co., California). Fig. 7, state 4 (*P. salinus,* Wabuska, Lyon Co., Nevada). Fig. 8, state 4 (*P. subdentatus,* Russell Reservation, Contra Costa Co., California). Fig. 9, state 5 (*P. subdentatus,* 18 mi S. Ravendale, Lassen Co., California). Fig. 10, state 5 (*P. salinus,* Lovelock, Pershing Co., Nevada). Fig. 11, state 6 (*P. subdentatus,* Santa Cruz Island, Santa Barbara Co., California). Fig. 12, state 6 (*P. subdentatus,* Gonzales, Monterey Co., California).

(16% and 14% respectively). PetDor state 1, however, occurs only as far south as Lassen County, California (33%) and Elko County, Nevada (9%), while state 5 extends northward into Lake (33%), Harney (28%) and Malheur (20%) counties, Oregon, and Elmore

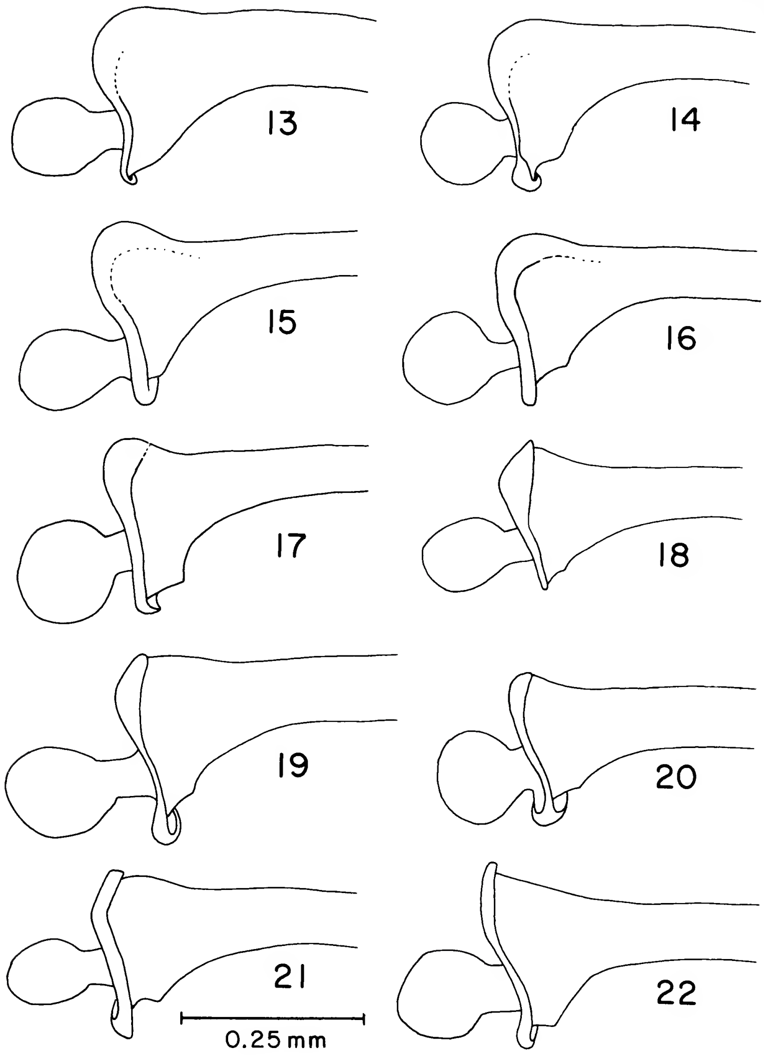
County (33%), Idaho. Thus neither of these characters fully supports the distributional boundaries of *P. salinus* and *P. owyheei* cited by Cole (1968): PetDor indicates the northern extent of *P. salinus* as central Oregon rather than southern Oregon, while the southern boundary of *P. owyheei* (northern California and Nevada) is supported; PpDor supports the northern extent of *P. salinus* as southern Oregon but indicates *P. owyheei* as occurring throughout Nevada rather than limited to the northern portions.

All specimens of *P. montanus* have PetDor state 5 and PpDor state 5 (Table 1), thus showing no geographic variation. *P. subdentatus* does show variation in these characters, with PetDor states 1, 3, 4 and 5 represented as well as all PpDor states (Table 1). However, this variation is distributed randomly throughout the range of the species (Figs. 29 and 30).

VENTER OF PETIOLAR PEDUNCLE (PETVENT)

In *P. occidentalis,* all states of PetVent are represented (Table 1). This agrees with the findings of Cole (1968), except for the presence of a prominent process (states 5 and 6) in 24% of the specimens from Dawson, Roosevelt and Rosebud counties, Montana.

Pogonomyrmex owyheei possesses the first five states of PetVent in decreasing frequency and lacks the sixth state (Table 1). *P. salinus* shows a similar trend, but possesses all states (Table 1) and a higher proportion of individuals with higher states. *P. subdentatus* has all states represented but in increasing frequency from state 1 to state 6 (Table 1). The presence of a large process on the venter of the petiolar peduncle is often used as a diagnostic character for *P. subdentatus* (Creighton, 1950; Cole, 1968) and the presence of states 4, 5 and 6 in populations of *P. salinus* in western Nevada may indicate gene flow between these two species. States 4, 5 and 6 occur in *P. salinus* only in or near areas containing populations of *P. subdentatus* (south central Oregon, western Nevada), while in all other areas *P. salinus* exhibits states 1, 2 or 3 (Fig. 31). Other characteristics of *P. subdentatus* (cephalic sculpturing, propodeal spine development, thoracic profile) do not appear in western Nevada populations of *P. salinus,* indicating only limited or no gene flow between *P. salinus* and *P. subdentatus.* There is a weak trend for state 1 to increase and states 2 and 3 to decrease as one moves outward from northwestern Nevada.



Figs. 13–22, states for base of antennal scape (Scape). Fig. 13, state 1 (*P. salinus*, 2 mi N Montello, Elko Co., Nevada). Fig. 14, state 1 (*P. salinus*, Sulphur, Humboldt Co., Nevada). Fig. 15, state 2 (*P. salinus*, T14N R6E, White Pine Co., Nevada). Fig. 16, state 2 (*P. salinus*, T18N R64E, White Pine Co., Nevada). Fig. 17, state 3 (*P. salinus*, Raft River Narrows, Cassia Co., Idaho). Fig. 18, state 3 (*P. salinus*, Montgomery Pass, Mineral Co., Nevada). Fig. 19, state 4 (*P. subdentatus*, Davis, Yolo Co., California). Fig. 20, state 4 (*P. salinus*, Kelton Junction, Box Elder Co., Utah). Fig. 21, state 5 (*P. subdentatus*, 18 mi S Ravendale, Lassen Co., California). Fig. 22, state 5 (*P. occidentalis*, Ogden, Weber Co., Utah).

Pogonomyrmex montanus was found to possess states 2 and 3 in equal proportions, a finding which agrees with the original description (MacKay, 1980).

SCAPE

The scape base of *P. occidentalis* varies from state 3 to state 5 (Table 1) but shows no geographic pattern, with the states occurring in all parts of the range in roughly equal proportions (Fig. 32). This agrees well with the observations of Cole (1968), although he did not recognize the extent of the variation.

All Scape states occur in *P. subdentatus* (Table 1). States 1 and 2, and 90% of the state 3 records occur in western Nevada; state 4 occurs equally in California and Nevada, and state 5 occurs primarily in California and Oregon, with a few (14%) records from Nevada (Fig. 33). Cole (1968) asserted that the scape base of *P. subdentatus* is equivalent to state 5, and distinct from that of *P. salinus.* This observation was apparently in error because some specimens found to have states 1 and 2 in this study were determined by Cole as *P. subdentatus* (specimens now in LACM).

Cole (1968) describes the scape base of *P. salinus* as "evenly and broadly rounded", while that of *P. owyheei* is "not evenly and broadly rounded." Cole's figures show the scape base of *P. salinus* as evenly rounded dorsally, without any trace of a basal flange, while that of *P. owyheei* has a distinct basal flange dorsally. Two aspects of this character are inconsistent with these statements. First, the geographic distributions of these character states are not concordant with the geographic distribution of the species supposed to possess them; and second, material determined by Cole (from LACM) does not always possess the appropriate states.

The geographic distribution of these character states does not agree with the distribution of *P. owyheei* and *P. salinus* as stated by Cole (1968). Scape state 1 (indicative of *P. salinus*) occurs primarily in Nevada, but has also been found at Twin Falls, Montana; Redmond, Cline Falls State Park, Summer Lake, and Hermiston, Oregon; and Burlington and Greybull, Wyoming (Fig. 34). Scape state 5 (indicative of *P. owyheei*) occurs in all areas expected except the northwestern portions of its range (Washington, British Columbia) where only Scape state 3 occurs. Scape state 5 occurs outside the putative range of *P. owyheei* at a site 3 miles southeast of Rowland, Nevada; at Bridgeport, California; and at several localities in Washington County, Utah. This would indicate that *P. salinus* extends north into central Oregon (Lake and Deschutes counties) with small populations farther north and east, while *P. owyheei* has populations in eastern California (Lassen and Mono counties) and southwestern Utah (Washington County).

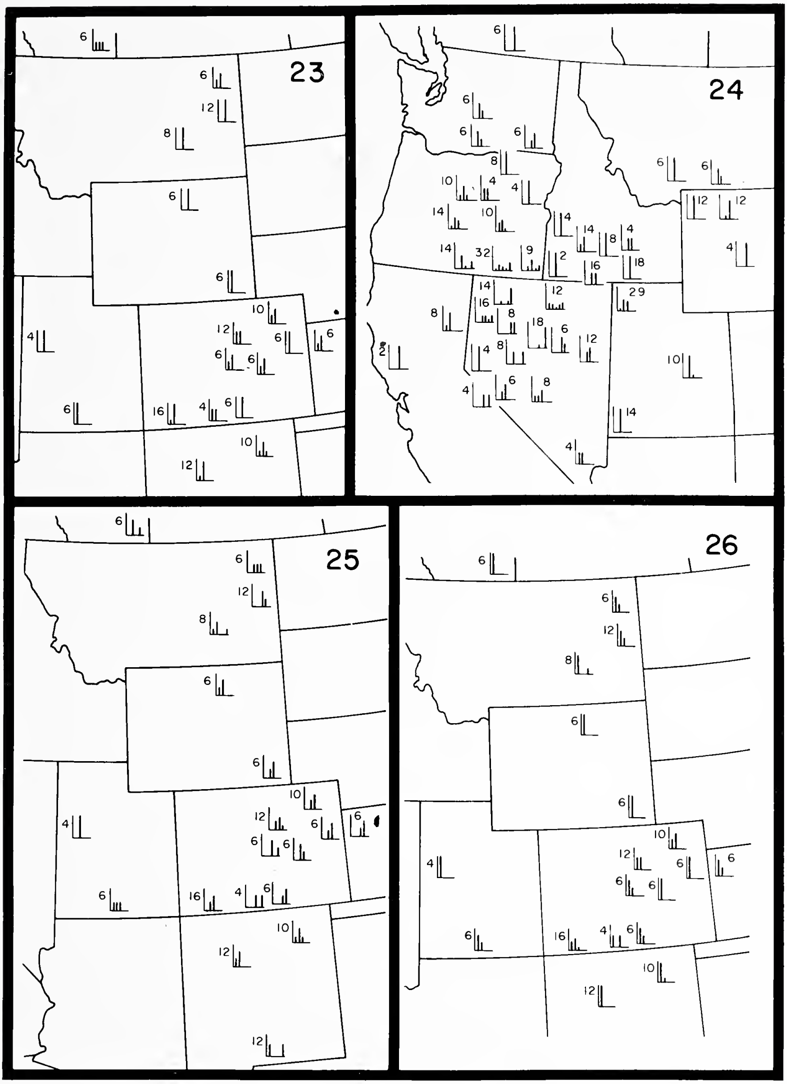
The second inconsistency involves specimens determined by Cole. Numerous specimens with Scape state 1 were determined as *P. owyheei* by Cole. These were collected in Nevada (Elko and Washoe counties), Oregon (Harney and Umatilla counties), and Wyoming (Big Horn County). Scape state 5 was found in two nest series determined as *P. salinus* by Cole from northern California (11.5 miles south of Termo and 18 miles south of Ravendale, Lassen County). These determinations show that Cole either allowed considerable variation in this character, or utilized other characters (alone or in combination) to identify these forms.

The *P. montanus* collections show no geographic variation in this character.

SCAPE INDEX (SI)

The SI of *P. occidentalis* varies from 65 to 78, with a mean of 66.9. It shows a weak cline, with low values in the eastern part of the range (Colorado, Kansas) and high values in the western portions (Utah, Nevada) (Fig. 35).

Cole (1968) found the SI of *P. owyheei* to vary from 83.0 to 100.0, while that of *P. salinus* varied between 83.5 and 84.0. A random sample of material determined by Cole (from LACM) was measured, and the SI varied from 69.0 to 79.0 (mean = 73.8, sd. = 2.20, n = 32) in *P. owyheei* and 70.0 to 84.0 (mean = 76.1, sd. = 3.18, n = 33) in *P. salinus*. The discrepancy between these measurements and those of Cole (1968) may be caused by differences in measurement techniques. Cole's range of SI values was greater for *P. owyheei* than for *P. salinus,* while material now available shows the opposite. This may be due to a small sample of *P. salinus* in Cole's study. Although the broad overlap in the ranges of SI values makes this character of little value in discriminating the taxa, the means are significantly different (t = 3.35, p = 0.0014).



Figs. 23–26, distribution of character states. Fig. 23, Gaster states for *P. occidentalis.* Fig. 24, Gaster states for *P. salinus* and *P. owyheei.* Fig. 25, PetDor states for *P. occidentalis.* Fig. 26, PpDor states for *P. occidentalis.*

Geographically, this difference may be explained by the presence of large scape values in southern Nevada (Fig. 36). Over the northern portions of the range of these two forms the SI values vary between 70 and 82, with a mean of 74.2, while in the southern portions (Clark, Eureka, Nye, White Pine counties, Nevada, and Mono County, California) SI varies from 74 to 84, with a mean of 77.8. This trend, however, is weak with large SI values occurring in some northern populations (i.e. SI = 82 in Lake County, Oregon) and small values in some southern populations (SI = 66 in Washington County, Utah).

TAXONOMIC CONCLUSIONS

P. montanus MacKay

P. montanus MacKay, 1980: 151 (W, M, F). Type Loc.: Hanna Flat, 4 km NW Fawnskin, San Bernardino Co., California, USA.

P. montanus is known only from the San Bernardino Mountains of southern California. It is retained as a full species in this study.

P. occidentalis (Cresson)

Myrmica occidentalis Cresson, 1865: 426 (W, F). Type Loc.: Colorado Territory, USA.

Myrmica seminigra Cresson, 1865: 427 (M). Type Loc.: Colorado Territory, USA. (Synonymy by Forel, 1886: 42.)

P. opaciceps Mayr, 1870: 971 (W). Type Loc.: New Mexico, USA. (Synonymy by Forel, 1886: 42.)

P. occidentalis ruthveni Gaige, 1914: 93 (W, M, F). Type Loc.: James Canyon, Elko Co., Nevada, USA. (Synonymy by Olsen, 1934: 507.)

P. occidentalis utahensis Olsen, 1934: 509 (W, M, F). Type Loc.: Zion National Park, Utah, USA. (Synonymy by Cole, 1968: 95.)

P. occidentalis may be separated from all other species in the complex by the offset tooth at the basal angle of the mandible. As demonstrated by Colley (1962), all other known characters occur in *P. owyheei,* as well as *P. salinus,* and are of no value in distinguishing this species. In no case did I find intermediate specimens between this species and *P. owyheei* or *P. salinus,* contrary to the findings of Allred (1982). The characters used in this study further support the distinctness of this species. The characters Gaster, PetDor, PpDor and Scape show a moderate degree of variation, but a random geographic distribution. This differs from closely related species in which clines are seen in many of these characters. Since there is a broad region of overlap (western Utah, Nevada, eastern California) of *P. occidentalis* and several other species, interbreeding would be expected to produce clinal patterns in both species involved. This was not observed in regions where *P. occidentalis* and related species are sympatric.

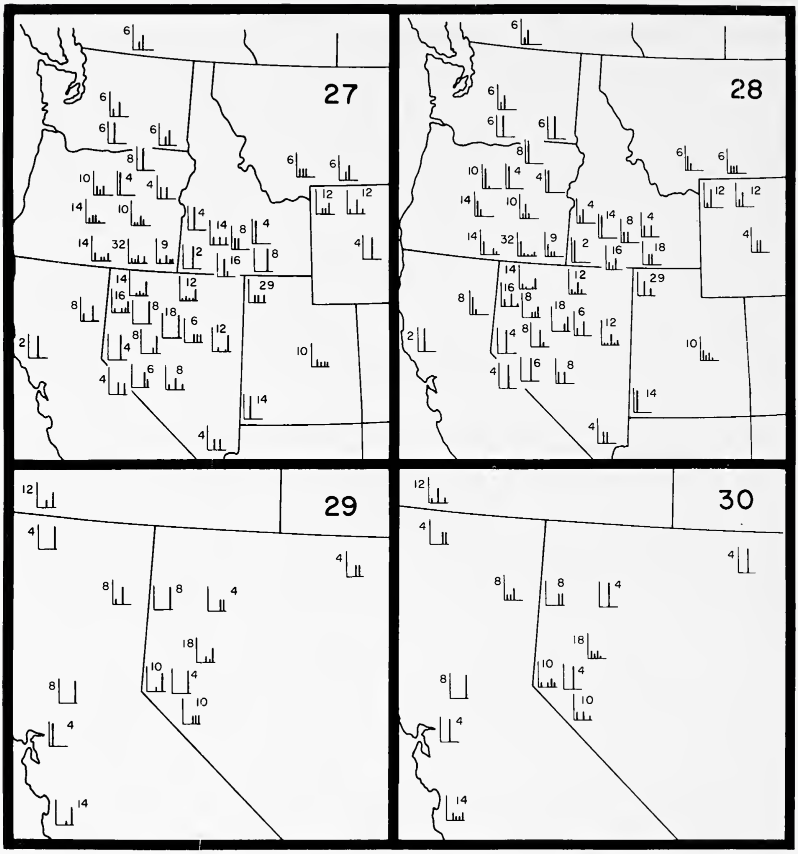
P. salinus Olsen

P. salinus Olsen, 1934: 510 (W). Type Loc.: near Soda Springs, Bridgeport, Mono Co., California, USA.

P. occidentalis owyheei Cole, 1938: 240 (W, F). Type Loc.: Indian Cove, near Hammett, Elmore Co., Idaho, USA. (New Synonymy)

Cole (1968) considered *P. owyheei* and *P. salinus* as distinct species and gave little discussion to the matter. The present study shows that many characters have clinal patterns not in support of Cole's view. The gaster shows a clinal pattern with smooth states (1 and 2) in the north and smooth and rough states (3, 4 and 5) in the south. This partly supports the distinctness of *P. salinus* by limiting it to the southern portions of the range, but does not support the notion that *P. owyheei* occurs only in the north. PpDor shows a similar clinal pattern, with greater variation in the southern portions of the range and less variation in the north. PetDor differs from both of these characters in that it shows *P. salinus*-like states as occurring north into central Oregon, while *P. owyheei*-like states do not occur south of northern Nevada. The scape also incorrectly indicates the distributions of these two forms. As determined by the shape of the scape, *P. salinus* would extend northward into central Oregon, while *P. owyheei* would extend southward into east-central California and southern Utah.

Many specimens determined by Cole (primarily in LACM) suggest that color and distribution played a role in his actual determinations: dark specimens from southern areas were identified as *P. salinus* while light-colored individuals from northern areas were identified as *P. owyheei.* Since color is somewhat subjective and difficult to quantify I made no attempt to do so but did record it while making determinations. Cole (1968) mentioned color in his treatment of these species but did not use it as a distinctive character in his keys or discussion.



Figs. 27–30, distribution of character states. Fig. 27, PetDor states for *P. salinus* and *P. owyheei.* Fig. 28, PpDor state for *P. salinus* and *P. owyheei.* Fig. 29, PetDor states for *P. subdentatus.* Fig. 30, PpDor states for *P. subdentatus.*

It is clear that *P. owyheei* represents northern populations of a single, variable species and is therefore a synonym of *P. salinus.* As can be seen from Figures 24, 27, 28, 31, 34 and 36, there are no distinct and consistent steps in the clines of the characters studied. This makes the recognition of subspecies difficult and of little value in this species.

P. subdentatus Mayr

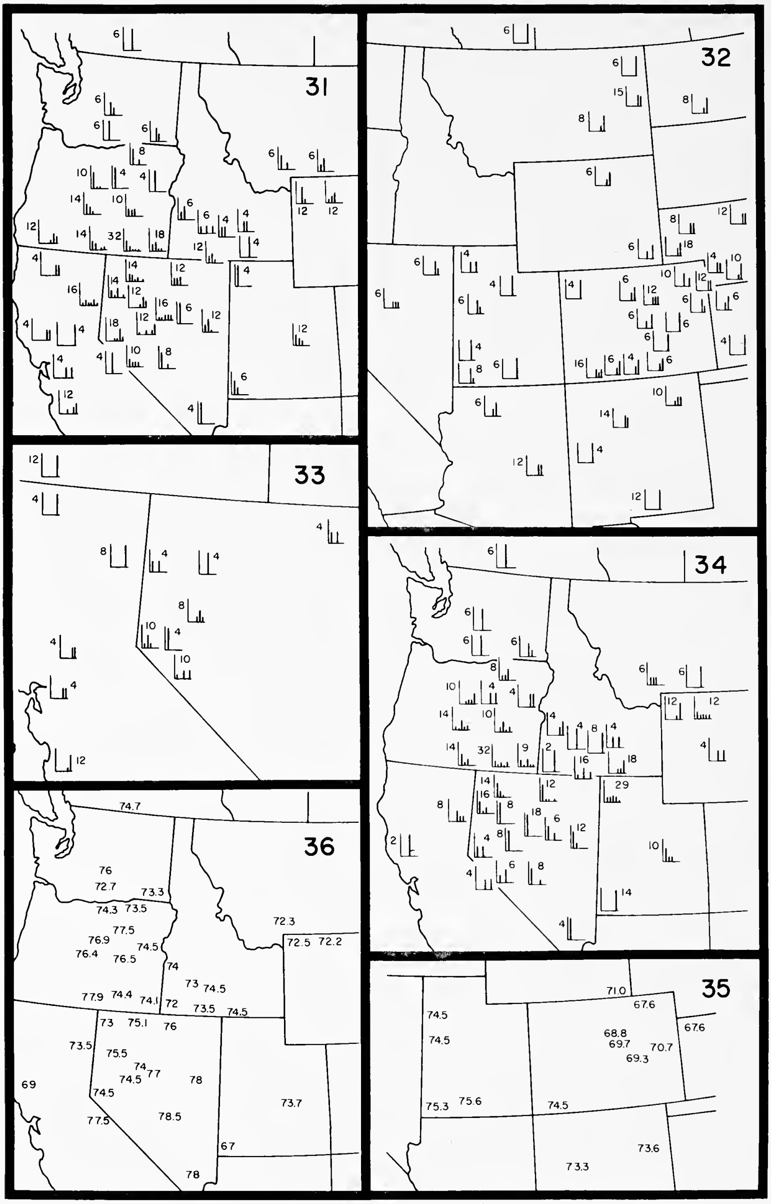
P. subdentatus Mayr, 1870: 971 (W). Type Loc.: California, USA.

P. subdentatus has been considered a full species since its original description. The usual characters given for its identification are the presence of a ventral process on the petiolar peduncle (Creighton, 1950), the arched profile of the thoracic dorsum and the cephalic sculpturing (Cole, 1968). The cephalic sculpturing shows only a small amount of variation among the species and has not been used in the present study. The process on the venter of the petiolar peduncle shows variation within and between species and was quantified as character PetVent. The arched profile of the alitrunk is unique to *P. subdentatus.*

The presence of a process on the venter of the petiolar peduncle and Scape states 1 and 2 in *P. subdentatus* and sympatric populations of *P. salinus* may cause confusion of some samples of these species, but the arched thoracic dorsum and reduced propodeal spines are characteristic of *P. subdentatus.* The presence of a PetVent process and Scape states 1 and 2 in some sympatric populations of *P. salinus* may indicate gene flow between these two species, but the lack of other characters of *P. subdentatus* in these populations distinguishes the species clearly and suggests no gene flow between them. Further study will be necessary to resolve this inconsistency.

KEY TO THE SPECIES OF THE *POGONOMYRMEX OCCIDENTALIS* COMPLEX, Based on Workers.

1a. Mandible with 6 teeth; venter of postpetiole with a strong, triangular tooth .... *P. anzensis*
1b. Mandible with 7 teeth; venter of postpetiole rounded, without a tooth-like process 2
2a. Interrugal spaces of head smooth and shiny, without punctation; dorsum of petiolar node without transverse rugae .... *P. subnitidus*
2b. Interrugal spaces of head densely punctate and opaque, with a beaded appearance; dorsum of petiolar node variable, but often with at least 1 ruga present posteriorly..............3



Figs. 31-36, distribution of character states. Fig. 31, PetVent states for *P. salinus, P. owyheei* and *P. subdentatus.* Fig. 32, Scape states for *P. occidentalis.* Fig. 33, Scape states for *P. subdentatus.* Fig. 34, Scape states for *P. salinus* and *P. owyheei.* Fig. 35, SI values for *P. occidentalis.* Fig. 36, SI values for *P. salinus* and *P. owyheei.*

3a. Propodeal spines absent or, if present, shorter than the distance between their bases; venter of petiolar peduncle smooth, without a process; frontal lobes expanded laterally, without a thickened border .... *P. brevispinosus*

3b. Propodeal spines distinctly longer than the distance between their bases or, if shorter or absent, then venter of petiolar peduncle may possess a broad and short to narrow and long process; frontal lobes slightly expanded laterally, with a thickened border (*occidentalis* subcomplex) 4

4a. Basal tooth of mandible offset, causing basal margin of mandible to form an angle medially .... *P. occidentalis*

4b. Basal tooth of mandible not offset, basal margin of mandible even over its entire length..............................5

5a. Propodeal spines absent or, if present, distinctly shorter than the distance between their bases; thoracic profile arched, with an angle present near the mesopropodeal suture; majority of workers from a given nest series with a well developed process or tooth on the venter of petiolar peduncle .... *P. subdentatus*

5b. Propodeal spines longer than the distance between their bases or, if shorter, then without a process or tooth on the venter of the petiolar peduncle; thoracic profile flat, without an angle near the mesopropodeal suture; venter of the petiolar peduncle generally without a process (present in some populations from western Nevada and eastern California)..................6

6a. Base of antennal scape angular, with flange present, and dorsum of petiolar and postpetiolar nodes with 5 or more moderate to heavy rugae superimposed over punctations on posterior half. (Known only from the San Bernardino Mountains of California) ....*P. montanus*

6b. Base of antennal scape rounded or angular; if angular, then dorsum of petiolar and postpetiolar nodes with less than 5 moderate rugae on posterior half. (Widespread)............ .... *P. salinus*

SUMMARY

The *occidentalis* subcomplex of *Pogonomyrmex* is defined as a subgroup of Cole's (1968) "*occidentalis* complex," consisting of five nominal species. Six taxonomically significant morphological characters are quantified and recorded from throughout the ranges of

each species. The character states are mapped to reveal clinal patterns and this information is used to help with systematic decisions.

P. occidentalis differs from all others in the subcomplex by its unique mandibular structure. The states of 5 of 6 characters studied show random geographic distribution and are of no value in differentiating this species from others. *P. owyheei* is a synonym of *P. salinus* (new synonymy). No single character or combination of characters could be found to separate these two forms. *P. subdentatus* possesses several unique, although subtle, characters and is retained as a full species. *P. montanus* is also maintained as a full species.

ACKNOWLEDGMENTS

I wish to thank Dr. Charles D. Michener for his assistance and guidance during this research. I also thank Drs. G. W. Byers, P. D. Ashlock and P. S. Ward for comments on the manuscript. The constant support and encouragement of M. K. Smith is gratefully acknowledged. Publication costs were provided in part by the Department of Entomology, University of California, Davis.

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A NEW GENUS OF AGENIELLINI FROM CENTRAL AMERICA (HYMENOPTERA: POMPILIDAE: PEPSINAE)*

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The spider wasp tribe Ageniellini is a diverse and successful group in the new world. The Nearctic species are assignable to three genera, *Phanagenia* Banks, 1933, *Auplopus* Spinola, 1841 and *Ageniella* Banks, 1912. None of these genera is restricted to the Nearctic Region.

Phanagenia comprises African and Oriental species as well as a single Nearctic representative. *Auplopus* is cosmopolitan with a number of species in temperate and tropical America. *Ageniella* is restricted to the New World. It is the largest genus of the tribe in North America with thirty-six species reported from north of the Mexican border. The Nearctic species of *Ageniella* have been placed in four subgenera (Townes, 1957) and the Neotropical species in seven, four of them confined to the neotropics (Evans, 1973). I do not consider the subgenus *Ameragenia* with representatives in extreme southern Texas and Florida to be a Nearctic element. Although figures are not available, there are probably more species in the Central and South American segment of the *Ageniella* fauna than in the North American.

In addition to *Auplopus* and *Ageniella* there are five additional genera in the neotropics, *Phanochilus* Banks, 1944, *Priocnemella* Banks, 1925, *Mystacagenia* Evans, 1973, *Dimorphagenia* Evans, 1973 and the genus described below, which are all apparently confined to that region.

An explanation of the abbreviations used in the following descriptions is given by Wasbauer and Kimsey (1985:4) and is summarized here.

**Manuscript received by the editor March 25, 1987.*

FD—facial distance. The length of the head in full frontal view, from the crest of the vertex to the apex of the clypeus.
LID—lower interocular distance. The minimum distance between the lower margins of the compound eyes.
MID—middle interocular distance. The maximum distance between the inner margins of the compound eyes.
OOL—ocellocular length. The minimum distance between the outer margin of the lateral ocellus and the inner margin of the compound eye.
POL—postocellar length. The minimum distance between the inner margins of the lateral ocelli.
TFD—transfacial distance. The maximum distance across the head from the outer margin of one compound eye to the outer margin of the other.
UID—upper interocular distance. The minimum distance between the upper margins of the compound eyes.

Atopagenia Wasbauer, new genus

Female. Large wasps, the size of small *Pepsis.* Head (fig. 1) with clypeus very long and wide, extending laterally well under compound eyes, anterior margin strongly gibbous; malar space well developed; apex of mandibles broad, tridentate (including apical cusp); mentum with a number of long, slender, dark hairs; palpi long, maxillary palpi extending beyond apex of anterior coxa; labrum not exposed in anterior view, its apex truncate; occipital carina extending dorsally onto vertex in a short loop. Mesosoma with disc of pronotum gently sloping anteriorly to a small, rounded, median dorsal projection; postnotum scarcely developed, very short, not expanded at midline; mesosternum with posterior carina sharply angled laterally; wings long, extending beyond apex of metasoma, anterior wing with marginal and submarginal cells approaching wing apex; first recurrent vein meeting second submarginal cell close to its apex; posterior wing with anal vein in an even curve, meeting discoidal vein beyond origin of cubitus; tibial spurs short, those at apex of posterior tibia of nearly equal length; anterior tibia without noticeable spines except short, slender spines at apex, without stout, curved spine at outer apex; posterior tibia smooth with unbroken dorsal carina extending nearly to apex; posterior basitarsi somewhat arched dorsally; distitarsi without ventral spines; claws toothed. Metasoma with first segment of typical agenioid form in dorsal view, sides concave, expanded at insertion on mesosoma, in lateral view without a suture separating an epipleurum; second sternum with transverse suture in extreme anterior position, connate medially with posterior margin of first sternum; pygidial area undifferentiated, dull, densely clothed with long, uniformly fine setae.

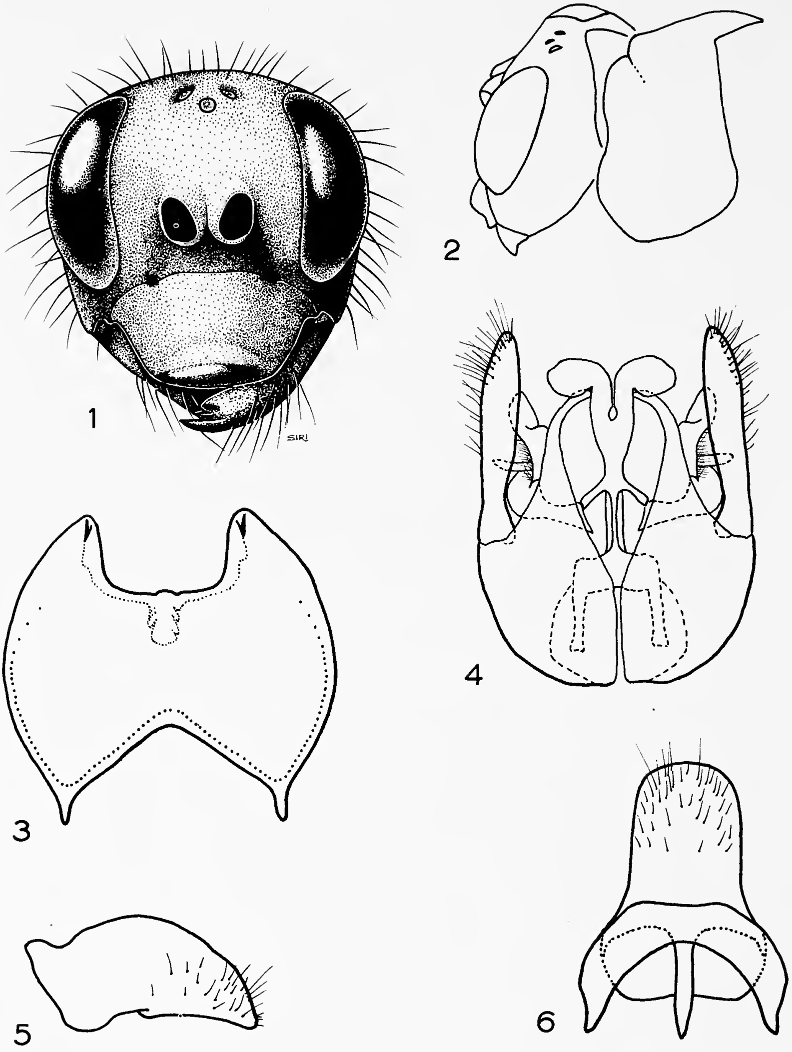
Male. Similar to female in most details, but head with clypeus and occipital carina unmodified; apex of labrum exposed in frontal view; mandibles slender, bidentate; anterior tibial spur barely exceeding apex of tibia; anterior and middle legs with distitarsi longer than preceding three segments taken together. Metasoma with first sternum convex; second sternum swollen anteriorly, swelling bordered posteriorly by curved, deeply impressed transverse groove; apical margin of sixth sternum (fig. 3) with large, rectangular emargination and paired apical spines; genitalia (fig. 4) with aedeagus bearing pair of accessory apodemes; basal hooklets single.

Type species. Atopagenia menkei Wasbauer, new species.

Etymology. Gr.: Atopos—odd or strange; agenia—beardless.

Atopagenia menkei Wasbauer, new species.

Holotype female. Black with faint blue to violet reflections imparted by appressed pubescence; small spots under compound eyes, apex of clypeus and apex of mandibles, ferrugineous. Length 29 mm. Anterior wing length 31 mm; both pairs uniformly dark to apex with strong violaceous reflections. Erect hair black, long, fine and abundant over most of body, absent on following areas: mesonotum, except for a few scattered hairs anteriorly, femora dorsally, anterior and middle tibiae and tarsi, the latter with a few short hairs dorsally, first metasomal tergum except at apex. Appressed pubescence dense, fine and dark on head and mesosoma, imparting a dull, velvety appearance, more dilute on somewhat shining metasoma. Head (fig. 1) rounded, about as wide as long, FD/TFD 1.05; ocelli forming a compact right triangle, laterals much closer to each other than to compound eyes, POL/OOL 0.57; front moderately narrow, MID/TFD 0.56; compound eyes nearly parallel, LID/UID 0.95; length of clypeus 0.59 times its width, apical margin strongly convex; length of malar space 0.56 width of mandible at base; antennae very long, slender, third segment 10.8 times as long as



Figs. 1–6. *Atopagenia menkei,* n. sp. Figs. 1–2. Holotype female. Figs. 3–6. Allotype male. Fig. 1. Head, anterior view. Fig. 2. Outline of head and pronotum, oblique lateral view. Fig. 3. Sixth metasomal sternum, ventral view (not flattened, vestiture omitted). Fig. 4. Genitalia, dorsal view. Fig. 5. Left gonostylus, lateral view. Fig. 6. Subgenital plate, ventral view.

wide, 1.43 times UID, apical segment 9.4 times as long as wide. Pronotum (fig. 2) with collar not much below level of disc, separated from anterodorsal projection by short concave face, posterior margin broadly angulate; mesepisternum not produced; propodeum short, slope even from front to rear, faintly striate with shallow median sulcus anteriorly; area laterad of spiracle produced into distinct tubercle; posterior tibiae and tarsi very hairy; brush on inner side of hind tibia complete, broad at base, narrowed toward apex; distitarsi very long, length of posterior distitarsus (excluding claws) 3.9 times its apical width; tarsal claws large with small, erect, basal tooth; anterior wing with stigma small; marginal cell 5.4 times as long as high, 0.38 times its length from apex of wing; third submarginal cell 2.12 times as high at apex as at base, 1.19 times as long as second submarginal, measured on cubitus; third transverse cubital vein curved before junction with cubitus; transverse median vein meeting media 0.46 of its length distad of basal vein; second recurrent vein meeting third submarginal cell at about middle and joining subdiscoidal vein 0.77 times the distance from base of discoidal to its intersection with wing margin.

Allotype male. Similar to female in color and pilosity, but without ferrugineous spots on face and clypeus. Length 18.0 mm. Anterior wing 18.3 mm. Head thin, temples not developed, slightly wider than long, FD/TFD 0.89; ocelli in a compact triangle, POL/OOL 0.56, posterior ocelli in a line with posterior corners of compound eyes; MID/TFD 0.62; compound eyes nearly parallel as in female; length of clypeus 0.49 times its width, apical margin slightly convex; antennae long and slender, third segment 6.25 times as long as wide, 1.10 times UID, apical segment 8.3 times as long as wide. Pronotum and mesepisternum as in female; postnotum short, 0.35 times as long as metanotum, transversely striate; propodeum less strongly curved, but striate as in female; wing color and venation as in female; posterior tibia and tarsi not hairy; tibia with unbroken dorsal carina as in female, but with dorsal row of slender curved spines; tarsal segments, except distitarsus laterally compressed, distitarsi long, that of posterior leg 5.3 times as long as apical width. Sixth metasomal tergum large; subgenital plate (fig. 6) broad, ligulate, flat, rounded at apex; genitalia with gonostylus attenuate at apex (fig. 5); parapenial lobes strongly curved toward midline; aedeagus expanded beyond middle and produced into pair of large, flattened, horizontal lobes at apex (fig. 4).

Type material. Holotype female (LACM): Costa Rica: Golfito, August 21, 1957 (Arnold Menke). Allotype male (LACM) and paratypes (1 female, 3 males, USU and author's collection): Panama: Canal Zone: Gamboa, 5 mi SE, March 1, 1959 (W. J. Hanson). According to Mr. Hanson's field notes, the allotype and paratypes were collected near a military access road through an area of rain forest which had been cut over, but had developed a subsequent overstory.

Remarks. Atopagenia appears to be only distantly related to other genera in the Ageniellini. The form of the female occipital carina and the pronotum of both sexes apparently is apomorphic in the tribe. There are at least some similarities to the Old World genus *Macromeris* in size, color and pilosity (especially of the legs), presence of a definite malar space, long antennae and retention in the male of the transverse groove on the second sternum. Other fundamental features of *Macromeris* are quite different, however. The first metasomal segment has a suture separating an epipleurum, the transverse groove on the second sternum of the female is not in an extreme anterior position, the anal vein of the posterior wing is strongly recurved, the pygidium of the female is noticeably differentiated, nearly bare and the basal hooklets of the male genitalia are double.

Because of the densely hairy ultimate tergum of the female, it is unlikely that *Atopagenia menkei* constructs cells of mud or similar materials as do females of at least some species of *Macromeris* and *Auplopus* (Williams, 1919: 79), but one is tempted to speculate that the unusual modification of the occipital carina and pronotum are adaptations for prey capture in confined situations.

Acknowledgements. I wish to express my thanks to Mr. Roy R. Snelling, Los Angeles County Museum (LACM) and to Dr. Terry Griswold, USDA, ARS, Logan, Utah for providing the material used here. Thanks are also due Mr. William J. Hanson, Department of Biology, Utah State University, Logan (USU) for providing notes on the Panama locality. Mr. Michael C. Day, Department of Entomology, British Museum (Natural History), London, kindly compared specimens with Cameron's material in the British Museum. Drs. Howard E. Evans, Colorado State University, Ft. Collins and Lynn S. Kimsey, University of California, Davis reviewed and made suggestions on the manuscript. In addition, Dr. Kimsey executed one of the drawings (fig. 1).

SUMMARY

A new genus and species of spider wasp, *Atopagenia menkei* is described in the pepsine tribe Ageniellini based on both sexes from Costa Rica and Panama. A brief discussion is given of the other new world genera in the tribe.

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THREE NEW MEGALYRIDS FROM SOUTH AMERICA (HYMENOPTERA: MEGALYRIDAE)*

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Introduction

The neotropical Megalyridae are very rare and virtually unstudied. Some confusion has resulted over the classification of *Iseura* Spinola, which was based on a single specimen from Brazil (Spinola 1853). Although the wasp is actually a cenocoeline braconid, it was incorrectly classified as a megalyrid by Dalla Torre (1900). This error was perpetuated by subsequent authors (Froggatt 1906, Fahringer 1928, Hedqvist 1959) who continued to treat *Iseura* as a megalyrid, though they expressed doubts about the correct classification of the genus. The holotype finally was examined by Hedqvist (1967), who correctly determined *Iseura* to be a braconid (I have also examined the holotype and concur with this identification). Therefore, to date, no authentic megalyrid species are described from South America.

Even so, Nelson and Platnick (1981) characterized the family Megalyridae as "moderately diversified" in South America, citing Kuschel (1960). Although Kuschel (1960) listed Megalyridae as occurring in South America, it is uncertain whether this observation was based on specimens examined, or merely a perpetuation of the incorrect *Iseura* classification. After surveying the Megalyridae from 25 insect collections, only four neotropical specimens have been found. These represent three new species, each representing a new genus. Although there are few available specimens, it is desirable to describe and name these at the present time, so the taxa may be included in a phylogenetic and biogeographic study of the Megalyridae, currently in progress by the author.

**Manuscript received by the editor March 28, 1987.*

MATERIALS AND METHODS

Collections and their abbreviations are given in the acknowledgments.

The morphological terminology used in this paper is mostly that of Shaw (in press). Microsculpture terminology is that of Harris (1979). Measurements and ratios are those used by Naumann (1985, in press). Body length (BL) is measured in dorsal view, excluding the antennae and ovipositor. Forewing length (FWL) is measured from the tegula to wing apex. Ovipositor length (OL) is measured from the apex of the hypopygium. Shape of the head is expressed as a ratio of head width (HW) to head length (HL), measured in dorsal view. Size and position of the ocelli is expressed by the ratio of distance between the lateral ocelli (POL) to the distance between compound eye and lateral ocellus (OOL), and the ratio of the maximum diameter of a lateral ocellus (OD) relative to the distance between lateral ocelli (POL). Size of the compound eye is expressed as a ratio of maximum diameter of the compound eye (MAE) relative to the width of the frons (FW), measured as the minimum distance between the compound eyes. Size and shape of the antenna is expressed as flagellar length/width ratios (F1L/F1W, etc.) Mesoscutum shape is expressed by a length/width ratio (MTL/MTW), and by the ratio of metasoma length relative to body length (MTS/BL).

Family Megalyridae

Diagnosis: Flagellum 12-segmented; subantennal groove present; mesoscutum usually with a median sulcus (absent in one oriental genus, but always present in neotropical species); pronotum with the mesothoracic spiracle completely surrounded by pronotal cuticle; hind wing venation reduced, Sc+R leading to R1 and Rs (as in Figs. 4-6).

KEY TO NEOTROPICAL MEGALYRIDAE (FEMALES)

1. Ocular carina absent (Figs. 1-2); apical segment of Rs in forewing indicated only by spectral venation, not sclerotized and tubular to wing margin (Figs. 4-5) 2
   Ocular carina present (Fig. 3); apical segment of Rs in forewing sclerotized and tubular to wing margin (Fig. 6) .... *Neodinapsis peckorum* Shaw

2. Ovipositor longer than metasoma length; antenna long and slender (as in Fig. 1) .... *Rigel chiliensis* Shaw
Ovipositor shorter than metasoma length; antenna short and compact (as in Fig. 2) .... *Cryptalyra plaumanni* Shaw

Genus **Rigel** Shaw, NEW GENUS

Type-species: *Rigel chiliensis* Shaw

Head: Hypognathous, wider than long; clypeus and frons convex, not excavated; frons and ocellar triangle densely punctulate; vertex punctulate to shagreened; occiput, gena, and malar space shagreened; eye ovoid, densely setose; ocular orbital carina absent; malar suture indistinct; subantennal groove broad (Fig. 1), not bordered by distinct carinae; occipital carina present, finely foveolate; occipital carina at base curving away from mandible; postgena narrow; antenna long and slender, apex reaching middle of metasoma; flagellum filiform; mandible 3-toothed; maxillary palpus apparently 4-segmented; labial palpus 3-segmented.

Mesosoma: Mesonotum, axilla, and scutellar disc punctulate to densely shagreened; median mesoscutal sulcus finely foveolate; axillae meeting at inner angles; pronotum, mesopleuron, metapleuron, and hind coxa shagreened; "pronotal" spiracle circular, without an internal fringe of setae; propodeal spiracle elongate, slit-like; propodeum areolate, without tubercles at postero-lateral corners; legs (as in Fig. 1); hind coxa without a longitudinal carina; hind tibial setae prone; fore and middle tibiae not apically rimmed with stout spines; fore and middle tibiae each with one apical spur, hind tibia with two spurs.

Wings (as in Fig. 4) hyaline, without any distinct banding pattern.

Metasoma: Elongate, subcylindrical, slightly compressed; faintly shagreened, but mostly smooth and shining; ovipositor (Fig. 1) much longer than metasoma and slightly arched; ovipositor sheaths long, slender, densely setose, tending to curl.

Etymology: After Rigel, a star in the constellation Orion.

Remarks: Most similar to *Megalyridea* Hedqvist, described by Hedqvist (1959) based on a specimen from Cape Province of South Africa. *Rigel* differs from *Megalyridea* by lacking a distinct carina along the dorsal margin of the subantennal groove, lacking a row of foveae along the genal orbit of the eye, and by having entirely hyaline wings. In contrast, *Megalyridea* has a carina along the dorsal margin of the subantennal groove, a row of foveae along the genal margin of the eye, and fore wing with distinct infumate bands.

Rigel chiliensis, NEW SPECIES

(Figs. 1, 4)

Holotype. Female, CHILE: Las Cruces, Cord. Parral, X.58, (L.E. Pena). (CNC)

Measurements and ratios: BL 3.5 mm; FWL 3.8 mm; OL 5.7 mm; OL/BL 1.63; HW/HL 1.57; POL/OOL 1.33; OD/POL 0.38; FW/MAE 1.13; F1L/F1W 5.2; F2L/F2W 10.0; F3L/F3W 10.0; F1L/F2L 0.65; F2L/F3L 1.0; F11L/F11W 2.67; F12L/F12W 3.0; F11L/F12L 0.89; MSL/MSW 0.57; MTL/MTW 2.7; MTL/BL 0.54.

Color: Black except trochanters, bases and apices of tibiae, tibial spurs, hypopygium, and ovipositor yellowish brown; tegula and wing venation dark brown.

Paratype female: Same as holotype, except OL 5.9 mm.

Male: Unknown.

Paratype data: 1 female, same data as holotype. (CNC)

Distribution: Chile.

Etymology: Named for its distribution.

Genus **Cryptalyra** Shaw, NEW GENUS

Type-species: *Cryptalyra plaumanni* Shaw

Head: Hypognathous, wider than long, globular; clypeus and frons convex, not excavated; frons, ocellar triangle, vertex, occiput, and gena dorsally punctulate; gena ventrally and malar space faintly shagreened; eye ovoid, minutely setose; ocular orbital carina absent; malar suture indistinct; subantennal groove broad, bordered along dorsal margin by a sharp carina (Fig. 2); occipital carina present, finely foveolate dorsally but not ventrally; occipital carina at base curving toward mandible; postgena narrow; antenna very short and compact (Fig. 2), apex barely reaching mesosoma; flagellum filiform, apical flagellomere sharply pointed; mandible 3-toothed; maxillary palpus apparently 4-segmented; labial palpus apparently 2-segmented.

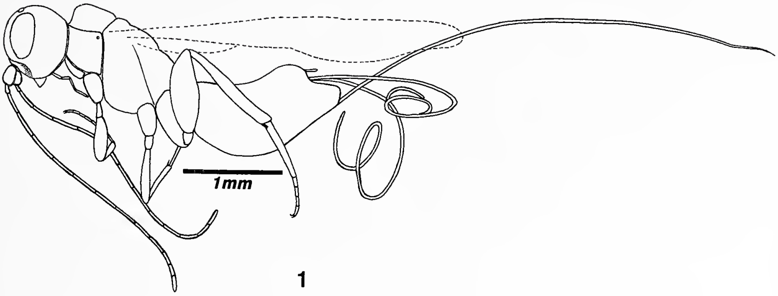

Fig. 1. *Rigel chiliensis,* lateral habitus.

Mesosoma: Mesonotum, axilla, and scutellar disc densely punctulate; median mesoscutal sulcus finely foveolate; axillae meeting at inner angles; pronotum, mesopleuron, metapleuron, hind coxa, and propodeum basally rugose; "pronotal" spiracle minute and circular, apparently without an internal fringe of setae; propodeal spiracle elongate, slit-like; propodeum apically areolate-rugose, with distinct tubercles at postero-lateral corners; legs (as in Fig. 2); hind coxa without a longitudinal carina; hind tibial setae prone to erect; fore and middle tibiae not apically rimmed with stout spines; fore, middle, and hind tibiae each with one apical spur.

Wings (as in Fig. 5) hyaline, without any distinct banding pattern.

Metasoma: Compact, subcylindrical, not compressed; faintly shagreened, but mostly smooth and shining; ovipositor (Fig. 2) much shorter than metasoma, arched apically; ovipositor sheaths very short, compact, and densely setose, about as long as T7.

Etymology: Derived from "crypto-" (Gr.) meaning hidden, and "lyra" (Gr.), a stringed instrument, as a reference to its short ovipositor.

Remarks: A very autapomorphic genus, quite distinct from any other known megalyrid. Its very short antenna with pointed apical flagellomere, propodeum with postero-lateral tubercles, and very short ovipositor sheaths (Fig. 2) are all unique for Megalyridae. Its relationship to other megalyrids is not readily apparent; however, two putative synapomorphies indicate a possible relationship to the Australian genus *Megalyra* Westwood: hind coxa rugose and hind tibia with one spur.

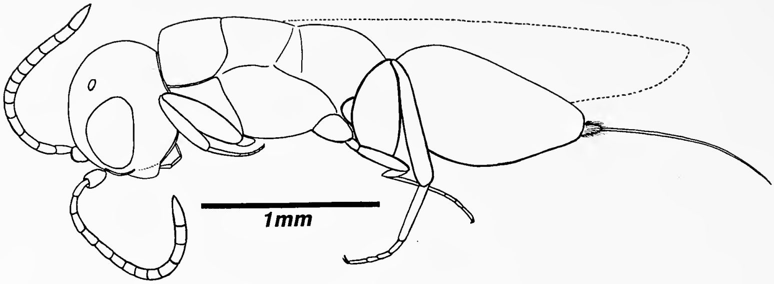

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Fig. 2. *Cryptalyra plaumanni,* lateral habitus

Cryptalyra plaumanni, NEW SPECIES
(Figs. 2, 5)

Holotype. Female, BRAZIL: Nova Teutonia, 22.II.1941, (F. Plaumann). (AEI)

Measurements and ratios: BL 2.9 mm; FWL 2.6 mm; OL 1.0 mm; OL/BL 0.34; HW/HL 1.52; POL/OOL 1.40; OD/POL 0.36; FW/MAE 0.83; F1L/F1W 1.67; F2L/F2W 1.67; F3L/F3W 1.67; F1L/F2L 1.0; F2L/F3L 1.0; F11L/F11W 1.67; F12L/F12W 3.0; F11L/F12L 0.56; MSL/MSW 0.56; MTL/MTW 1.60; MTL/BL 0.41.

Color: Brown except ocellar triangle, occipital carina, mesosomal sutures and sulci, meso- and metapleuron, propodeum, hind coxa, and metasoma black; pedicel, basal flagellomeres, tarsi, and ovipositor yellowish brown; wing venation dark brown.

Male: Unknown.

Remarks: Notable for its minute body size and very short ovipositor. It is the smallest megalyrid ever described. Only a few of the undescribed Australian species are nearly as small.

Distribution: Brazil.

Etymology: Named for the collector of the holotype.

Genus **Neodinapsis** Shaw, NEW GENUS

Type-species: *Neodinapsis peckorum* Shaw

Head: Hypognathous, wider than long; clypeus and frons convex, not excavated; frons, ocellar triangle, vertex, and occiput foveate-reticulate; gena and malar space punctate-rugose; eye ovoid, glabrous; ocular orbital carina present along genal margin from subantennal groove to temple (Fig. 3); space between eye and ocular orbital carina foveate; malar suture faintly indicated at apex of subantennal groove; subantennal groove broad, bordered along dorsal margin by a sharp carina; occipital carina present, finely foveolate; occipital carina at base curving toward mandible; postgena narrow; antenna long and slender, extending at least to middle of mesosoma (F7-12 missing from holotype); flagellum (at least F1-6) filiform; mandible 3-toothed; maxillary palpus apparently 4-segmented; labial palpus 3-segmented.

Mesosoma: Mesonotum densely punctate; mesoscutal sulcus finely foveolate; axilla, scutellar disc, and mesopleuron punctulate-shagreened; axillae meeting at inner angles; pronotum rugose; "pronotal" spiracle circular, without an internal fringe of setae; metapleuron and hind coxa shagreened; propodeal spiracle elongate, slit-like; propodeum areolate, without tubercles at postero-lateral corners; legs (as in Fig. 3); hind coxa without a longitudinal carina; hind tibial setae prone; fore and middle tibiae not apically rimmed with stout spines; fore and middle tibiae each with one apical spur; hind tibia with two spurs.

Wings (as in Fig. 6) very faintly infumated, but without any distinct banding pattern.

Metasoma: Elongate, subcylindrical, gradually narrower apically but not compressed; faintly shagreened, but mostly smooth and shining; ovipositor (Fig. 3) just slightly longer than metasoma and slightly arched; ovipositor sheaths long, slender, and densely setose.

Etymology: Derived from "neo-" (Gr.) meaning new, and *Dinapsis,* after the ethiopian megalyrid genus (Waterston 1922).

Remarks: Clearly related to the lineage comprising *Dinapsis* + *Ettchellsia,* which shares the following synapomorphies with *Neodinapsis:* Rs branching from Rs + M (Fig. 6), Rs apically tubular and sclerotized to the wing margin (Fig. 6), and ocular orbital carina present (Fig. 3). *Neodinapsis* differs from these genera by its shagreened hind coxa without a longitudinal carina, prone hind tibial setae, and areolate propodeum. *Dinapsis* and *Ettchellsia* have a

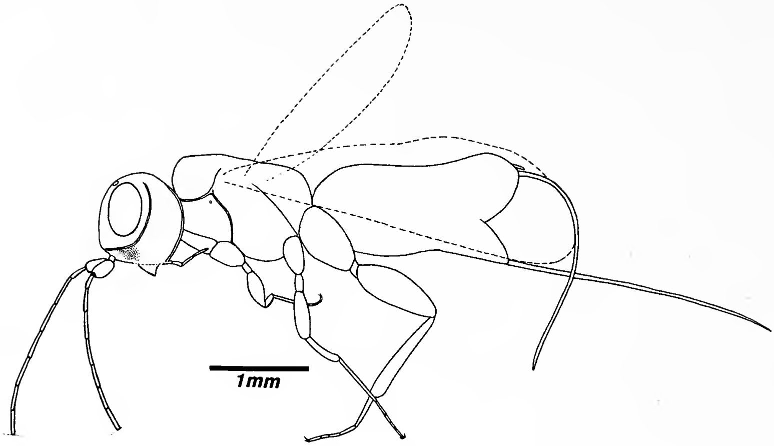

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Fig. 3. *Neodinapsis peckorum,* lateral habitus.

smooth hind coxa with a longitudinal carina, erect hind tibial setae, and carinate propodeum. *Neodinapsis* is the only known neotropical megalyrid with the Rs apically tubular, sclerotized, and reaching the wing margin (Fig. 6).

Neodinapsis peckorum, NEW SPECIES
(Figs. 3, 6)

Holotype. Female, CHILE: Cautin, 21 km NE Pucon, Lago Caburga, 15.XII.84–10.II.85, (S. & J. Peck), FIT, 600 m, mixed forest remnant. (CNC)

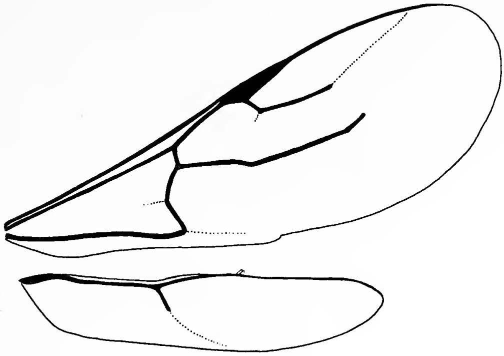
Measurements and ratios: BL 4.3 mm; FWL 3.5 mm; OL 2.8 mm; OL/BL 0.65; HW/HL 1.53; POL/OOL 2.43; OD/POL 0.18; FW/MAE 1.22; F1L/F1W 7.0; F2L/F2W 7.5; F3L/F3W 8.0; F1L/F2L 0.93; F2L/F3L 0.94; (F7–12 missing); MSL/MSW 0.46; MTL/MTW 2.0; MTL/BL 0.51.

Color: Black except tibial spurs, ovipositor, and wing venation brown.

Male: Unknown.

Distribution: Chile.

Etymology: Named for the collectors of the holotype.



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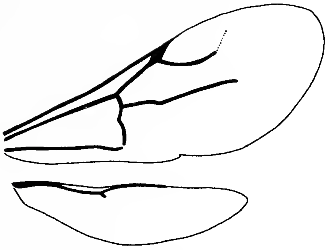

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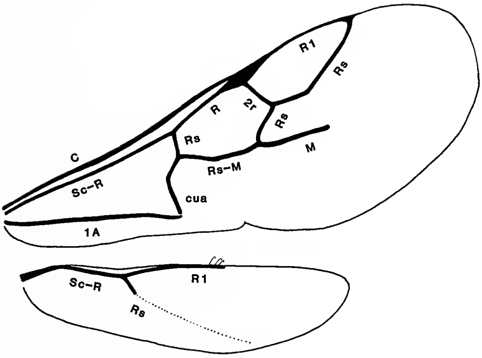

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Fig. 4. *Rigel chiliensis,* wings. Fig. 5. *Cryptalyra plaumanni,* wings. Fig. 6. *Neodinapsis peckorum,* wings.

ACKNOWLEDGMENTS

The following institutions and individuals loaned the neotropical specimens used in this study:

(AEI) American Entomological Institute, Gainesville, Florida (Dr. Henry Townes)
(CNC) Biosystematics Research Institute, Ottawa, Ontario (Drs. G. Gibson & L. Masner)

Holotypes of megalyrids from other regions were loaned by:

(AMNH) American Museum of Natural History, New York (M. Favreau)
(ANIC) Australian National Insect Collection, Canberra (Dr. I. Naumann)
(BMNH) British Museum (Natural History), London (Dr. I. Gauld)
(MNHP) Museum National d'Histoire Naturelle, Paris (J. Weulersse)
(NMVM) National Museum of Victoria, Melbourne (Mr. K. Walker)
(QMB) Queensland Museum, Brisbane (Mr. E. Dahms)
(TMB) Termeszettudomanyi Museum, Budapest (Dr. J. Papp)
(UMO) University Museum, Oxford (Dr. C. O'Toole)
(UPP) University of the Philippines, Laguna (Dr. C. Baltazar)
(ZMHB) Zoologisches Museum, Humboldt Universitat, Berlin (Dr. F. Koch)
(ZML) Zoological Museum, Lund (R. Danielsson)
(ZMUA) Zoologisch Museum, Universiteit van Amsterdam (W. Hogenes)
(ZMUC) Zoologisk Museum, Universitets Copenhagen (Dr. B. Petersen)

SUMMARY

Three new megalyrid genera and species from the Neotropical region are described and illustrated: *Rigel chiliensis* Shaw, *Cryptalyra plaumanni* Shaw, and *Neodinapsis peckorum* Shaw. These are the first Megalyridae described from South America. A diagnosis for the family and a key to neotropical species are given. Preliminary ideas on phylogenetic relationships are discussed.

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FORAGING AND RECRUITMENT IN PONERINE ANTS: SOLITARY HUNTING IN THE QUEENLESS *OPHTHALMOPONE BERTHOUDI* (HYMENOPTERA: FORMICIDAE)

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Johannesburg 2001, South Africa.

Introduction

Recent studies have indicated that, in ponerine ants, a eusocial organization is viable without the presence of a queen caste. In *Rhytidoponera* (Haskins and Whelden, 1965; Ward, 1983; Pamilo *et al.,* 1985) and *Ophthalmopone berthoudi* (Peeters and Crewe, 1985), some of the workers (= gamergates; Peeters and Crewe, 1984) engage in sexual reproduction. Although there is still reproductive division of labor within the colonies, the loss of the queen caste represents a retrogression since the replacement egg-layers lack specialized ovaries. It is of interest to discover whether other aspects of the colonial organization of permanently queenless ponerines have changed with this modification in the reproductive structure. One consequence of this change is that queenless colonies have low levels of relatedness among nest inhabitants (there are many mated laying workers), and Ward (1981, 1983) has suggested that this leads to lower levels of altruistic behavior. Thus Ward would expect colony defence and foraging efficiency to be less well-developed in these species. The natural history of more species of queenless ponerines needs to be documented in order to test the validity of this opinion.

The genus *Ophthalmopone* belongs to the tribe Ponerini (subtribe Poneriti), and is derived from *Pachycondyla* (W. L. Brown, pers. comm.). *O. berthoudi* Forel occurs in Angola, Zambia, Zimbabwe, Mozambique, and the eastern part of South Africa (Prinz, 1978). The workers are monomorphic, and it is exclusively termitophagous. Alfred Ilg described columns of hunting ants in *O. ilgi*

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Manuscript received by the editor August 22, 1986.

(reported in Forel, 1928), and it has been assumed that group-raiding behavior occurs in the whole genus (Wheeler, 1936; Wilson, 1958). The colonies of *O. berthoudi* are polydomous (Peeters, 1984).

NATURAL HABITAT AND METHODS

This study was carried out in one locality in Mkuzi Game Reserve (north-eastern Natal, South Africa), during 1981–1983. Over 100 working days were spent in the field. Mkuzi is semi-arid (Goodman, 1981), with a hot humid summer from mid-September to the end of March. The rainfall is highly seasonal, peaking in February and lowest in June. The greatest variability in the mean monthly rainfall occurs during the dry winter months. The colonies of *Ophthalmopone berthoudi* occurred in open woodland with a grass component less than 1%. The micro-distribution of these ground-dwelling ants is influenced by soil characteristics. They nest in sandy clay loam which is free-draining (i.e. no sub-surface clay pans). The surface is slightly capped and compacted; this increases the run-off and decreases the infiltration. The ponerine community at this location also included *Plectroctena mandibularis* and *P. conjugata, Pachycondyla* sp. (*soror*-complex) and *P. krugeri.*

Various nests were selected for intensive study, and every ant coming in or out of these was colour marked. Some ants were also collected inside the nests and marked. Spots of paint were applied to 1–5 pre-selected dorsal positions and, with a choice of five colours (Humbrol enamel paint), a sufficient number of unique combinations was generated. The ants did not lose their marks with time because painted ants were observed for several months and unexpected color codes were never recorded (the paint holds well to the pubescent cuticle). The activities of individual ants were monitored for varying numbers of days, with the help of a portable tape recorder. Many of the nests were excavated at the end of field visits.

FIELD OBSERVATIONS

Nest description

Nests consisted of a number of underground chambers and galleries with no distinct spatial arrangement, and seldom extended deeper than 50 cm. Nest entrances were simple holes in the ground with little or no accumulation of soil around the hole. Active termite tunnels were sometimes intimately associated with the ant nests, and we suggest that the ants modify abandoned termite tunnels and use them as nests.

Since adults and brood were frequently carried between nests, we soon determined that a single colony occupies more than one nest site (= polydomy). Colony units were made up of 2–7 nests, and these nests were separated by distances varying from 30 cm to 75 m. None of the nests were connected underground, even those with entrances very close to each other.

Individual nests contained variable numbers of adults (mean = 186 ± 151 s.d., range = 20 - 840, n = 34) and brood. Four colonies had all their component nests excavated, and the following estimates of total population were obtained (mean = 517):
January 1981: 3 nests, 453 adults (84, 142, 227).
April 1981: 3 nests, 838 adults (445, 75, 318).
December 1981: 2 nests, 311 adults (261, 50).
February 1982: 5 nests, 464 adults (168, 124, 72, 80, 20).

Patterns of activity

The ants were observed outside their nests throughout the year, although the level of above ground activity decreased during the dry winter months. A subjective impression was that foragers then spent more time away on single hunting expeditions, and that they returned with fewer termites. This is probably linked to decreased termite availability; the dry soils and the low temperatures at night lead to a reduction in the nocturnal activity of the termites.

Diurnal patterns of activity varied during the year. The ants remained outside the nests throughout the day during winter, but during the rest of the year, above ground activities stopped during the middle of the day. The biphasic summer pattern (04h30–10h00; 17h00–sunset) appeared to be regulated by soil temperatures. Indeed, foragers returning to their nests towards the end of the morning period of activity repeatedly climbed up short grass stems. They remained there for short periods before they ventured on the ground again and ran across to the next plant. When the ground surface became very hot (50° C), the ants stayed inside their nests. On cool, cloudy or rainy summer days, foraging continued for longer periods and even for the whole day.

Activities around the nest entrances

Excavation occurred frequently after rain, with soil being brought out of the nests to the surface. Nest sanitation was a distinct activity, whereby workers came up to the surface and discarded pellets of termite remains, as well as empty cocoons. The former consisted of jaws, limbs, and other bits of exocuticle, which were all packed into a distinctive rough-looking ball. These pellets were carried for 1–5 m before being left on the ground; they were never discarded close to the nest entrances. Individual cleaners repeatedly dropped their pellets in the same place.

No natural instances of predation on *O. berthoudi* were recorded, but it is suspected that lizards feed on the ants. A number of arthropods (beetles, spiders, ant lion larvae) were observed trying to steal the termites retrieved by foragers.

Carrying behavior: adult and brood transfer

Adult carrying occurred daily and was preceded by a stereotyped "invitation behavior". This involved vigorous antennation and was similar to that described by Möglich and Hölldobler (1974) for *Rhytidoponera metallica*. However, the carrying posture in *O. berthoudi* is completely different (Fig. 1), with the recruit carried on its side underneath the other ant. Not all invitation interactions were followed by carrying, and the outcome seemed influenced by the age and motivation of the participants.

Adults were carried between existing nests of the same colony. Single cocoons, single larvae of all sizes and packets of 3–14 eggs were also frequently transported above ground. Males were carried between nests during January–February. Different recruiters that were active between the same pairs of nests seldom followed the same route, and the paths were sometimes strikingly different. This is further evidence that the nests are not connected together by chemical trails.

Nest emigration is a frequent occurrence in ponerine ants. Species which do not lay chemical trails for social coordination use social carrying or tandem running (e.g. Möglich and Hölldobler, 1974; Fukumoto and Abe, 1983; Hölldobler, 1984; Traniello and Hölldobler, 1984; Fresneau, 1985). Both these primitive recruitment techniques are preceded by the same invitation behavior, and in *Pachycondyla obscuricornis* they are used alternatively to recruit

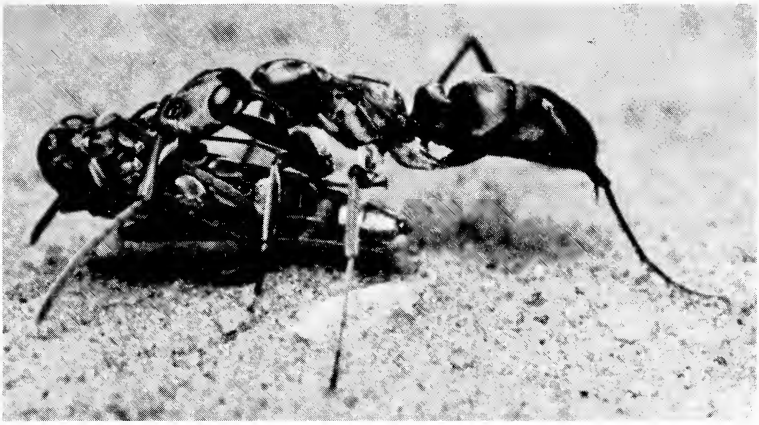

Figure 1. Worker of *Ophthalmopone berthoudi* carrying a male between two nests—workers are carried in an identical way.

sexuals or workers (Traniello and Hölldobler, 1984). In *O. berthoudi,* social carrying is not only used during the evacuation of old nests and the settlement of new ones, but is a habitual, routine event between established nests. An ant carried to another nest in a colony remains associated with it; if it was active above ground, it will return to this new nest after future performance of its task. While being carried, an ant is also provided with visual navigation cues which enable her to return to the nest of origin. When marked recruiters and recruits came apart outside the nests, the latter were unable to proceed but could walk back to the nest from which they originated. A detailed analysis of the pattern of recruitment between nests will be presented elsewhere. While the proximate adaptive significance of inter-nest transfers is unclear, they have the effect of maintaining contact between the nests of polydomous colonies.

Foraging behavior

O. berthoudi feeds exclusively on termites. The ants only hunted those species which foraged in accessible places, and termite nests were never raided. Cooperative hunting was never observed. Three termite species seemed to make up most of the ants' diet. *Macrotermes natalensis* and *Odontotermes badius* forage principally on wood-, grass-, or leaf-litter on the surface, covering these with a thin layer of soil and feeding beneath this protective cover. Chemical cues contained in fresh soil sheeting of these two termite genera are detected by scout ants of *Megaponera foetens* (Longhurst and Howse, 1978); this effect was not investigated in the present study. Foragers of *O. berthoudi* broke open the soil sheeting or looked for natural openings. Termites were captured one by one; the prey was held in the ants' mandibles, impaled on the sting and flung underneath the body to the rear. After catching up to 15 termites in this way, the foragers gathered most of the semi-immobilized bodies and stung them once again. They packed the termites between their mandibles and brought them back to the nest. *O. berthoudi* also preyed on *Hodotermes mossambicus,* which are grass-harvesters on the surface, and which sporadically exit in small groups from underground galleries. The ants located these visually, and captured single termite workers which were immobilized with the sting. Successful foragers only remained inside their nest for a short while before they reappeared (in laboratory nests they leave their prey in the entrance chambers), and revisited the same locations. Foragers were often found with missing limbs, and such injuries are presumably sustained during hunting.

Recruitment never occurred, and single foragers independently exploited a food source until it was exhausted. Social facilitation was observed in laboratory nests however; the return of successful foragers induced others to go out and hunt, but to no particular location. The lack of cooperation between hunters is associated with the absence of trails in this species. The distinctive trail-laying gait was never observed, and simple experiments showed that foragers do not become disoriented when soil ahead of them is disturbed. Instances of tandem running were never seen. Some kind of discrete marking was sometimes observed however. Workers stood momentarily still and rubbed the ventral tip of their gaster sideways over objects lying on the ground (e.g. pebbles, dead leaves, sticks,...); marking was never done directly onto the bare ground. This behavior was especially conspicuous around nest entrances after rain, and also occurred when some foragers walked away from their nests. We suggest that ants which are unfamiliar with a new area outside their nests lay these marks and then use them as personal orientation cues on their return. Similarly, scouts in *Pachycondyla tesserinoda* deposit and use scattered chemical orientation marks which have no recruiting effects (Jessen and Maschwitz, 1985).

Foraging originated from every nest and marked hunters were always recorded as returning to their nest of origin in a colony. Some foragers did not hunt around their own nests, and travelled long distances to hunt in areas nearer other nests in the colony, where they had been observed to be previously active. On consecutive days, the same individuals returned to the same part of their colony's home range.

Discussion

Ophthalmopone berthoudi invariably hunts alone; this is in conflict with previous references to this genus in the literature. There is no cooperation among foragers, either through the transfer of information about the location of new sources of prey, or through direct assistance during the killing and retrieving of prey. Many other species of ponerines are also solitary predators (Table 1), although they are in many cases more opportunistic in their choice of prey. Group retrieving (involving a small number of workers) is occasionally seen in some species of solitary hunters (when prey is too large or numerous to carry), but this cooperation is not always a consequence of recruitment, i.e. a huntress can attract nestmates in her immediate vicinity through the release of alarm pheromones (*Amblyopone pallipes;* Traniello, 1982), which is not equivalent to returning to her nest to recruit one or more nestmates to the prey (e.g. *Rhytidoponera purpurea;* Ward, 1981). In *Plectroctena conjugata* (Peeters, unpublished), several foragers are sometimes led together to a hunting area, but they capture prey and return to the nest independently.

Solitary predation contrasts with the elaborate systems of recruitment and cooperative hunting displayed by other ponerine species. Fletcher (1973) has critically reviewed column-raiding in the Ponerinae. The comparative overview in Table 1 reveals that simple and complex hunting strategies occur in different species irrespective of phylogenetic relationships. Thus *O. berthoudi* and *Megaponera foetens* are closely related (W. L. Brown, pers. comm.) but

Table 1. Overview of the foraging techniques exhibited in the Ponerinae (only a few species of *Leptogenys* have been included). The process of hunting living prey (=predation) is broken up into raiding (getting to the prey) and retrieving, a distinction made by Wilson (1958). "Group" refers to a small number of participants (less than 10–15), while "column" involves many ants walking together in one of several distinct files. The species mentioned are all predatory, and they belong to the following tribes and sub-tribes (Brown, 1958, 1960, 1975, pers. comm.): (1) Amblyoponini; (2) Cerapachyini; (3) Ectatommini; (4) Platythyreini; (5) Ponerini, a: Odontomachiti, b: Poneriti, c: Leptogenyiti.

Recruitment technique associated with foraging	Species recorded in the literature (and tribe)		Hunting strategy	References
no chemical trails, no recruitment	*Amblyopone pluto*	(1)	solitary	Gotwald & Lévieux 1972
	A. pallipes	(1)	solitary	Traniello 1982
	Rhytidoponera sp. 12	(3)	solitary*	Pamilo et al. 1985
	Ectatomma ruidum	(3)	solitary	Lachaud 1985
	Platythyrea conradti	(4)	solitary	Lévieux 1976
	Odontomachus bauri	(5a)	solitary	Jaffe & Marcuse 1983
	Ophthalmopone berthoudi	(5b)	solitary	this study
	Diacamma rugosum	(5b)	solitary	Fukumoto & Abe 1983
	Dinoponera gigantea	(5b)	solitary	Haskins & Zahl 1971
	Pachycondyla obscuricornis	(5b)	solitary	Traniello & Hölldobler 1984
	P. (=Neoponera) apicalis	(5b)	solitary*	Fresneau 1985
recruitment by tandem-running	*Pachycondyla tesserinoda*	(5b)	solitary, group retrieving large prey	Maschwitz et al. 1974
	Mesoponera caffraria	(5b)	solitary, group raiding and retrieving	Agbogba 1984
	Hypoponera sp.	(5b)	solitary, group retrieving (large prey)	Agbogba 1984

rudimentary chemical recruitment (short-lived trails)	*Rhytidoponera chalybaea*	(3)	solitary, group retrieving*	Ward 1981
	R. purpurea	(3)	same, with long-range trails to aphids	Ward 1981
	Plectroctena mandibularis	(5b)	solitary, group retrieving (large prey)	Fletcher 1973
	Paltothyreus tarsatus	(5b)	solitary, group raiding and retrieving*	Hölldobler 1984
	Leptogenys attenuata	(5c)	solitary, also group raiding (2–5 ants)	Fletcher 1971
advanced chemical recruitment (more persistent trails, larger groups)	*Cerapachys turneri*	(2)	column raiding (on ant nests)	Hölldobler 1982
	Paraponera clavata	(3)	solitary†, group foraging to nectar	Breed & Bennett 1985
	Pachycondyla laevigata	(5b)	column raiding, solitary retrieving?	Hölldobler & Traniello 1980
	P. commutata	(5b)	column raiding and retrieving	Mill 1984
	Megaponera foetens	(5b)	column raiding (complex)	Longhurst & Howse 1979
	Simopelta oculata	(5b)	column raiding (on ants)	Gotwald & Brown 1966
	Leptogenys chinensis	(5c)	group raiding (2–6), solitary retrieving	Maschwitz & Schönegge 1983
	L. nitida	(5c)	group raiding (few ants) and retrieving	Fletcher 1971
	L. kitteli	(5c)	column raiding (40–60) and retrieving	Baroni Urbani 1973
	Onychomyrmex	(1)	swarm raiding (destination of column is not predetermined)	Brown 1960, Hölldobler et al. 1982

* also scavengers † along established trunk trails

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	Odontomachus hauri	(5a)	solitary	Jaffe & Marcuse 1983
	Ophthalmopone berthoudi	(5b)	solitary	this study
	Diacamma rugosum	(5b)	solitary	Fukumoto & Abe 1983
	Dinoponera gigantea	(5b)	solitary	Haskins & Zahl 1971
	Pachycondyla obscuricornis	(5b)	solitary	Traniello & Hölldobler 1984
	P. (=Neoponera) apicalis	(5b)	solitary*	Fresneau 1985
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* also scavengers † along established trunk trails

exhibit solitary hunting and column raiding respectively, and members of the genus *Pachycondyla* exhibit a range of hunting strategies. Furthermore, representatives of each of four tribes hunt in well-coordinated raids (Table 1). These data emphasize that foraging characteristics are the product of the unique selective pressures facing each species. The evolution of these characteristics is not governed by anatomical constraints, e.g. all members of the sub-tribe Poneriti seem to have the exocrine glands necessary for recruitment, but only some of them hunt in groups. In addition, some solitary-hunting species have recruitment capabilities which they do not use during foraging, e.g. *Diacamma rugosum, Dinoponera gigantea* and *Pachycondyla (=Neoponera) apicalis* use tandem-running during nest emigration only (Fukumoto and Abe, 1983; Overal, 1980; Fresneau, 1985).

Wilson (1958) suggested that group hunting only becomes selectively advantageous with respect to certain prey preferences. This is evident for species which prey on large arthropods or on the brood of other ants. However, strictly termitophagous species include both solitary and column hunters, i.e. a number of strategies are appropriate to exploit this strongly-clumped prey. Column raiding appears to have evolved a number of times and from different behavioral antecedents (Furthermore, different exocrine glands are involved in recruitment.), and this term thus describes a range of "variations on one theme". Indeed in some species, group raiding is followed by solitary retrieving of the prey. The occurrence of group hunting is unlikely to be related to one ecological factor only.

There has not been a phylogenetic trend towards the elaboration of patterns of cooperation and recruitment during predation in the Ponerinae, and these characteristics can vary from species to species regardless of the nature of the reproductive system. Indeed, group foraging is characteristic of the genus *Leptogenys,* and this behaviour is unaffected by the change to gamergate breeding which has occurred in *L. schwabi* (M. Zini, in prep.). Thus we reject the possibility that the simple hunting strategy seen in *O. berthoudi* is a secondary modification caused by a reduction in altruism in colonies with numerous matrilines. We note that solitary-hunting species with a highly-specific diet are more vulnerable to seasonal fluctuations in prey availability. Rather than implying that elimination of the queen caste would result in a simplification of social relationships, attempts should be made to understand how it might have arisen as an *effect* of various attributes of the life histories.

ACKNOWLEDGMENTS

We are grateful to William L. Brown Jr. for his information on the phylogenetic relationships among the Ponerinae, and to Barry Bolton for ant identifications. Peter Goodman provided logistic assistance in the field, and the Natal Parks Board gave permission to work in Mkuzi Reserve. Anthony Bannister took the photograph in Figure 1. We thank R. H. Crozier, W. L. Brown, and M. W. Moffett for comments on this manuscript. This study was funded by grants from the University of the Witwatersrand and the C.S.I.R., and the manuscript was prepared while CP was supported by the Australian Research Grants Scheme.

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Editorial Office, Psyche
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Cambridge, Mass. 02138

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ISSN 0033-2615

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 94 1987 No. 3–4

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CAMBRIDGE ENTOMOLOGICAL CLUB

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PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: $18.00, domestic and foreign.

Checks and remittances should be addressed to Treasurer, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138.

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Psyche, vol. 94, no. 1–2, for 1987, was mailed October 6, 1987

The Lexington Press, Inc., Lexington, Massachusetts

PSYCHE

Vol. 94 1987 No. 3–4

A MORDELLID-MELOID MIMICRY

By M. Deyrup[1] and T. Eisner[2]

The Mordellidae are small wedge-shaped beetles commonly found in one of the most dangerous of all insect habitats, the open inflorescences of plants. Their chief protection against the many predators that frequent flowers is a series of convulsive leaps followed by rapid flight, as acknowledged in their common name, the "tumbling flower beetles" (Crowson, 1981). Their escape from a predator's grasp is facilitated by their wedge shape and covering of smooth, backward-pointing hairs, while their movement and purchase among stamens and floral hairs may be assisted by rows of tibial and tarsal setae strongly reminiscent of the combs of fleas. These escape mechanisms, while undoubtedly effective against many predators (including entomologists), have the disadvantage that they involve abandonment of the feeding site.

At our study area in southern Florida (Archbold Biological Station, Highlands Co.) one species of mordellid appears to belong to a mimetic complex, a strategy by which the beetles might forestall attack. The mordellid, *Mordellistena comata* LeConte, is a relatively uncommon insect that is found during late summer on flowers of yellow Asteraceae, especially *Heterotheca subaxillaris* (Lamarck) Britton and Rusby, and *Balduinia angustifolia* (Pursh) Robinson. The reddish pronotum and black elytra of this beetle (Fig. 1, bottom) confer a strong resemblance to several species of nemognathine meloids, especially *Gnathium francilloni* Kirby (Fig. 1,

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**Manuscript received by the editor July 6, 1987.*

Fig. 1. The meloid *Gnathium francilloni* (above) and its mimic, the mordellid *Mordellistena comata*, on flowers of *Heterotheca subaxillaris*. Photographs taken at same magnification. Body length of *Gnathium* = 4.5 mm.

top). At one location in a dense stand of *H. subaxillaris* covering an area of about 50 × 50 m, we counted 250 specimens of *G. francilloni* and 6 of *M. comata.* The meloids often occurred in groups of 2 or 3 (31 pairs were *in copula*), while the mordellids occurred singly. Visually, as small specks of reddish-brown and black on the brilliant yellow floral discs, the two species are difficult to distinguish. The differences apparent at very close range were not obvious to us at a distance. We had long been familiar with *Gnathium* at our field site before we noticed the *Mordellistena* among them.

Nemognathines can be expected to be protected chemically by cantharidin, the well-known terpenoid toxin present in meloid blood (Carrel and Eisner, 1974). Meloid beetles typically reflex-bleed when disturbed, a behavior that we could readily induce in *G. francilloni,* as in other species of *Gnathium,* by gentle pinching of the body and legs. *M. comata,* we believe, may avoid harassment through mimicry of these protected models. Whether it is itself fully palatable and therefore (in a chemical sense) a Batesian mimic, remains unanswered. The literature offers no clue to the presence of chemical defensive agents in mordellids. Tests that we did with another species of mordellid, *Mordella atrata* (Melsheimer), proved this beetle to be edible: six individuals (freshly killed or rendered moribund by freezing) that we offered at our field site in a small dish to tame wild scrub jays (*Aphelocoma c. coerulescens*) were taken in quick succession by one bird, together with pieces of peanut offered as accompanying morsels. The same bird ate another 29 of 32 *M. atrata* that were similarly offered several days later, and a second bird ate two individuals of this lot, leaving only one of the beetles uneaten.

Examination of *G. francilloni* and *M. comata* by ultraviolet video-viewing (Eisner et al. 1969) showed no differences in ultraviolet reflectance characteristics. Both beetles are ultraviolet absorbent over their entire body surface. To the insect eye, therefore, the beetles should also appear similar in coloration.

M. comata and *G. francilloni* have more or less overlapping geographic ranges, according to the fragmentary data available (Blackwelder and Arnett, 1975). There are additional species of meloids, such as *Nemognatha nemorensis* Hentz, and one additional mordellid, *Mordellistena marginalis* Say, that occur on flowers and seem to belong to the red-pronotum, black-elytra mimetic complex. At the Archbold Biological Station this general complex includes about 90 species, belonging to various insect orders; most of these species cannot yet be assigned to specific mimetic associations of species found together in the same microhabitat.

The Mordellidae appear to be an ancient family of floricolous beetles (Crowson, 1981), and the scarcity of mimetic species might seem surprising. The small size of most species and their distinctive shape do not preadapt them for visual convergence with most of the stinging or distasteful species found on flowers. *M. comata* may be viewed as adaptively "fortunate" in co-occurring with a small, distasteful, floricolous species.

ACKNOWLEDGMENT

We thank Dr. Norville Downie, Lafayette, Indiana, for identifying the mordellids and meloids.

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PATTERNS OF MATING AND FECUNDITY IN SEVERAL COMMON GREEN LACEWINGS (*NEUROPTERA: CHRYSOPIDAE*) OF EASTERN NORTH AMERICA*

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Recently, much interest and innovative research have focussed on the mating systems of animals (Thornhill and Alcock, 1983; Willson and Burley, 1983). Our interpretation and understanding of reproductive behavior, for example, has undergone a metamorphosis in the last few years. In the recent past, such common reproductive activities as courtship were viewed as steps to overcome some sort of physiological threshold in the female of the species (Marler and Hamilton, 1966, chapter 3), or, alternatively, as mechanisms to prevent the interbreeding (hybridization) of different species (Mayr, 1963). However, principally since the publication in the mid 1970's of works by Alexander (1975, 1977) and Wilson (1975), evolutionary biologists have adopted a rather different view of courtship and other reproductive behavior. This perspective is a more inclusive one, stressing the evolutionary or selective benefits to individuals of behaving the way they do during sexual activity. Courtship is more properly viewed as a series of test questions posed by the courting individual to its potential partner. The answers to these questions help the individual decide where the other individual is located; what species and sex that individual is, to avoid costly mistakes in mating; and how good a mate that individual will make, in terms of its vigor, strength, and success at intrasexual competition or at securing resources for its partner. In fact, the ultimate goal of reproductive behavior is success in transmitting an individual's genes to the next generation, through the production of viable, fit offspring.

Individual reproductive success can be achieved in a variety of ways. Females can have very high fecundity, or they may provide more care or resources for fewer offspring. Additional strategies are

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**Manuscript received by the editor September 25, 1987*

open to males, which need only produce energetically "cheap" sperm rather than expensive eggs. On the one hand, a male can copulate with as many females as time and conditions allow; alternatively, he may be more careful to ensure, through attention and guarding, that the sperm transferred are actually used by the female to produce offspring (Waage, 1983). The stage is set in many animals for sexual inequality: males may embark on highly polygynous reproductive lives, while females choose fewer times and more carefully among the scrabbling suitors. With such inequities comes unfairness, especially among males: if one male can inseminate many females, but each female accepts only a few males, then many other males must never get the opportunity to mate. High variance in reproductive success among males is the basis for strong sexual selection on males (Darwin, 1859, 1871), which in turn is thought to sculpt the obvious morphological and behavioral dimorphism between the sexes that exists in the majority of animal species.

It is often assumed, but rarely documented, that individual males of sexually dimorphic species inseminate many females, and can produce many more progeny than can individual females. Conversely, it follows that species displaying little sexual dimorphism should be reasonably equivalent in the reproductive potential of the two sexes. Insects are well suited for testing predictions of sexual selection theory, because they exhibit inexhaustible diversity of life-history strategy (Dingle and Hegmann, 1982) and are often easy to observe and manipulate in the field and laboratory. For example, green chrysopid lacewings show a convenient range of sexual dimorphism, from extreme in *Meleoma* Fitch spp. (Bickley and MacLeod, 1956), through moderate in the common *Chrysopa oculata* Say (Smith, 1922), to negligible in the *carnea*-group within the genus *Chrysoperla* Steinmann (Henry, 1983). Fortunately, most lacewing species adapt well to laboratory culturing, so simple studies measuring individual reproductive success are both feasible and reasonably representative of conditions in nature. Here, we concentrate on the reproductive biology of two well known, closely related species of the *carnea*-group, but we include some preliminary data on several other species characterized by greater sexual dimorphism.

The principal protagonists are the sympatric, closely related North American species *C. plorabunda* (Fitch) and *C. downesi* (Smith). *C. plorabunda* is a common meadow-dwelling form with multiple generations per year, while *C. downesi* is a darker green conifer-associated species that produces but one annual generation (Tauber and Tauber, 1976; Henry, 1980a). Each species, but especially *C. plorabunda,* has been well studied because of its importance in biological control (New, 1975; Hassan, 1978). Also, both species have figured prominently in investigations of sympatric speciation through disruptive selection (Tauber and Tauber, 1977a, b; 1982) and song divergence (Henry, 1980a, 1983, 1985a, b). Extensive fecundity data, relating egg production to diet or age, have been published for these and several other important green lacewings (Rousset, 1983). However, the extent of polygyny and polyandry, or the effect of multiple matings on fertility and fecundity, have not been determined for any chrysopid. Yet such basic information about mating habits and consequences is prerequisite to understanding several broader issues—particularly, the consequences of different life-history patterns and reproductive strategies, the dynamics of rapid speciation through acquisition of assortative mating patterns (West-Eberhard, 1983; Henry, 1986), and mass rearing and release in programs of biocontrol.

Methods and Materials

Data for this paper were generated over several years, as part of a larger project investigating courtship singing behavior, reproductive isolation, and speciation in sibling species of the genus *Chrysoperla* (Henry, 1983, 1985a, b, 1986). Adult green lacewings of *C. plorabunda, C. downesi,* and several additional species were collected from the field during the warmer months and maintained throughout the year in small, outbred colonies of 25 to 50 individuals. Most species were available locally, within 15 miles of Storrs, Connecticut; however, *C. downesi* and most of the *Meleoma emuncta* (Fitch) came from coniferous forests on the E. N. Huyck Preserve in Rensselaerville, New York. Additional *C. downesi* in 1982 and 1983 were from populations in central Vermont (Echo Lake), southern New Hampshire (Mount Monadnock), and northwestern Massachusetts (north of Quabbin Reservoir). And late in 1986, we included several individuals of *C. plorabunda* from near Moscow, Idaho, in the study. Laboratory colonies of all species were maintained as described earlier (Henry, 1979, 1980a, b) and kept at 26±2°C. An artificial diet consisting of equal proportions (by weight) of honey, yeast hydrolyzate (Difco™), water, and Wheast™ was available in excess to all adults. *Chrysopa oculata,* the only species studied requiring adult prey for proper egg maturation (Tauber and Tauber, 1973), was given *Aphis fabae* Scopoli raised on greenhouse-grown *Nasturtium* sp. *Meleoma emuncta* adults were fed a mixture of assorted pollens and honey (J. Johnson, Univ. of Idaho, pers. com.). All larvae were fed ether-killed *Drosophila* spp. every 2–3 days. Photoperiod was manipulated for *C. downesi* to break adult reproductive diapause (Tauber and Tauber, 1976); for other species, constant long-day (17L:7D) light regimes were maintained.

We took three simple experimental approaches: (1) Field-captured, gravid females were allowed to oviposit freely without re-mating. From this, we could assess the extent of egg productivity possible from sperm in reserve under natural conditions. (2) Young (two-week-old), laboratory-reared virgin females were mated as often as they would accept previously unmated males, while others of the same cohort were mated just once; whenever possible, copulation duration was noted. Egg production and sexual receptivity were monitored for each female throughout the experiment. This approach was designed to determine the extent of polyandry, the number of eggs produced per copulation, and the relationships among sexual receptivity, re-mating, copulation duration, and egg-laying. Sexual receptivity, which is lost in female lacewings after copulation, was assessed by playing back species-appropriate songs to the insects and waiting for "answers" (abdominal dueting behavior [see Henry, 1985a, b]). To minimize the effects of aging on fecundity, insects that had been sexually mature for more than two weeks were excluded from these studies. Maturity, in turn, was judged by the onset of sexual receptivity. (3) Finally, individual two-week-old males were re-mated to unmated, receptive females at 1–3 day intervals, until they could no longer copulate. This provided estimates of sperm transferred and accepted per copulation, degree of polygyny, and minimum total lifetime reproductive potential for each male. Females were selected from cohorts of the same age as the males. Since a single male could easily mate with many females, we were forced in one case (male H of Table 6) to recruit two-week-old virgin females after the 18th copulation.

All three approaches above shared one simple but important protocol: count every egg and determine whether or not it had been fertilized. Counting was facilitated by the egg stalk so typical of the green lacewings: each egg could be clipped cleanly from its substrate and placed on the filter paper floor of a 10 cm plastic petri dish for storage. Fertility was indicated by darkening of the initially green egg within two days of oviposition at about 26°C. Unstalked eggs, glued directly to the substrate or dropped to the ground, were also monitored for darkening and included in any counts if fertile. Eggs were clipped, counted, and monitored three times per week, unless otherwise specified. Clipped eggs from one session were saved until the next, so that their fertility or sterility could be guaranteed. Since just 5 to 10 percent (at most) of any individual female's eggs were ever inviable, the results tabulate only fertile, developing eggs.

Sample sizes varied considerably from one experiment to another, due to the opportunistic nature of the studies. For example, egg counts were performed on 8 field-captured, gravid females of *Chrysopa oculata* and 6 of *Chrysoperla harrisii* (Fitch), but only three of such females of *C. rufilabris* (Burmeister) and one of *C. downesi* were available, and *C. plorabunda* was neglected altogether. Similarly, multiple-mating experiments on females were completed only with *C. plorabunda* (21 females) and *C. downesi* (17 females). Individuals that produced fewer than 400 eggs were excluded, since our interest was in maximal fecundities. Male multiple-mating studies were limited to *C. plorabunda* (8 males), *C. downesi* (2), and *C. oculata* (2). Finally, a few data correlating fertility with copulation duration were taken, but only for *C. plorabunda* (27 matings) and *C. downesi* (15 matings).

Means and standard deviations were calculated from the data using a computer spreadsheet (LOTUS 1, 2, 3™). Samples were tested for normality by a Kolmogorov-Smirnov routine, and deemed significantly different by two-tailed t-tests and confidence limits of 99%, using the statistical functions of the computer program ASYSTANT+™.

Voucher specimens have been deposited in the insect collection of the Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs.

RESULTS

Egg Counts: Field-captured, Gravid Females.

Egg productivity by wild females of *C. oculata, C. harrisii, C. rufilabris, C. downesi,* and *M. emuncta* are shown in Tables 1 and 2 (no field-collected *C. plorabunda* were tested). For all species except *M. emuncta,* totals per female averaged between 700 and 1000 eggs: insignificantly different from one another. Such totals also reflect

Table 1. Average fecundity of females of six chrysopid species, from field and laboratory data. Data are means and standard deviations; sample sizes are entered parenthetically. Oviposition lifespan, in days, is the period during which a female continuously produced fertile eggs.

	Chrysoperla plorabunda	*C. downesi*		*Chrysoperla harrisii*	*Chrysoperla rufilabris*	*Chrysoperla oculata*		*Meleoma emuncta*
	(Laboratory)	(Lab.)	(Field)	(Field)	(Field)	(Lab.)	(Field)	(Field)
Total Eggs	780 ± 240 (21)	769 ± 233 (17)	991 (1)	744 ± 146 (6)	905 (±) 117 (3)	683 ± 119 (6)	761 ± 299 (9)	132 ± 41 (8)
Eggs: 1st Cop.	502 ± 310 (21)	527 ± 276 (17)	--	--	--	--	--	--
Eggs: 2nd Cop.	243 ± 195 (17)	311 ± 221 (11)	--	--	--	--	--	--
Eggs: 3rd Cop.	93 ± 119 (9)	141 ± 70 (3)	--	--	--	--	--	--
Number Cops.	2.48 ± 1.18 (21)	1.94 ± 0.87 (17)	--	1 (6)	1 (3)	1 (5)	1 (8)	--
Ovip. Lifespan	64 ± 21 (18)	53 ± 19 (17)	48 (1)	32 ± 1.4 (6)	36 ± 1.4 (3)	54 ± 6.2 (4)	36 ± 11.5 (8)	--

single-mating reproductive potentials of individuals of those species, because other experiments described elsewhere in this paper indicate that female lacewings do not store appreciable quantities of sperm from one mating to another. Certain field-caught individuals within each species were remarkably fecund, especially considering that none was re-mated after capture. For example, some females of *C. oculata* and *C. rufilabris* oviposited more than 1000 fertilized eggs, while one female each of *C. harrisii* and *C. downesi* nearly matched that level (Figs. 1, 3, Table 2). Except for slightly higher early rates of egg-laying by *C. oculata,* the overall patterns shown are quite similar in all of the above species, and in fact are much the same as that seen in monogamous *C. plorabunda* raised in the laboratory (Fig. 2). The egg production by all once-mated females of all species, whether laboratory-reared or field-captured, is summarized in Table 2.

Egg Counts: Continuously Re-mated Females.

The *C. plorabunda* and *C. downesi* females mated 1–6 times, the former species averaging a total of 780 eggs and the latter 769 (Tables 1, 3, and 4). Both species averaged two matings over an individual's lifespan. Oviposition spanned a mean of 64 days in *C. plorabunda* and 53 days in *C. downesi,* but the high variance indicates no significant interspecific difference.

Lifetime patterns of egg-laying, sexual receptivity, and mating varied considerably among individuals of both species. Some females produced consistently high numbers of eggs for prolonged periods from their first fertilization, without ever recovering sexual receptivity or re-mating. Examples of this pattern can be seen in both *C. plorabunda* (86-4, Fig. 2) and *C. downesi* (FLD1, Fig. 3). More commonly, a female became sexually receptive and re-mated after a shorter time, just as her egg productivity began to dip (Figs. 2, 3, Table 5). If immediately re-fertilized, such individuals oviposited large numbers of eggs again and receptivity disappeared, but without re-mating egg production soon ceased, suggesting sperm depletion. A third, rare subset of individuals recovered sexual receptivity many days before their egg productivity declined, as seen in females E (*C. plorabunda*) and B and E (*C. downesi*) in Table 5. Actually, receptivity in such insects waxed and waned rather erratically, and none succeeded in re-mating until egg production truly diminished.

Table 2. Total fertile egg production, without re-mating, by individual female lacewings of six species, from both field and laboratory-reared insects. Averages and standard deviations are entered at the bottom of the table.

Species:	*Chrysoperla plorabunda* (Laboratory)	*Chrysoperla downesi* (Lab. and Field)	*Chrysoperla harrisii* (Field)	*Chrysoperla rufilabris* (Field)	*Chrysopa oculata* (Lab. and Field)	*Meleoma emuncta* (Field)
I	743	463	551	779	480	88
N	822	636	581	876	486	89
D	893	644	717	1061	539	107
I	1160	793	776	--	545	110
V	--	840	911	--	629	129
I	--	991	930	--	652	144
D	--	--	--	--	709	167
U	--	--	--	--	788	218
A	--	--	--	--	809	--
L	--	--	--	--	967	--
S	--	--	--	--	1126	--
	--	--	--	--	1289	--
Avg: ST. Dev:	958 ± 146 (4)	781 ± 132 (6)	744 ± 146 (6)	905 ± 117 (3)	776 ± 245 (12)	132 ± 41 (8)

In general, females that mated more than once produced the majority of their eggs from the first copulation (Tables 3 and 4). However, a subsequent pairing could yield large numbers of eggs if earlier copulations had little issue (e.g., I, Table 3, and B, Table 4). At their peak of egg productivity, females of either species could oviposit nearly 40 eggs per day. Despite varying rates of egg-laying and radically different lifetime patterns of re-mating, the most fecund individuals consistently laid about 1200 eggs altogether.

Field-captured *Meleoma emuncta* females had the lowest fecundity of any of the lacewings studied (avg. 132 eggs/female, Table 2). This low fecundity may be due in part to unknown dietary or environmental requirements for optimal growth and reproduction (Tauber 1969); the species is notably difficult rear (J. Johnson, pers. com.).

Male Reproductive Potential: Continuously Re-mated Males.

Males of *C. plorabunda, C. downesi,* and *C. oculata* could mate several times (Table 6). One *C. downesi* mated with 10 different females at 24-hour intervals, and *C. plorabunda* males inseminated maxima of 22 and 30 females. The highest value was posted by an individual of *C. plorabunda* that was re-mated at 2-day rather than 24-hour intervals; in fact, this male remained reproductively competent for much of his long lifespan (210 days). Generally, the data from egg counts described a decline in male fertility with time, suggesting irreversible sperm depletion. However, the active individual was conspicuously different, maintaining high fertility even after many copulations: for example, his 20th female oviposited 620 eggs, as many as produced by females paired with fresh, virgin males. The reproductive potential of males consistently exceeded that of females in all three species studied. Again, the exceptional *C. plorabunda* male fathered many more offspring than any other individual: over 9600, vs. 2253 for the runner-up. The performance of this extraordinary individual, compared with the next-most-fertile male, is graphed in Fig. 4.

Egg Production vs. Copulation Time.

Chrysoperla plorabunda had consistently shorter matings than its sibling, *C. downesi* (Table 7). Highest individual fecundity in the former species was associated with copulation durations of 8–10 minutes, whereas in *C. downesi,* longer copulations (19–65 minutes)

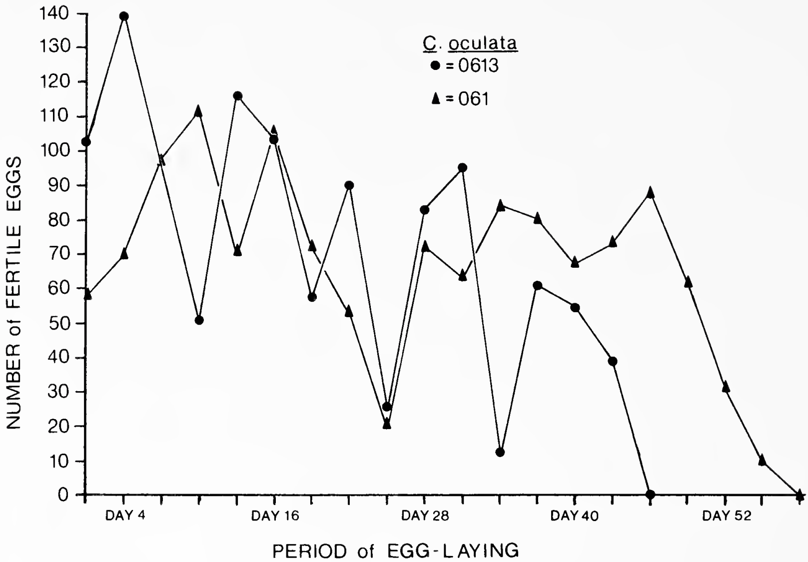

Figure 1. Fertile egg production as a function of time in two females of *Chrysopa oculata*, collected from the field. Eggs were clipped every 3 days.

were optimal. *C. downesi* varied considerably more than *C. plorabunda* in the time spent *in copulo*, although high variance typified both species.

Discussion

Female Fecundity.

Fecundity data on many lacewing species are well summarized in Rousset (1983). Our results differ strikingly from those of other workers, in the sheer numbers of eggs produced by individual lacewings under a variety of mating protocols. For example, even single-mated females of *C. plorabunda, C. downesi, C. harrisii, C. rufilabris,* and *C. oculata* produced 1000 or more fertile eggs (Table 2), which is significantly more than previously reported for any lacewing. Multiply-mated females increased this figure further, to 1207 in *C. plorabunda* and 1286 in *C. downesi* (Tables 3 and 4). (The champion was actually a single-mated *C. oculata* that deposited 1289 eggs in 55 days.) The literature reports individual maxima of only 617 for *C. oculata* (Smith, 1922), 850 for *C. plorabunda* (= *C. carnea* [Stephens]; Hagen and Tassan, 1966), and 189 for *C.*

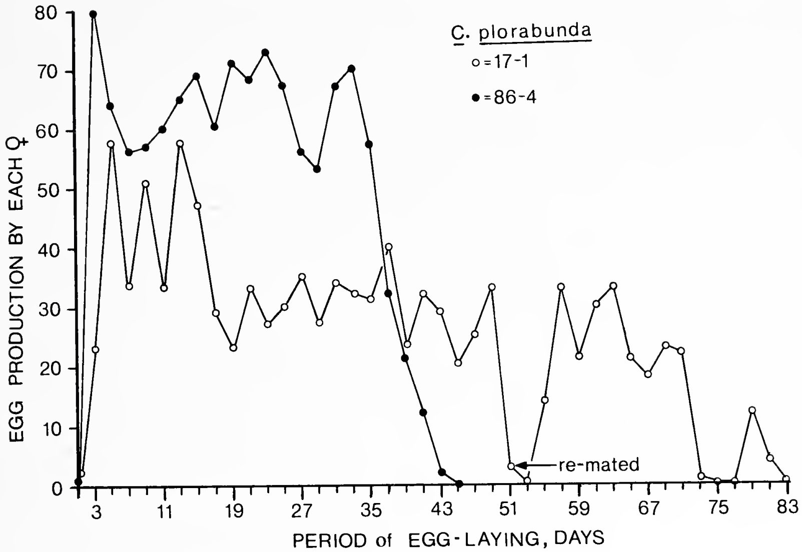

Figure 2. Fertile egg production as a function of time by two females of *Chrysoperla plorabunda,* mated in the laboratory on Day 1. Eggs were clipped on a 2, 2, and 3 day timetable each week.

rufilabris (Hydorn and Whitcomb, 1979; Ru *et al.,* 1976), all reared on diets very similar to those we used. We are unable to explain these discrepancies, except to note that great variability characterizes the reproductive potential of lacewings of all species. Occasionally, for example, we found ourselves rearing a stock of insects with consistently low fecundity and high larval mortality, despite continuing efforts to avoid inbreeding. Whether such episodes were the results of genetic factors or disease was never resolved, but analogous problems could have unnaturally curbed egg productivity in the studies of others.

An important and perhaps unexpected result of this work was the observed uniformity of maximal individual egg production from species to species. On the one hand, it may not be too surprising to find similar maximal fecundities in very closely related, sibling species like *C. plorabunda* and *C. downesi;* but more distantly related taxa like *C. rufilabris* and *C. harrisii* and even representatives of distinct genera like *Chrysopa oculata* also had similar individual lifetime egg totals. Actually, even the life-history patterns of the

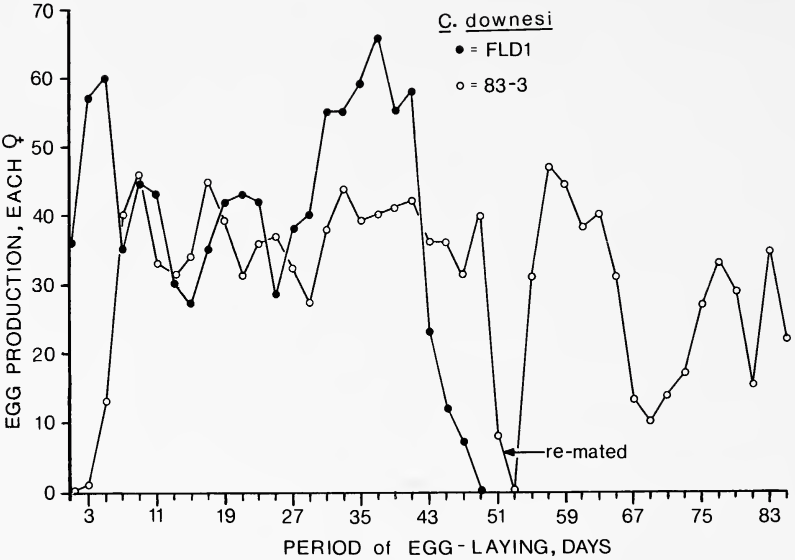

Figure 3. Fertile egg production as a function of time for two females of *Chrysoperla downesi,* mated on day 1 (83-3) or collected from field (FLD1). Eggs were clipped on a 2, 2, and 3 day timetable each week.

siblings *C. plorabunda* and *C. downesi* differ so much that their similar fecundities seem anomalous: the former species is multivoltine, whereas the latter is univoltine. In any case, it seems clear that individual females of either *C. plorabunda* or *C. downesi* can fertilize about 80 percent of their lifetime supply of viable eggs with the sperm of a single male, although this may not happen very often in nature, for reasons to be discussed shortly. Principi (1949) obtained similar results for *C. formosa* Brauer, suggesting that a fertilization pattern like this may be widespread in Chrysopidae. Females in some other insect orders have also been shown to fertilize most of their eggs with the sperm of their first mate: *Drosophila melanogaster* Meigen is a good example (Pyle and Gromko, 1978).

The relatively low fecundity of *Meleoma emuncta* (Table 2) may not be typical of the species or genus, for Tauber (1969) counted 347 fertile eggs from one female fed an artificial diet fortified with levulose and choline chloride. In that study, a specimen of *M. dolichartha* (Navas) produced 313 eggs from the same diet. As mentioned

Table 3. Fecundity of individual females of *Chrysoperla plorabunda* that were re-mated to satiation. Ovip. Days = oviposition lifespan, as in Table 1. Only fertile eggs were tabulated.

	Individuals																				
Matings	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
1st	497	793	271	893	809	698	786	822	14	301	410	186	138	95	1160	305	512	642	743	104	353
2nd	351	88	32	--	216	273	211	--	777	484	200	391	409	315	--	216	21	62	--	27	62
3rd	359	62	25	--	16	--	--	--	--	--	163	--	--	--	--	37	7	3	--	260	--
4th	--	--	469	--	--	--	--	--	--	--	--	--	--	--	--	--	--	16	--	22	--
5th	--	--	184	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6th	--	--	81	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ovip. Days	71	67	84	52	80	118	72	39			49	81	86	65	39	74	56	49		48	26
Total	1207	943	1062	893	1041	971	997	822	791	785	773	577	547	410	1160	558	540	723	743	413	415
Tot. Cops.	3	3	6	1	3	2	2	1	2	2	3	2	2	2	1	3	3	4	1	4	2
Eggs/Cop.	402	314	177	893	347	486	499	822	396	393	258	289	274	205	1160	186	180	181	743	103	208

Table 4. Fecundity of individual females of *Chrysoperla downesi*, re-mated to satiation. See Table 3.

	Individuals																
Matings	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
1st	796	64	840	37	509	388	840	793	991	475	571	636	102	644	463	303	512
2nd	101	824	446	107	502	320	--	--	--	399	200	--	353	--	--	145	22
3rd	--	80	--	104	--	238	--	--	--	--	--	--	--	--	--	--	--
4th	--	--	--	274	--	--	--	--	--	--	--	--	--	--	--	--	--
Ovip. Days	37	55	84	59	72	79	45	48	48	69	79	26	52	39	39	48	16
Total	897	968	1286	522	1011	946	840	793	991	874	771	636	455	644	463	448	534
Tot. Cops.	2	3	3	4	2	3	1	1	1	2	2	1	2	1	1	2	2
Eggs/Cop.	449	323	429	131	506	315	840	793	991	437	386	636	228	644	463	224	267

Table 5. Relationship of fertile egg production to sexual receptivity in several individual females of *Chrysoperla plorabunda* and *C. downesi.*

	Chrysoperla plorabunda									*Chrysoperla downesi*					
Individual	1	2	3	4	E	G	L	M	N	B	J	C	K	M	E
Oviposition days While Unreceptive	41	61	65	65	67	67	65	69	53	39	65	83	73	49	51
Number of Eggs Laid While Unreceptive	717	1167	928	535	916	974	570	527	405	692	874	1278	736	448	681
Eggs/Unreceptive Day	17	19	14	8	14	15	9	8	8	18	13	15	10	9	13
Oviposition Days While Receptive	10	10	4	10	14	8	6	6	6	18	2	2	6	2	22
Number of Eggs Laid While Receptive	56	40	15	23	125	23	7	20	5	276	0	8	35	7	330
Eggs/Receptive Day	6	4	4	2	9	3	1	3	1	15	0	4	6	4	15
Number of Matings	3	3	3	3	2	2	2	2	2	3	2	2	2	2	2

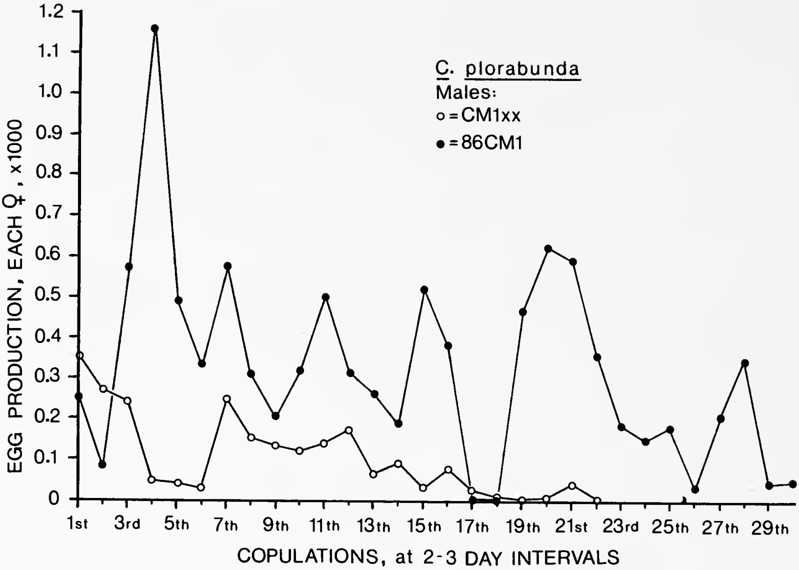

Figure 4. Total fertile egg production by the successive mates of two males of *C. plorabunda*, mated every 2 days (CM1xx) or every 2–3 days (86CM1). Young females were made available to 86CM1 after his 18th copulation.

earlier, species of *Meleoma* often have specialized dietary or photoperiod requirements that can complicate any measurements of fecundity. Actually, the number of eggs produced by females employed in our study was undoubtedly higher, because we cannot assess the number laid in the field prior to capture.

Female Polyandry.

It has long been known that female lacewings will mate more than once. Smith (1922) observed this in *C. oculata,* and second matings have been tabulated for European *C. perla* (L.) by Philippe (1971) and *C. plorabunda* by Jones *et al.* (1977), among others. The present study documents for *C. plorabunda* and *C. downesi* just how often a female will re-mate. Unlike many other insects—such as damselflies (Waage, 1983), scorpionflies (Thornhill, 1980), and crickets (Loher and Rence, 1978)—these green lacewings lose sexual receptivity after mating, and must nearly exhaust their stored supply of sperm before copulating again. Alternatively, it may be that stored sperm dies or is discarded by the female, or in some other way becomes unavailable to her; but the simplest explanation of our results is that sperm gets used up. As seen in Figs. 2 and 3 and Table 5, receptivity and re-mating are strongly correlated with dips in egg production, after which oviposition increases again to earlier levels. That the new surge of egg production is the result of and uses the new sperm is supported by two cases in which *C. downesi* females, originally mated to conspecifics, were later mated to *C. plorabunda* males; the new offspring were all F_1 hybrids with typical F_1 hybrid song phenotypes.

The extent of polyandry in these insects reflects the interaction of three factors: rate of egg-laying, number of usable sperm transferred from the male, and oviposition lifespan. Our data indicate that maximal rates of egg-laying and maximum oviposition lifespan are approximately equivalent in all lacewing species studied to date. For example, females in peak condition produce 40–60 eggs per day; field-captured *C. oculata, C. rufilabris,* and *C. harrisii* show generally higher values than laboratory-raised *C. plorabunda* or *C. downesi* (Table 1). Reports from the literature are more or less similar, ranging from the 20–40 eggs per night cited by Tassan *et al.* (1979) and Duelli (1981) for *C. plorabunda,* to the 48 per night mentioned by Ickert (1968) for *C. perla.* Similarly, oviposition duration is approximately the same in both *C. plorabunda* and *C. downesi* regardless of sperm availability (but is irretrievably diminished by senescence even in virgin females after two or at most three months; see Table 5). In contrast, the quantity of sperm contributed per copulation, interpolated from fecundity measured between matings, shows high variance, and may be the principal determinant of polyandry. Females that chance to receive relatively little sperm with successive copulations will repeatedly recover sexual receptivity and re-mate, whereas those receiving large amounts of sperm early in life will live out a significant or even dominant portion of their allotted reproductive lives depositing eggs fertilized by their first partners. Thus, the most frequently mated females like C and T of Table 3 and D of Table 4 produced only a few viable offspring from early inseminations. Female senescence can be seen most clearly when older, virgin females are mated to fresh males: invariably, egg production is significantly less than that of younger ones. At least some of the wide variance in fecundity can be attributed to age differences at first copulation. We found little evidence to support Philippe's (1971) suggestion, concerning *C. perla,* that sperm from each copulation fertilizes the eggs produced during a relatively constant number of oviposition days: in his study, 24.

In many ways, female polyandry in lacewings is much like that in *Drosophila,* particularly *D. melanogaster.* These females re-mate a few times during their lifetimes, but often fertilize most of their eggs with the sperm of one male (Pyle and Gromko, 1978). In *D. melanogaster,* about 78% of the sperm must be depleted before the female will re-mate (Ibid.). And although a female's total complement of eggs can in theory be fertilized from one copulation, multiple matings nonetheless increase lifetime egg productivity by a small but significant amount (Gromko *et al.* 1984). These flies, like lacewings, achieve such fecundity patterns by a similar mechanism: females totally lose sexual receptivity after copulating, and regain it only when stored sperm has been nearly depleted.

Male Polygyny.

The results of the male multiple-mating experiments are the most difficult to interpret (Table 6, Fig. 4). For the most part, individual males of *C. plorabunda* and *C. downesi* showed a rather steep decline in their ability to inseminate females with successive matings. Both tested males of *C. downesi* conform to this pattern, so that after two or three matings, they were unable to father more than a few progeny, even though each mated 10 times. Similarly, most of the 8 *C. plorabunda* males appeared to run low on sperm after a series of consecutive matings; for these and the *C. downesi* "normal" males, reproductive potential was only slightly greater than that of females, averaging between 1000 and 2000 progeny over a lifetime (Table 6). However, one male of *C. plorabunda* sired over 9600 offspring during his 3.5 month reproductive life, mating 30 times. What appears to be a decline in his fertility at the time of his 17th and 18th matings actually reflects the old age of the females used as his mates; once younger partners were recruited, post-copulation fecundity increased to levels nearly as high as those recorded early in the male's life (Fig. 4). Of course, it can be argued that data based on so few males are of little use. However, we were not so much concerned with average male mating performance and fertility as we were with maximal values, to determine whether individual males could inseminate many females and sire several thousands of offspring. Consequently, the results here can only underestimate the real reproductive potential of males of these species; a single vigorous, prolific individual is sufficient to highlight the differences between males and females.

In many insects, especially Lepidoptera, spermatogenesis is completed before adulthood (Chen and Graves, 1970; Chaudbury and Raun, 1966; Retnakaran, 1970; Jumper and Cannon, 1975). Other insects continue manufacturing sperm as adults, e.g., Coleoptera (Jumper and Cannon, 1975; Chang and Riemann, 1967); or cockroaches, like *Nauphaeta cinerea* (Olivier) (C. Busher, pers. obs.). Although no experiments have confirmed this, it seems reasonable to assume that insects that continue to produce sperm through their adult lives should be capable of manufacturing more of it than those endowed with a fixed quantity at adult eclosion. Research on spermatogenesis in green lacewings has not addressed this issue. Some data for *C. plorabunda* suggest a lepidopteran, fixed-quantity pattern (Sheldon and MacLeod, 1974; Jones *et al.,* 1977), and other studies on *C. perla* imply adult maturation and possibly adult manufacture of sperm (Philippe, 1970, 1972). It is known that individual spermatozoans in lacewings of *Chrysoperla, Anisochrysa,* and *Chrysopa* are quite large, measuring nearly 1 mm in length (Baccètti *et al.,* 1969; Rousset, 1983). Considering how much space 9000 long sperm would occupy, our results with male 86CM1 (=H of Table 6) strongly suggest continuous, on-demand sperm manufacture, at least in *C. plorabunda* and its close relatives.

These findings bear directly on the significance of sexual selection in lacewing species. Clearly, the potential is present for intense, asymmetrical sexual selection among males, because individual reproductive potential is so much higher in males than in females. In theory, a mere handful of males could monopolize the reproductive activities of a large number of females. If a given male could easily locate the receptive females in the area, and if those females had a way of choosing certain males over others, then he could experience disproportionately high reproductive success by either appealing to females or outcompeting other males. In nature, however, the situation is probably very different. Within a group of individuals living in close proximity, a male would most often encounter previously inseminated females that were unreceptive to his courtship songs. Secondly, males of *Chrysoperla* spp. are unable to call rare receptive females to them over long distances: their songs carry only centimeters, between individuals on contiguous substrates (Henry, 1980a). Thirdly, any male that can duet with a female is acceptable to her if she is sexually receptive (Henry, 1979, 1983, 1985a, b, 1986).

Table 6. Fertile egg production by the successive mates of individual males of three lacewing species, mated every 1–3 days to different females in the laboratory.

	C. downesi		*C. plorabunda*								*C. oculata*	
Matings	A	B	A	B	C	D	E	F	G	H	A	B
1st	680	510	104	809	786	271	893	512	353	251	629	359
2nd	549	27	27	167	367	21	591	469	269	81	709	788
3rd	4	645	0	123	370	--	17	--	239	573	--	809
4th	50	85	114	0	30	--	--	--	46	1160	--	--
5th	1	42	194	4	--	--	--	--	40	490	--	--
6th	49	9	0	--	--	--	--	--	28	331	--	--
7th	0	15	1	--	--	--	--	--	247	575	--	--
8th	1	2	0	--	--	--	--	--	151	308	--	--
9th	0	12	--	--	--	--	--	--	132	203	--	--
10th	0	0	--	--	--	--	--	--	117	318	--	--
11th	--	--	--	--	--	--	--	--	139	498	--	--
12th	--	--	--	--	--	--	--	--	169	314	--	--
13th	--	--	--	--	--	--	--	--	62	259	--	--
14th	--	--	--	--	--	--	--	--	88	185	--	--
15th	--	--	--	--	--	--	--	--	29	517	--	--
16th	--	--	--	--	--	--	--	--	76	378	--	--

Table 6. Continued.

	C. downesi		*C. plorabunda*								*C. oculata*	
Matings	A	B	A	B	C	D	E	F	G	H	A	B
17th	--	--	--	--	--	--	--	--	23	0	--	--
18th	--	--	--	--	--	--	--	--	2	0	--	--
19th	--	--	--	--	--	--	--	--	0	465	--	--
20th	--	--	--	--	--	--	--	--	3	620	--	--
21st	--	--	--	--	--	--	--	--	38	589	--	--
22nd	--	--	--	--	--	--	--	--	2	354	--	--
23rd	--	--	--	--	--	--	--	--	--	182	--	--
24th	--	--	--	--	--	--	--	--	--	145	--	--
25th	--	--	--	--	--	--	--	--	--	175	--	--
26th	--	--	--	--	--	--	--	--	--	28	--	--
27th	--	--	--	--	--	--	--	--	--	205	--	--
28th	--	--	--	--	--	--	--	--	--	345	--	--
29th	--	--	--	--	--	--	--	--	--	39	--	--
30th	--	--	--	--	--	--	--	--	--	45	--	--
Total	1334	1347	440	1103	1553	292	1501	981	2253	9633	1338	1956
Tot. Cops	10	10	8	5	4	2	3	2	22	30	2	3
Eggs/Cop.	133	135	55	221	388	146	500	491	102	321	669	652
Avg/Indiv:	1341			Avg/Indiv:		2220				Avg/Indiv:		1647
Std. Dev.:	7			Std. Dev.:		2863				Std. Dev.:		309
N:	2			N:		8				N:		2

Finally, field experience tells us that individual lacewings are moderately dispersed rather than tightly clumped in space, so that rarely if ever will two males be present to compete for the privilege of mating with a receptive female. For that matter, even in the laboratory under conditions designed to encourage such competition, males never interfere with and barely even notice one another's courtship activities. As a consequence, we feel it likely that reproductive success is reasonably egalitarian among healthy males, despite their potential as individuals for high sperm production and multiple copulations. Thus, the intensity of sexual selection is little different for males than for females of *Chrysoperla* of the *carnea*-group, for reasons first clearly outlined in Emlen and Oring's important review (1977) of environmental influences on mating systems. Sexual dimorphism, which is coupled to the degree of asymmetry of sexual selection, is minimal in these species, as expected from the above argument (although see Hafernik *et al.* [1986] for a discussion of sexual dimorphism without sexual selection).

GENERAL CONCLUSIONS.

The same basic patterns of reproductive biology characterize all the green lacewings of this study. In the future, sexually dimorphic taxa should be studied; here, we have concentrated on a sexually monomorphic genus, *Chrysoperla.* In this genus, lifetime fecundity is high and reasonably equivalent in several common species. Polygamy of both males and females is the rule, although females can fertilize most of their eggs with sperm acquired from one copulation. Sexual receptivity mediates re-mating in females, and is only recovered when stored sperm is nearly depleted or otherwise unavailable. The time between matings varies greatly with the success of insemination; because sperm must be almost used up by egg-laying before re-mating occurs, one is forced to the conclusion that males transfer variable quantities of sperm to different females. The causes of such variability in a given male are unknown, since the success of insemination shows no reliable correlations with either the number of previous matings or the duration of copulation. Potential for lifetime reproduction is much higher for males than for females because males can produce nearly unlimited quantities of sperm, but this potential probably goes unrealized in nature, because males have no reliable way of finding the few sexually

Table 7. Fertile egg production versus copulation duration characterizing 27 individual females of *Chrysoperla plorabunda* and 15 of *C. downesi.*

		Chrysoperla plorabunda			
Dura.	5–7 min	8–10 min	11–13 min	14–18 min	19–65 min
Number	9	271	114	27	--
of	14	305	119	104	--
Eggs	85	351	166	168	--
Laid	102	698	353	194	--
Per	301	786	410	--	--
Individual	387	793	512	--	--
After	484	809	--	--	--
Mating	743	893	--	--	--
	777	--	--	--	--

		Chrysoperla downesi			
Dura.	5–7 min	8–10 min	11–13 min	14–18 min	19–65 min
Eggs	--	54	512	9	21
per	--	463	796	27	64
Individual	--	--	--	138	161
after	--	--	--	171	644
Mating	--	--	--	303	824
	--	--	--	--	840

receptive females in a population at a given time. The resulting approximate equality of sexual selection in the two sexes encourages low sexual dimorphism, as observed, although we acknowledge that there can be other causes of slight sexual dimorphism. Further speculation on subtle strategies of mate choice or sperm rejection by females or of sperm competition within the female's storage system should probably await experiments to test specific hypotheses.

ACKNOWLEDGMENTS.

This study was supported in part by National Science Foundation award BSR-8508080 to the first author and by the Research Foundation of the University of Connecticut. We thank Jane O'Donnell, William Cook, Raymond Pupedis, Carrie Toth, Julie Weber, and Gary Zanauskas, all presently or formerly of the University of Connecticut, for help in collecting and maintaining living lacewings. Our thanks are also extended to the staff of the E. N. Huyck Preserve, Rensselaerville, N.Y., for permission to collect at that site, and to

James Johnson, University of Idaho, for sending live material from western North America. Carl Schaefer (University of Connecticut) unsparingly criticized and edited an early version of the manuscript, and two anonymous reviewers made additional helpful suggestions.

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CIRCADIAN RHYTHM IN THE TROPICAL ANT *ECTATOMMA* (HYMENOPTERA: FORMICIDAE)*

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Introduction

In early 1960 I surveyed the daily activity rhythms of three tropical ponerine ants, *Paraponera clavata, Ectatomma tuberculatum,* and *E. ruidum,* first on Barro Colorado Island (BCI), Panama, then in the laboratory upon return home. The study of *Paraponera* was reported previously (McCluskey & Brown 1972). That of *Ectatomma* presented here is of interest in spite of being based on limited material, because it is one of the few studies of rhythmicity of ants in controlled conditions; the two species appeared opposite in time-of-day out of the nest, in both field and laboratory; and the rhythm of *E. tuberculatum* persisted in constant conditions.

Methods and Materials

All the observations for either species, whether field or laboratory, were on one nest (except Fig. 1, field *E. ruidum,* two nests); hence the conclusions are based on replicate days, rather than nests.

In the field, the best ant counts for the *tuberculatum* nest were on an adjacent vine, whereas the counts for *ruidum* were mostly on the ground. This accords with Levings & Franks' (1982) statement that *E. ruidum* forages mainly at ground level, whereas *E. tuberculatum* forages mainly at shrub level. Night counts were made by dim red flashlight.

At the end of January workers from the *tuberculatum* nest and from one of the two *ruidum* nests were taken back to E. O. Wilson's laboratory at Harvard. They were kept in a darkroom at a constant temperature of 27.5 ± 1.5°C. (The shaded ground temperature on BCI averages 25–26°C all year [Levings 1983].) In alternating light and darkness (LD) there was fluorescent light, 400 lux, for 12 hours

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*Manuscript received by the editor June 24, 1987.

daily. There was clear ruby light during the dark hours, and continuously during constant darkness (DD).

The group of ants of each species was placed in a two-chambered nest. Each chamber was a clear plastic box about 10 cm in diameter and depth. One chamber was darkened and had water and sugar water provided; the other served as an arena, dry and fully exposed to the light regime, and the counts were made there. To avoid interference with the ant rhythms, food was renewed only when observations were to be omitted for the following hours or days.

RESULTS

Field

Figure 1 shows the number of *E. tuberculatum* out, as assayed on the vine. A prominent increase occurred at dusk. The number was high during at least the first half of the night, and was low from dawn through the day. Fewer counts were made in the rest of the area around the nest entry (not shown), but they corroborated the high-night, low-day pattern.

The pattern for *E. ruidum,* on the other hand, was diametrically opposite, high in the day and low at night, as based on two nearby nests of *ruidum* observed on the same days as *tuberculatum* (Fig. 1).

Laboratory Light and Dark

The number of *E. tuberculatum* out in the arena started rising from soon after light-off, to the highest peak early in the night (Fig. 2). The number fell after the lights came on, remaining low through the light period, as in the field. The rise after light-off and the fall after light-on had also been seen in LD over a month earlier, good because so soon after collection from the field (but not shown here because so few night counts were made then).

The *E. ruidum* counts were higher in the light period than at night (Fig. 2), and thus opposite to *tuberculatum* observed the same days.

Constant Darkness

What is the evidence for persistence of rhythm in the absence of the light-dark cycle? For each of the first 3 days of DD (Feb. 9–11), ant counts were made during what *had* been the light and the first of the dark part of the LD cycle. There was no obvious rhythm for *E. ruidum,* possibly because of so low a number of ants out in the

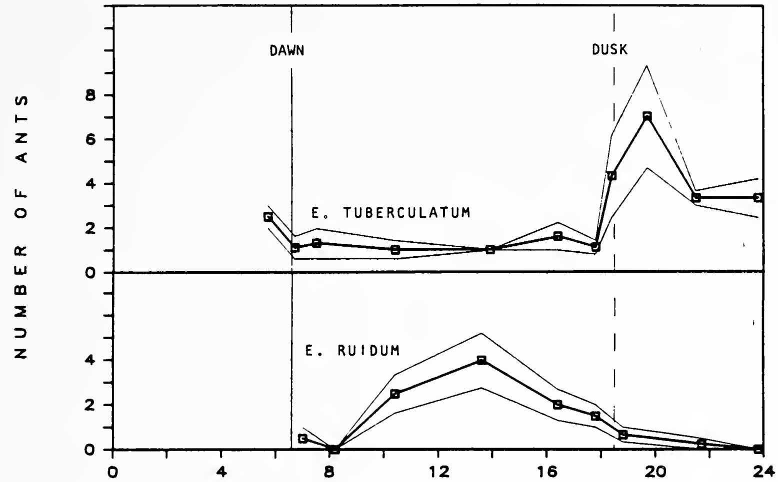

Fig. 1. Above-ground field rhythm on BCI. *E. tuberculatum,* ants on vine within 2 m of nest; mean ± SE, n = 3–4 (i.e., each mean is based on 3–4 days as replicates for given hour on graph), Jan. 10–11 and 17–21; $P < .01$ for difference among hours (one-way ANOVA). *E. ruidum,* 2 nests, ants within .5 m of nest. N = 2-4 (nest and/or day replicates), Jan. 10–11 and 17–19; $P = .01$.

arena, always in contrast with the high number for *tuberculatum;* and the record is not shown.

E. tuberculatum was checked in two ways, DD following LD, and DD following light exposure at night. Fig. 3 serves to illustrate both, because the patterns were similar relative to what had been the light period. In DD (Feb. 9–11) following LD the arena count resembled that in LD in that it was low near what had been the light-on hour and high near what had been light-off. The data are too few to compute an accurate free-running period; but for the total 3-day span of counts a cosine least-squares fit (Halberg et al. 1972) to a trial period of 24 hours is good ($P < .01$), thus suggesting a persistent rhythm. And the counts for the various times of day differ consistently (using the 3 days as replicates, ANOVA $P < .001$), again suggesting persistence.

If rhythmicity is truly endogenous it should still appear after reversal of day-night phase. So the lights were turned on at 2000 Feb 13 for 12 hours (i.e., through the night), then left off continuously

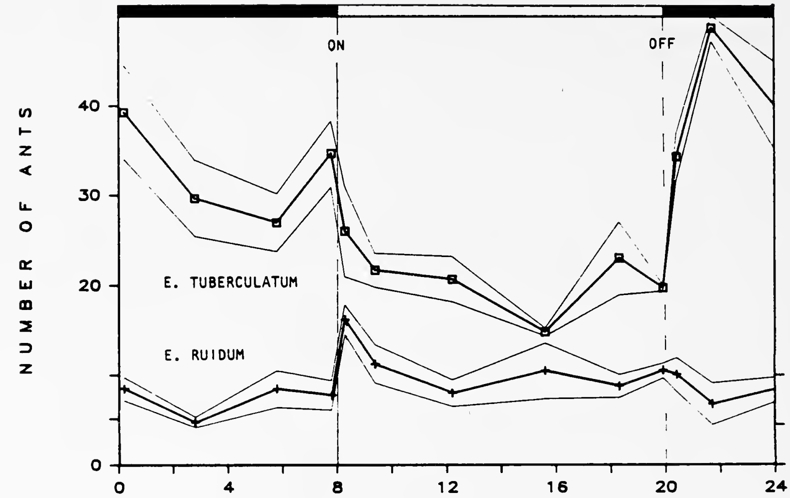

Fig. 2. LD arena rhythm of group of workers from BCI colony. Ants out in arena, mean ± SE, days as replicates (one-way ANOVA), Mar. 10–14. *E. tuberculatum, P*< .001; *E. ruidum,* P = .01.

again. Counts were started at 0600 Feb 15. They rose toward the highest near light-off of what had been the single night light exposure (2000–0800 in Fig. 3). The hourly pattern is consistent from day to day (ANOVA P < .001). [Still assuming a 24-h free-running period, the peak in Fig. 3 appears somewhat early: the peak hour of a cosine-fitted (P < .001) curve was about 0500, instead of 0800 (i.e., the new 'dusk' hour) as expected if the rhythm had been completely inverted.]

(In DD Mar. 15–18, the pattern was much less clear, and neither it nor records later in March–April are shown.)

Discussion

What do these observations say about rhythmic behavior in *E. tuberculatum*? 1) The colony was notably rhythmic in the field, the ants appearing outside the nest primarily at night. 2) A colony fragment in lab constant temperature exhibited a similar rhythm, indicating that it is not simply a reflection of cyclic field temperature. 3) In constant darkness there was evidence for persistence of rhythm, indicating that it is not simply a response to the light-dark cycle of the field, either.

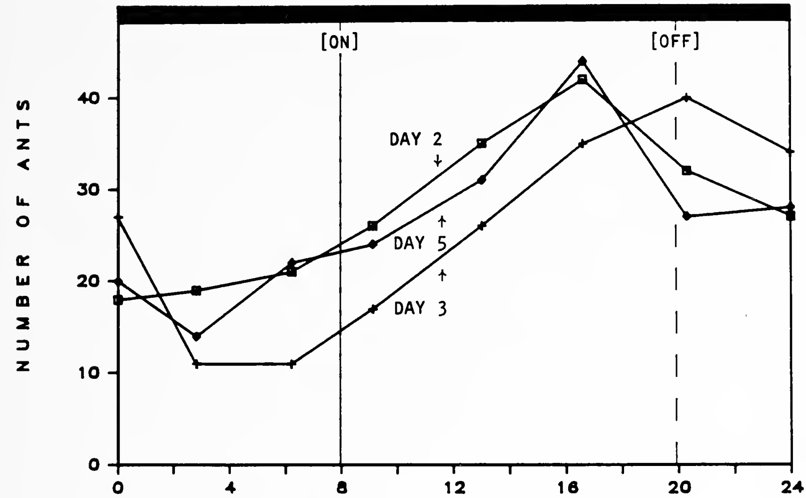

Fig. 3. Same group of *E. tuberculatum,* in same artificial nest, as in Fig. 2. DD arena rhythm, following single exposure to light for 12 h starting Feb. 13 at 2000. Day 2 = Feb. 15–16, 3 = Feb. 16–17, 5 = Feb. 18–19.

This suggests a rhythm that is circadian in the strictest sense—internally controlled. The evidence stopped short of this for workers of the other two species studied simultaneously, *Paraponera* (McCluskey & Brown 1972) and *E. ruidum* (reported here); there was good rhythm in the lab, but no apparent persistence in constant darkness. However, in those two species, the colony fragment and/or hourly count of ants was much smaller; and this or other limiting conditions may well have obscured display of persistence. On the other hand, it should be noted that the male and female *Paraponera* studied at the same time did show a persistent rhythm.

There is interesting field evidence for internal control of timing in workers of another BCI species, a leaf-cutting ant (Hodgson 1955). The ants were already in the nest openings an hour before dawn, too early for environmental cues of the approach of dawn; yet even strong light did not reveal them there or bring them forth at earlier hours of the night.

For each species of *Ectatomma* the LD timing corresponded to that in the field. And in both field and laboratory, the two species were out of the nest at opposite times of day. If these particular nests are indeed characteristic of the species, we would see here an exception to the general trend of similarity in rhythm among the species of a genus (McCluskey 1973, 1974). A clear exception is the genus *Myrmecocystus,* where the members of one subgenus are diurnal, and of another subgenus, nocturnal (Snelling 1976).

The field rhythm for the *E. tuberculatum* colony was the same as for the one reported by Wheeler (1986), also on BCI, but in July and October, during the rainy season (though the two days were neither rainy nor overcast). My January observations were made during the transition to the dry season. For her colony there was a mass exit at dusk, with continued high foraging during the night, reduced to a very low level through the day. However, in Costa Rica in September she saw much foraging in the morning as well as at night, with no mass exit at dusk. (The habitat was different, e.g., dry forest rather than moist forest as on BCI.)

Long ago as these observations were made, I still remember them vividly—such a clear demonstration of circadian rhythm in the worker caste, not always seen in experience with other species. It made the strenuous around-the-clock observations worthwhile.

Summary

Workers from one colony each of *E. tuberculatum* and *E. ruidum* were studied on Barro Colorado Island, then in the laboratory. The peak number out near the field nest was early night for *tuberculatum,* but during the day for *ruidum.* In LD the rhythms were likewise opposite. In DD the *tuberculatum* rhythm persisted. Noteworthy here is the apparent species difference in phase of rhythm, in both field and laboratory; and the persistent rhythm, not always so obvious in the worker caste of ants.

Acknowledgments

This research was supported by postdoctoral fellowship NSF 49101 at the Biological Laboratories of Harvard University. I thank W. L. Brown, Jr., for his aid in determining the ant species, as well as in so many other ways while together on the BCI trip, and now for reading the manuscript; and E. O. Wilson for making all this possible, and for such a free use of his laboratory.

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A REVIEW OF THE SUBSPECIES CONCEPT IN THE EUMENINE GENUS *ZETA* (HYMENOPTERA: VESPIDAE)*

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Menke and Stange (1986) reported the establishment of the potter wasp *Zeta argillaceum argillaceum* (L.) in Dade County, Florida. This is the first species of this neotropical genus to be found in the United States. While identifying a small collection of Florida eumenines for Dr. Peter J. Landolt of the USDA Insect Attractants Lab in Gainesville, I discovered an additional specimen of this species from Dade County. It represents a color form, or "subspecies", different from that reported by Menke and Stange (1986). In this note I discuss recognition of subspecies in *Zeta,* and demonstrate that most are artificial taxa. Plasticity in coloration is a common phenomenon in Hymenoptera, and has even been shown to be experimentally manipulable in Vespidae (MacLean *et al.,* 1978). Yet recognition of subspecies purely on the basis of color differences remains a common practice in vespids, including *Zeta,* and other aculeates. The recent revision of the genus by Giordani Soika (1975) recognizes only four species in *Zeta,* but these are divided into no fewer than 15 subspecies, 10 of which are in *argillaceum!* These are all based on color, and in the continental forms the distributions frequently overlap. I have examined most of these "subspecies", and conclude that they do not merit formal recognition. Most of them are synonymized below. I have not treated the subspecies of the Antillean *abdominale.* Acronyms for collections are those of Heppner and Lamas (1982).

Zeta argillaceum (L.)

Sphex argillacea Linnaeus, 1758: 569. (type ♀ BMNH)—"Surinami."
Vespa canaliculata Olivier, 1792: 672. Type depository unknown—"Cayenne."
Vespa diadema Fabricius, 1798: 263. (ZMUC)—"Cajennae."

**Manuscript received by the editor June 3, 1987*

Eumenes orbignii Saussure, 1852: 69. ♀ (MNHP)—"Bolivie, Chiquitos." NEW STATUS.

Eumenes orbignyi (!) Saussure, 1853, Table alphabétique: 273.

Eumenes canaliculatus var. *dives* Zavattari, 1912: 129. ♀ (lectotype NHMV, designated by Giordani Soika, 1975: 122)—"Ecuador: Guayaquil." NEW STATUS.

Eumenes lineatifrons Cameron, 1912: 227. ♀ (BMNH).

Zeteumenes canaliculata for. *riojana* Bertoni, 1934: 110. Type probably lost—"La Rioja." NEW STATUS.

Zeteumenes argillaceus hubrichi Giordani Soika, 1969: 383. ♀ ♂ (type ♀ Zool. Staatsammlung, Monaco)—"Argentina: Granja." NEW STATUS.

Zeta argillaceum incarum Giordani Soika, 1975: 116, 126. ♀ ♂ (type ♀ USNM)—"Peru: Valle Chanchamayo, 800 m." NEW STATUS.

Zeta argillaceum distinguendum Giordani Soika, 1975: 117, 124. ♀ ♂ (type ♂ Zool. Staatsammlung, Monaco)—"Argentina: Buenos Aires, Tandil." NEW STATUS.

Zeta argillaceum apurimacense Giordani Soika, 1975: 117, 125. ♀ ♂ (type ♂ BMNH)—"Peru: Apurimac, Cuzco-Abacay Road, Apurimac Crossing at Cuya, 1900 m." NEW STATUS.

Zeta argillaceum pallidior Giordani Soika, 1975: 117, 127. ♀ ♂ (type ♀ stated to be at CU, but not found)—"Messico: 3 miglia a N di Alpuyeka, 3440 ft." NEW STATUS.

Zeta argillaceum peruense Giordani Soika, 1975: 118, 126. ♀ ♂ (*peruensis;* type ♀ BMNH). NEW STATUS.

A male collected at the USDA Lab in Dade Co., Florida on Nov. 6, 1981 by Dr. Landolt and now in the MCZ most closely resembles *hubrichi,* originally described from Argentina. The specimen is primarily reddish brown with limited yellow maculations as follows: the pronotum rimmed both anteriorly and posteriorly, the mesepisternum in part, a line in front of the parategula, and the scutellum laterally and metanotum entirely. The second metasomal tergum is not darker than the successive terga. However, this pattern is either developed or approached in specimens determined as other subspecies in the collections of the MCZ (most of the specimens listed in Giordani Soika, 1975, as being in the USNM are in fact in the MCZ, and there are numerous other similar errors), CU and USNM. Careful examination of series of these subspecies showed discrepancies with Giordani Soika's (1975) key, as well as transitional forms and distributional overlap. I have seen specimens of nine of the ten subspecies of *argillaceum* in the collections of the MCZ, CU and USNM, and cannot consider them distinct. The following discussion documents the synonymy.

The difficulties begin with the first couplet of Giordani Soika's subspecies key, which gives as alternatives (my translation):

> "Ferruginous, or brown-ferruginous, and black without yellow markings. In some examples (transitional to *hubrichi*) part of the posterior margin of the pronotum and apex of tergum I may be yellow."
> vs.
> "Yellow markings fairly extensive both on thorax and abdomen."

This vague couplet fails for numerous specimens in the MCZ from Brazil, Nova Teutonia, determined by Giordani Soika as *orbignii,* as well as other specimens from Paraguay and Argentina. This subspecies is supposed to key to the first alternative, but may have the yellow markings as extensive as in *hubrichi* or *distinguendum,* which are supposed to key to the second alternative. But examination of these specimens further shows that the distinction between the typical subspecies and *orbignii* does not hold up. The typical form is distinguished from *orbignii* only by having the second tergum darker than successive terga and the mesosoma. Typical *argillaceum* is confined to the Guianas, while *orbignii* is listed in Giordani Soika (1975) as occurring in Trinidad, Brazil, Bolivia, Peru, Paraguay, Uruguay and Argentina—although he himself (pp. 116 and 119) noted transitional forms in Brazil, Paraguay and Argentina. The specimens in the MCZ, CU and USNM show great variation in the darkness of tergum II *throughout* the range of *orbignii.* There are specimens assignable to the typical subspecies from Trinidad, Brazil, Peru, Paraguay and Argentina (as well as Venezuela and Colombia). Recognition of *orbignii* as a subspecies separate from the typical form is therefore unwarranted. The specimens cited by Giordani Soika as transitional to *hubrichi* also belong here. Two specimens labelled as such by Giordani Soika are in the collections of CU and the USNM, and they have the terga dark. One other "subspecies" keys to the first alternative of the first couplet, and belongs here. This is *incarum* Giordani Soika, described from the Cordillera in Peru. I have seen two specimens from CU. It is the only subspecies distinguished in the key by a morphological feature, namely the relative length of the hair on the scutum. However, this also occurs in the subspecies *peruense,* as well as numerous other species of eumenines found at higher elevations throughout the world. It seems to be primarily an ecological correlate. There is no other difference—the metasomal terga are black or brown, as in typical *argillaceum.*

The remaining seven subspecies are supposed to key to the second alternative. They are not really distinct from one another. The character distinguishing *dives* and *riojanum* in Giordani Soika's key, whether the pronotum is entirely or only partly yellow, is both trivial and not really true. For example, one of the MCZ specimens of *riojanum* from Belen-Los Nacimentos (seen by Giordani Soika, but cited as deposited in the USNM), and three CU and one USNM specimens from La Rioja have the pronotum nearly entirely yellow—supposed to characterize *dives.* The subspecies *peruense* in turn differs from these two forms in the amount of black on the mesepisternum and pronotum, as well as the relatively long hair on the scutum. These are all trivial features; the color in *peruense* differs only in having the black sometimes more extensive on the pronotum and mesepisternum, but there are specimens in the USNM with the pronotum completely yellow, and the amount of black on the mesepisternum varies considerably in specimens of all three subspecies. The length of the hair is probably an ecological correlate, as noted above. The characters cited in the key as distinguishing *hubrichi* from the three preceding subspecies all occur in *dives* and *riojanum.* The subspecies *pallidior* is in turn distinguished from these four forms by reduction of the black markings; it is Mexican while the others are South American. A specimen in the MCZ from Costa Rica: Guanacaste Prov., Playa Brasilito has the black markings limited to the base of terga I and II, the base of the metapleuron and the scutum. A specimen at CU from Panama, Coco Solo CZ is similar, but has a mesal black line on the scutum and most of the metapleura black. These specimens are thus intermediate both in color and range. The subspecies *distinguendum* is distinguished from these five forms only by having the propodeum black, whereas it is primarily yellow or ferruginous in the other subspecies. However black markings may appear in specimens of these other subspecies, and their extent varies in specimens of *dives* from Peru and Ecuador in the USNM. Recognition of any of these six forms as subspecies is therefore unjustified. Further, although I have not seen specimens of *apurimacense,* the characteristics by which it is distinguished from *distinguendum* in the key are subject to the same kind of variation as those just discussed. These are the extent of yellow on the dorsum of the thorax and ferruginous on the first metasomal tergum. I am confident that *apurimacense* is no more than another minor local variant, and have no hesitation in synonymizing it.

Finally, as mentioned above the initial couplet as written fails to separate the subspecies into two distinct groups, but can a distinction be made? Specimens supposed to key to the first alternative are typically darker than those supposed to key to the second alternative: the metasomal terga are usually black or brown in the first group and light reddish in the second; the yellow markings are usually much more extensive in the latter. The darker form is distributed from the Guianas south to Argentina, primarily east of the Cordillera, whereas the lighter form is distributed along the Cordillera north to Central America. But these forms overlap in northwestern Argentina (cf. Giordani Soika, 1975), Paraguay (MCZ specimens from Mborero and Molino-cué), Peru, Colombia (an MCZ specimen of "typical *argillaceum*" is from Meta: Carimagua) and Venezuela (MCZ and USNM specimens). Nor are they always distinct in color. Variation in the extent of yellow was already discussed, and the darkness of the metasoma is also uncorrelated with distribution. For example, specimens of *distinguendum* I have examined have the metasoma as black as dark specimens of *orbignii,* while pale specimens of the latter have the metasoma light reddish. So even just these two groups cannot really be diagnosed. Recognition of subspecies is in my view a poor way of dealing with color variation in vespids anyway, but in this species it is untenable.

Zeta confusum (Bequaert & Salt)

Eumenes confusus Bequaert & Salt, 1931: 768. ♀♂ (type ♀ MCZ)— "CUBA. Soledad". The following label data were not mentioned in the description: collected by Geo. Salt, March 28, 1925, at *Spodeas purpurea.*

Eumenes confusus var. *pinetorum* Bequaert & Salt, 1931: 771. ♀♂ (type ♀ CMP)—"Nueva Gerona, ISLE OF PINES (G. Link)". NEW STATUS.

The subspecies in *confusum* are at least allopatric, but examination of the material in the collection of the MCZ confirms that these subspecies are not really distinct. The subspecies *pinetorum* was distinguished from the typical form by reduced yellow markings on the mesosoma and the metasoma being "ferruginous" red, as opposed to orange red. I have examined the holotype of the typical form, ten paratypes (these latter specimens were not labelled as such, but the locality data correspond to those listed in the original description), and the two paratypes of *pinetorum* mentioned by Bequaert and Salt (1931) as deposited in the MCZ (and listed by Giordani Soika as deposited in the USNM). I have seen 13 additional specimens pinned in the same unit tray as typical *confusum,* from various localities in Cuba: Havana, San Blas, Baraguá and simply "Cuba" or no locality (some also seen by Giordani Soika). However, one is from the Isle of Pines, and so assignable to *pinetorum*. These specimens show extensive variation in the extent of yellow on the mesosoma and the color of the metasoma, so that the color distinction does not hold up here either. Since *pinetorum* is thus *not* "a distinct color form" (Bequaert and Salt, 1931), I synonymize it with the typical form.

SUMMARY

Subspecies concepts in the eumenine genus *Zeta* are discussed. Examination of subspecies in the genus distinguished by color alone indicates that the distinctions between them do not hold up, and the following are synonymized: *orbignii* (Saussure), *dives* (Zavattari), *riojanum* (Bertoni), *hubrichi* (Giordani Soika), *incarum* Giordani Soika, *distinguendum* Giordani Soika, *apurimacense* Giordani Soika, *pallidior* Giordani Soika and *peruense* Giordani Soika with typical *argillaceum* (L.); *pinetorum* (Bequaert & Salt) with *confusum* (Bequaert & Salt).

ACKNOWLEDGMENTS

I thank Peter J. Landolt for sending the Florida specimen which occasioned this work. J. K. Liebherr made the specimens of Cornell University available for study. Arnold S. Menke arranged the loan of material from the U.S. National Museum, and made valuable comments on the manuscript. This research has been supported by NSF Grant BSR-8508055 to the author.

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THE ROLE OF SCOUTING IN SLAVE RAIDS BY *POLYERGUS BREVICEPS* (HYMENOPTERA: FORMICIDAE)*

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Introduction

The formicine ant genus *Polyergus* contains four species, all of which are obligatory social parasites of the related genus *Formica.* Slave ants are obtained during group raids, in which a swarm of *Polyergus* workers penetrates a nest of *Formica,* disperses the adult workers and queen, and carries off the pupal brood (Topoff et al. 1984, 1985). Although many of these pupae are subsequently consumed in the slave-maker's nest (Kwait and Topoff 1984), a significant portion of the *Formica* brood is reared through pupal development. Workers eclosing from this pupal population subsequently perform their typical functions (i.e., foraging, feeding, nest defense) as permanent members of a mixed-species nest.

Ever since the pioneering studies on *Polyergus rufescens* by Huber (1810) and Emery (1908), on *P. lucidus* by Talbot (1967) and Harman (1968), and on *P. breviceps* by Wheeler (1916), it has been well known that slave-making raids are usually initiated by a small group of workers called scouts. These individuals locate target colonies of *Formica,* return to their colony of origin, recruit nestmates, and lead the raiders back to the *Formica* nest. Despite the generalization that *Polyergus* slave raids are typically preceded by scouting, virtually no field studies exist showing the actual paths travelled by scouts, or their overall importance in initiating slave raids. In their study of laboratory colonies of *P. lucidus,* Kwait and Topoff (1984) found that most raids were indeed directed towards

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**Manuscript received by the editor May 2, 1987.*

Formica schaufussi nests that were scouted on the same day. And in a preliminary field study, the removal of scouts on each of 3 days in the field resulted in the absence of slave raids.

In this paper we report the results of longitudinal field studies on two colonies of the western slave-making ant *Polyergus breviceps.* In the first study, we discovered that scouts use a biphasic search strategy, consisting of an initial linear component, followed by random search within a limited sector. An additional finding was that scouts may use three different routes on the outbound run, return trip, and slave raid respectively. In the second study, in which we removed all scouts during a period of 19 days, we verified their importance for raid onset.

PATH OF SCOUT

Materials and methods

All studies on scouts were conducted at the Southwestern Research Station, located 5 km west of Portal, Arizona. At an altitude of 1646 m, the ground in this habitat is covered with bunch grass and contains extensive leaf litter from alligator juniper, Arizona oak, and Chihuahua pine. The period for this study was July 10–30, 1986. To facilitate the detection of *Polyergus breviceps* scouts, one colony was enclosed by a circular, aluminum-flashing fence (15 cm high), using the *Polyergus* nest entrance as the center. The radius of the enclosure was 7 m, which insured that all ants reaching the fence were scouts (and not the circlers, which routinely emerge and mill around the nest entrance prior to raiding). To enable scouts to move in and out of the enclosure, the fence contained four gaps (15 cm wide) at 90-degree intervals, starting at the north end. Beginning at 1400 hr (MST), one person walked continuously around the circular fence. Scouts reaching the fence usually ran along the inside wall, and left the enclosure immediately upon encountering the nearest gap. Sometimes, a scout ran back and forth along the same small section of the fence's inner wall. On these occasions, a garden trowel was placed in the scout's path. When the scout moved onto the trowel, it was lifted and placed on the ground on the outer side of the fence. The path of each scout was marked by placing the stick end of cotton swabs (painted yellow and numbered sequentially) into the ground behind the scout, at approximately 1-m intervals. Because of the grass and leaf litter, this procedure required two persons, the first to constantly monitor the scout's path, and the second to place the numbered markers. Using a compass and a rolling measuring wheel, a map was made depicting the scout's path.

Results

During the three-week period of this study, 18 scouts were followed on 12 different days. Of these 18 scouts, five were tracked only on their outbound trip to a target colony of *Formica gnava.* For three other scouts, we succeeded in following their return trip as well. On five occasions, our tracking was abruptly halted when the scout was seized and killed by a spider. The remaining five scouts disappeared beneath the leaf litter before reaching a target colony.

The outbound paths of all scouts consisted of two distinct phases. Because of the essential similarity in movement among the scouts, the route illustrated in Figure 1 can serve as a typical example of scouting behavior. The target *Formica* nest on this day was located approximately 40 m to the west of the *Polyergus* nest. Phase one of scouting began when individuals left the swarm of ants circling around the nest, and moved in a relatively constant compass direction. For the scout on the afternoon of July 23, this straight run extended about 30 m to the west (the range for phase-one scouting on all days was 25–45 m). During this phase the scouts ran continuously, without stopping to search for *Formica* colonies. The second phase of scouting involved a qualitatively different pattern of movement, with scouts changing direction after running small distances over all compass directions. More importantly, it was only during this second phase that scouts periodically stopped and searched beneath rocks and patches of leaf litter. On July 23, this searching phase extended the scout's path for an additional 10 m to the west, with the north and south displacement combined covering about 14 m. Thus the searching phase of this particular scout covered an area of approximately 140 m^2.

A representative map of the complete sequence of successful scouting, followed by a slave raid, is illustrated in Figure 2. To clarify the distinctness of the paths, the erratic phase-two movements of the scout were replaced by a line extending from the end of the phase-one run, directly to the target nest. The most significant finding here is occurrence of three non-overlapping routes for the outbound run, return trip, and slave raid respectively. After locating

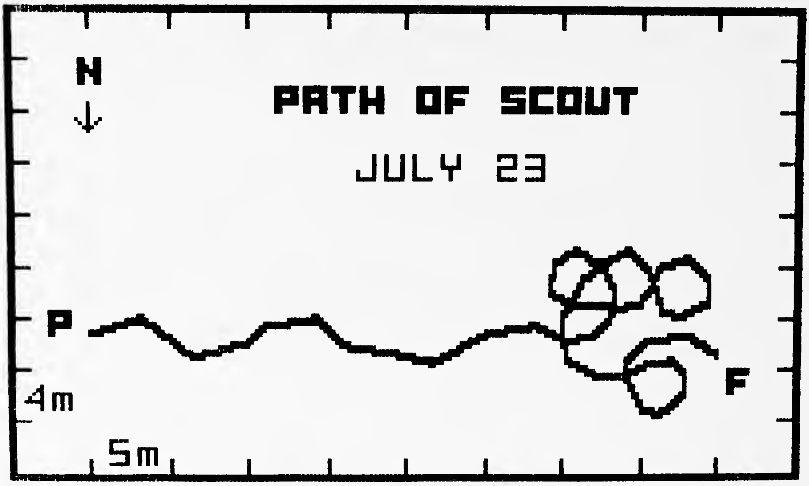

Fig. 1. Outbound path of *Polyergus* scout, consisting of a linear phase, followed by a circuitous (searching) phase. Scales of distance are shown at the lower left corner. N = north; P = location of *Polyergus* nest; F = location of *Formica* nest.

a *Formica* nest, the scout's return route paralleled its outbound course, but was displaced about 1 m to the east. The slave raid back to the *Formica* colony was displaced an additional 2 m to the east. Because the scout was not marked, we can not be certain that the slave raid was led by the same individual. Nevertheless, our previous studies with marked scouts (Topoff et al. 1984) indicate that successful scouts of *P. breviceps* typically run (at least intermittently) at the head of raid swarms.

IMPORTANCE OF SCOUTS FOR SLAVE RAIDS

Materials and methods

To determine the importance of scouts for initiating slave raids, another aluminum-flashing fence (15 cm high, 7 m radius, and containing four exits spaced at 90-degree intervals) was constructed around a second colony of *P. breviceps.* Every afternoon, from 1400 hr to 1800 hr, the perimeter of the enclosure was continuously monitored for the presence of scouts. For each scout, we recorded the time of arrival at the fence and the compass direction in which it was travelling. Each scout was then removed and placed in a holding container until the end of the day, at which time all the captured

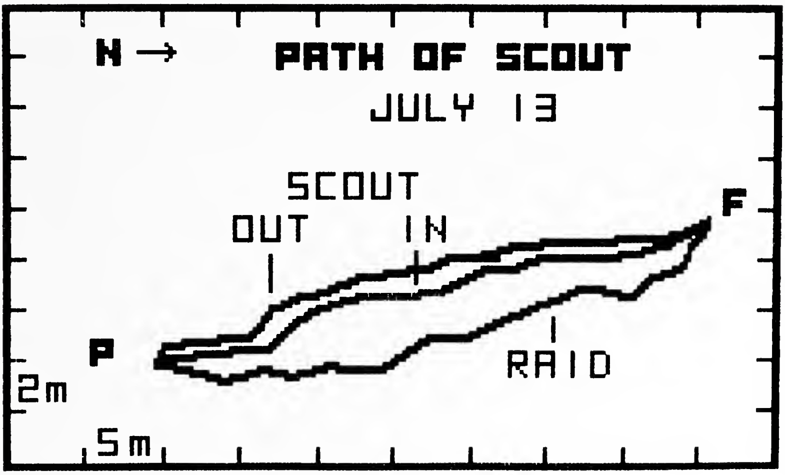

Fig. 2. Comparison of routes taken by *Polyergus* scout during outbound trip, return run, and subsequent slave-raid. Scales of distance are shown at the lower left corner. N = north; P = location of *Polyergus* nest; F = location of *Formica* nest.

scouts were placed at the nest entrance. This procedure for eliminating scouting was repeated for 19 consecutive days during the period July 2–July 20. Starting on July 21, and continuing until August 4, the fence was removed to permit unlimited scouting. Without the barrier, it was not possible to determine accurately the number of scouts departing each day. During this phase of the study, we simply verified that scouting occurred, and noted the time of raid onset.

Results

A comparison of the frequency of slave raids by *P. breviceps* with and without scouts is summarized in Table 1. The Table does not include data from days when scouting was prevented by rain or heavy overcast. Slave raids occurred on only 2 of 11 days (18%) during the period of scout removal. The two raids that occurred on 7/12 and 7/20 were stopped at the fence (by sealing the exits) to ensure that no *Formica* pupae would be brought back to the nest. When the fence was removed to permit scouting, the frequency of slave raids jumped to 69%, as 9 raids were conducted on 13 different days ($\chi^2 = 7.4$, df $= 1$, $P < 0.01$). All but one of these raids resulted in the capture of *Formica* brood, and the only unsuccessful one (July 23) was aborted by an abrupt thunderstorm.

Table 1. Comparison of slave-raid frequency with and without removal of scouts

Date	No. of Scouts	Scouts Removed	Slave Raid
7/02	8	+	-
7/05	7	+	-
7/06	3	+	-
7/09	1	+	-
7/10	5	+	-
7/11	1	+	-
7/12	15	+	+
7/13	24	+	-
7/15	21	+	-
7/17	13	+	-
7/20	16	+	+
7/21		-	+
7/22		-	+
7/23		-	+
7/24		-	+
7/25		-	++
7/27		-	-
7/28		-	+
7/29		-	-
7/30		-	+
7/31		-	-
8/01		-	+
8/04		-	+

++ denotes two raids on same day

DISCUSSION

Polyergus breviceps is similar to other obligatory parasites in that workers do not search for food. Nevertheless, the location of target nests by scouts can be thought of as indirect foraging, because much of the raided *Formica* brood is fed to the *Polyergus* workers and queen by their resident slaves. It is therefore not surprising that the searching pattern of *Polyergus* scouts illustrated in Figure 1 is almost identical to that described for the ant *Cataglyphis bicolor,* which forages alone for dead arthropods (Harkness and Maroudas 1985). In this desert-dwelling species, foragers also move away from the nest in a linear path, followed by random searching throughout a particular sector. *Cataglyphis* can measure angular directions from the pattern of polarized light (Wehner and Menzel 1969), so it could forage in a straight line until it found food, and then return to its home nest on the same bearing. But Harkness and Maroudas (1985) show that the sideways search pattern decreases the time for the return trip, and the same argument could easily hold for *Polyergus.* In addition, the linear phase of the scout's route ensures minimum overlap among the sectors searched by all of the scouts on any given day.

Polyergus is also similar to *Cataglyphis* (and other formicine ants) in its ability to orient to polarized light, and we recently demonstrated that scouts use visual (and not chemical) orientation during their outbound and return run, and when leading the raid swarm back to the target nest (Topoff et al. 1984). Further support for this hypothesis stems from our map of the complete route taken by a scout on July 13 (Fig. 2), in which a different path was taken for each of the scout's three runs. A model based upon chemical cues would predict a single path for the outbound run, return trip, and slave raid respectively. However, because a chemical trail is deposited during the slave raid, we have not ruled out the possibility that scouts might follow trails deposited on previous days.

The initiation of slave-making raids by scouts has so far been reported for the myrmicine genera *Strongylognathus, Harpagoxenus, Leptothorax, Epimyrma,* and *Chalepoxenus,* and in the formicine genera *Formica, Polyergus,* and *Rossomyrmex* (see review by Buschinger et al. 1980). In both subfamilies, details of scouting show several striking similarities. For example, scouts of the myrmicine ant *Harpagoxenus sublaevis* tend to be experienced workers which are at least one year old (Buschinger 1968; Buschinger and Winter 1977). This is almost identical to the findings of Kwait and Topoff (1984) for the formicine *Polyergus lucidus,* in which ants functioned as scouts only during their second season after eclosing.

A second convergence between the two subfamilies concerns the role of scouting as a prerequisite for raiding. In a laboratory study of the myrmicine species *Harpagoxenus americanus* and *Leptothorax duloticus,* Alloway (1979) recorded a total of 23 slave raids. For both genera, scouting preceded all of the slave raids, and scouting never took place when raids did not occur. In a similar study with *P. lucidus,* Kwait and Topoff (1984) removed scouts from laboratory nests on each of 7 days, during which time no slave raids occurred. Furthermore, observations showed that 25 out of 27 raids were directed towards *Formica schaufussi* nests that were scouted on the same day. The remaining two raids were directed at target nests that were scouted on the previous raid day. Our present field study with *P. breviceps* confirms the importance of scouting in the natural habitat. Because all scouts collected were returned to their nest in late afternoon, the colony's "interpretation" might have been that these scouts were simply unsuccessful in locating a colony of *Formica.* If this were the case, an adaptive colony response would be to send out more scouts on successive days. Note (in Table 1) that the number of scouts from July 7–July 11 ranged between 1 and 8, but that 15–25 scouts were collected between July 12 and July 20. It is plausible to hypothesize that the magnitude of scouting can be varied according to the colony's requirements, but a more rigorous, statistical analysis must await a larger sample size.

The data from July 12 and 20 also show that raids can be organized even when scouting has not taken place for at least one week, but we do not know how recruitment takes place when this occurs. When groups of *Polyergus* are led by same-day scouts, the raid typically mimics the biphasic nature of scouting. Thus, the raid starts with a relatively linear movement away from the nest, during which the swarm advances without stopping. This is followed by the second phase in which the ants periodically stop advancing, fan out in all directions, and search under rocks and leaf litter (Topoff et al. 1984). It will be interesting in future field studies to observe how slave raids proceed when not organized by same-day scouts. Under such circumstances, the linear phase of raiding might be eliminated, so that the *Polyergus* swarm is forced to advance in a more deliberate manner, with more numerous searching stops even close to the nest. Finally, formicine ants such as *Formica rufa* exhibit site allegiance, a process that is based upon individual memory of spatially-organized visual cues (Rosengren and Fortelius 1986). Using individually-marked *Polyergus,* we now plan to determine whether each scout has a particular compass direction and sector in which it regularly searches for *Formica* colonies.

SUMMARY

Slave raids by *Polyergus breviceps* are initiated by one or more scouts which locate target colonies of *Formica gnava,* and recruit nestmates to participate in group raids. Field studies in southeastern Arizona showed that scouting comprises two distinct phases. The first is a linear movement away from the nest, during which no

searching occurs. This is followed by sideways movements, a phase characterized by intensive searching under rocks and leaf litter throughout a limited sector. Sometimes, the scout takes a different route on the outbound run, return trip, and slave raid respectively. The distinctness among these three paths is consistent with the hypothesis that scouts rely primarily on visual orientation. The importance of scouts was determined by their systematic removal, resulting in the absence of raiding on 9 out of 11 days. When scouting was subsequently permitted, raids occurred on 9 out of 12 days.

ACKNOWLEDGMENTS

We thank Kim Cazier and Terry Inman for their assistance in the field. This study was supported by NSF Grant BNS-8402041, and by PSC-CUNY Grant 6-66346.

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THE IDENTITY OF THREE FABRICIAN CHRYSIDID SPECIES (HYMENOPTERA)

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As part of a world revision of the family Chrysididae it has been necessary to borrow or study in situ as many of the oldest types as possible because of potential confusion about their identity. The species described by Fabricius represent a particular problem. He named many of the commonest European species, as well as other less common ones. Although the majority of Fabrician type specimens are still extant, it is clear that the chrysidid types were never seen by most later workers. In several instances the Fabrician species was assumed to be one thing when in fact it belonged to an entirely different genus. One example of this was *Chrysis festiva* Fabricius, which has always been considered a *Pentachrysis,* or *Chrysis* with 5 apical abdominal teeth (Mocsáry 1889, Dalla Torre 1892, Bischoff 1913). However, *festiva* is actually a species of *Parnopes,* as discussed by Kimsey (1987). The three species below present similar problems.

Omalus gloriosa (Fabricius), N. STATUS

Chrysis gloriosa Fabricius 1793: 242. Holotype female; "Barbaria" (Kiel Coll., Copenhagen).

The name *gloriosa* has long been used for one of the most commonly collected species of *Holopyga* in the Palearctic Region (Dahlbom 1854, Mocsáry 1889, Dalla Torre 1892, Bischoff 1913). *Holopyga amoenula* Dahlbom was listed as a junior synonym of *gloriosa* by Bischoff (1913) and later by Bodenstein (1939), which made *gloriosa* the defacto type of *Holopyga.* However, *amoenula* is the designated type.

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Manuscript received by the editor April 7, 1987.

Examination of the *gloriosa* type revealed that it is actually an *Omalus,* conspecific with *Omalus auratus* (Linnaeus) 1758, and therefore a junior synonym of that species.

Holopyga fervida (Fabricius)

Chrysis fervida Fabricius 1781: 457. Type ?; Italy (lost ?).
Chrysis fervida Fabricius 1787: 283. Four specimens; Spain (Kiel Coll., Copenhagen).
Holopyga fervida of authors.

Kimsey (1986) designated a lectotype of this species in the Lepeletier collection in the Museum National d'Histoire Naturelle, Paris from a series of specimens labeled as Fabrician types. However, these specimens were from the Paris area. In the oldest description of this species (1781) Fabricius gives Italy as the type locality. Zimsen (1964) was unable to locate this type (or types ?). As a result, it must be assumed that the original type has been lost. Fabricius later described the species from 4 specimens from Spain. Therefore the specimen from Paris labeled lectotype is actually an invalid type.

In his 1787 description of *fervida* Fabricius states "An distincta species?". Whether this means that these specimens represent a different species from the one he described in 1781 is unclear. However, since he did call these *fervida* and the original specimen(s) cannot be located, it is important to designate one of these a neotype. Designation of a neotype is necessary for 2 reasons: (1) one of these 4 specimens is a species of *Hedychridium,* not *Holopyga,* and (2) *fervida* is a common European species, so the name should be associated with a type specimen. Therefore, I am designating a female from the Kiel Collection, which is in reasonably good condition and is a typical *fervida* as described by other workers.

Chrysis purpurata Fabricius

Chrysis purpurata Fabricius 1787: 283. Lectotype male; "Halae Saxonom" (Kiel Coll., Copenhagen). New designation.
Chrysis iris Christ 1791: 405. No type data available. New synonymy.
Euchroeus purpurata of Latreille 1809: 49 (#578).

As with *gloriosa* the name *purpurata* has been used for the commonest species of *"Euchroeus"* in Europe. This species was designated as the type of *Euchroeus* by Latreille 1809. Unfortunately, examination of the 3 syntypes of *purpurata* in the Kiel Collection revealed that they are typical *Chrysis* and not what is supposed to be

Euchroeus. The shape and dentition of the apical rim of the abdomen, body color, punctation and facial structure indicate that *purpurata* is the senior synonym of *Chrysis iris* Christ. Because Latreille (1809) designated *purpurata* the type of *Euchroeus*, and this species is in fact a typical *Chrysis* Linnaeus, *Euchroeus* is therefore a junior synonym of *Chrysis*. Although some argument could be make for conserving the name *Euchroeus* this is a relatively rare group of species occurring in the Palearctic and Ethiopian Regions, which has never had a major revision. The next available name for this genus is *Brugmoia* Radoszkowski 1877 (type: *Brugmoia pellucida* Radoszkowski 1877).

SUMMARY

The true identity of 3 chrysidid species, *Chrysis gloriosa, fervida* and *purpurata,* described by Fabricius are determined. A lectotype is designated for *purpurata*. *Chrysis gloriosa* is a junior synonym of *Omalus auratus* (Linnaeus) 1758. *Chrysis purpuratus* is the senior synonym of *iris* Christ 1791; it is also the type of *Euchroeus* Latreille, making *Euchroeus* a junior synonym of *Chrysis* Linnaeus. The next available name for the genus previously called *Euchroeus* is *Brugmoia* Radoszkowski 1877. *Chrysis fervida* is actually a *Holopyga,* and a neotype is designated for this species.

ACKNOWLEDGMENTS

The kind assistance of Ole Lomholdt made this study possible. This research was supported by NSF Research Grant No. BSR-86-00341.

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NEW SPECIES OF AFRICAN *CHRYSIS* (HYMENOPTERA: CHRYSIDIDAE)*

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In the past few years I have examined several thousand Chrysidini from Africa in connection with a generic revision. The bulk of this material came from museums and private collectors. In addition I personally collected some specimens in Kenya and South Africa. Most of the original types of African species have been studied.

Commonly collected species of Afrotropical *Chrysis* which have broad distributions are *lincea* Fabricius, *stilboides* Spinola, *mediocris* Dahlbom, *antennata* Mocsáry, *dira* Mocsáry, *angolensis* Radoszkowski, *aurifascia* Brullé, and *mionii* Guérin. All of these were described more than 75 years ago, some much longer. Nearly 150 additional species of *Chrysis* (plus synonyms) are known to occur in the Region, although they are less commonly taken. Most of these were named by A. Mocsáry, R. du Buysson, and E. Edney. The use of Malaise traps by F. W. Gess, C. M. Eardley, and others in the past 15 years has increased the catch of previously "rare" species, and also the proportion of males. Based on the *Chrysis* I have seen, the list of Afrotropical species in this genus should easily reach 250.

Some of the more distinctive unnamed forms are described below with indication of collectors and museum repositories. Abbreviations used in the descriptions are: F-I etc., flagellomeres; TFC, transverse frontal carina; MOD, median ocellus diameter; T-I etc., terga; S-I etc., sterna.

Museum repositories are identified by the cities in which they are located.

BUDAPEST, Hungarian National Mus.; CAMBRIDGE, Mus. of Comparative Zoology, Massachusetts; CAPE TOWN, South African Mus.; COPENHAGEN, Zoological Mus., Denmark; DAVIS, University of California Bohart Museum.; GAINESVILLE-AI,

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Manuscript received by the editor July 1, 1987.

American Entomological Institute, Florida; GAINESVILLE-FS, Florida State Collection of Arthropods; GENOA, Natural History Mus., Italy; GRAHAMSTOWN, Albany Mus., South Africa; LUND, University Mus., Sweden; PRETORIA-NC, National Collection of Insects, South Africa; PRETORIA-TM, Transvaal Mus., South Africa; TERVUREN, Congo Mus., Belgium.

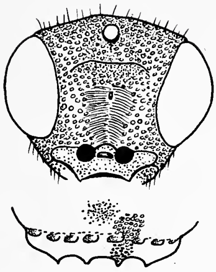
Chrysis aspredinis Bohart, new species

HOLOTYPE MALE: Length 7 mm. Body rather robust, green, becoming blue and purplish blue, F-I green in front, wings lightly stained. Punctation coarse and close, a little finer on vertex and T-II-III but close. F-I 2.8× as long as broad; face unusually broad, scapal basin punctate in outer one-third, microridged and depressed in middle one-third; TFC distinct, biconvex (Fig. 1); malar space 1.5 MOD; subantennal space 1 MOD. Pronotum shorter than scutellum, median groove weak; metanotum rounded; mesopleuron edentate, episternal and scrobal sulci distinct, latter broad; propodeal projection slender, sharp, incurved behind. Midline of T-II a little raised. T-III slightly saddled, a small median prepit depression, lateral margin concave except for a large rounded hump in basal one-fourth; pit row deep, pits distinct, 4 sharp but short distal teeth grouped inside lateral margins (Fig. 1); S-II spots large, nearly touching, occupying about one-half of sternum.

FEMALE: About as in male. Length 8 mm; F-I 3.2× as long as broad, scapal basin with coarse lateral punctures.

Male holotype, (PRETORIA-TM), SOUTH AFRICA: Cape Prov., van Rhynsdorp, VII-VIII-1927 (G. van Son). Paratype male, same data as holotype (DAVIS).

DISCUSSION: The odd shape of the short T-III which is broad with distal teeth well inside the lateral margin (Fig. 1), the median prepit depression, basolateral hump, and unusually coarse punctation are features of the *splendens* group. Other species besides *aspredinis* are *dentipleuralis* (Brauns), *munita* Buysson, *splendens* Dahlbom, and *vansoni* (Brauns). From all of these, *aspredinis* differs by its unmodified metanotum, simpler TFC, absence of a delimited midocellar area, and larger S-II spots.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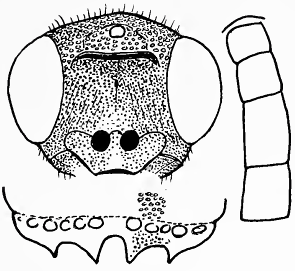
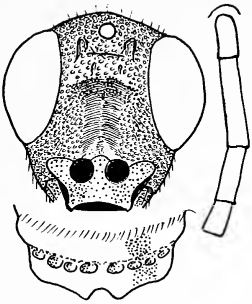
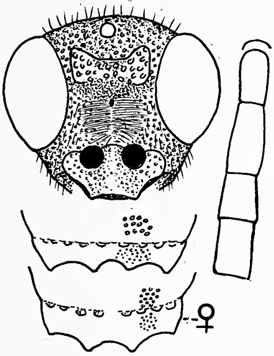
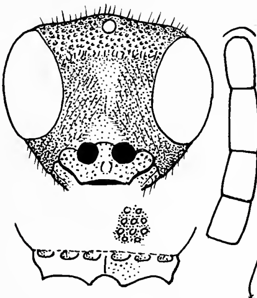

2. brothersi ♂


3. capana ♀



4. capicola ♂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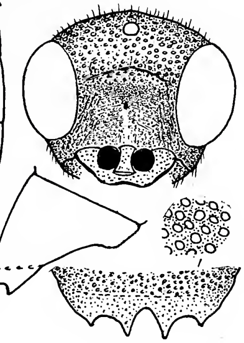
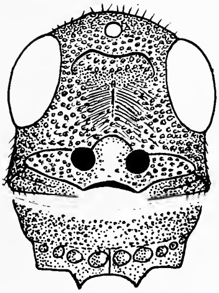
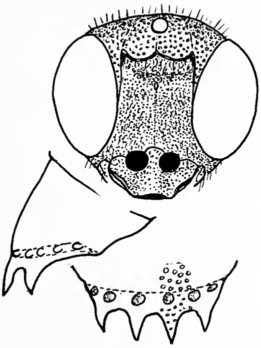
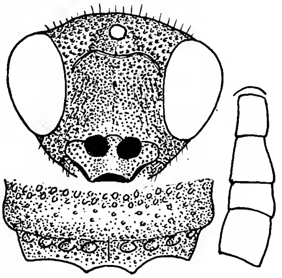

6. evexa ♀


7. genosa ♀


8. kenyana ♀


9. krugerana ♂

Figs. 1, 7, face and apex of T-III; 2, 3, 4, 5, 9, also pedicel to T-III of antenna (enlarged). Figs. 6, 8, face, T-III lateral and apex dorsal.

Chrysis brothersi Bohart, new species

HOLOTYPE MALE: Length 7 mm. Body robust, blue to bluish purple, ocellar area and broad median stripe on mesonotum purple; tarsi reddish brown, F-I blue in front, wings weakly stained. Punctation medium coarse, somewhat spaced on T-II-III. F-I as broad as long (Fig. 2), a little longer than pedicel, three-fifths as long as F-II; scapal basin punctate, dense silvery hair in outer two-fifths; TFC strong, midocellar area margins arising from sublateral angles; midocellus lidded; malar space 1.3 MOD; subantennal space 1.6 MOD. Pronotum shorter than scutellum, median groove well developed; metanotum rounded; mesopleuron bidentate, episternal and scrobal sulci distinct; propodeal projection pointed, very lightly convex behind. Midline of T-II weakly indicated; T-III rounded before moderately deep pit row, prepit bulge hardly raised, lateral margin sinuate, 4 sharp and acute distal teeth well within lateral margin, median emargination deep (Fig. 2), submedian one more shallow; S-II spots medium, round, narrowly separated.

FEMALE: About as in male. Length 7.5 mm. More green than blue, F-I 1.8× as long as broad, about as long as F-II, T-III a little saddled, distal teeth evenly spaced.

Male holotype (GRAHAMSTOWN) SOUTH AFRICA: Cape Prov., 30 km se, Hoedspruit, XI-14-78 (D. J. Brothers, C. F. J. Guillarmod). Paratypes, female, SOUTH AFRICA: Transvaal Prov.: Langjan Nature Reserve, I-24-82 (C. D. Eardley, PRETORIA-NC); female, Mogol Nature Reserve, XI-23-79 (S. J. van Tonder and G. L. Princeloo, DAVIS).

DISCUSSION: The short male F-I (Fig. 2), rounded metanotum, T-III teeth inside an expansion, and medium-sized round S-II spots narrowly separated, all place *brothersi* near *zuluana* Mocsáry. The latter differs by the much finer punctation and extensive microsculpture.

The species is named for a collector of the holotype, the well-known hymenopterist, Dennis Brothers.

Chrysis capana Bohart, new species

HOLOTYPE FEMALE: Length 7 mm. Body slender, green, F-I mostly green in front, wings lightly stained. Punctation moderate and close on vertex and notum, somewhat spaced on T-I, finer and a little spaced on T-II, fine and close on T-III. F-I 4.3× as long as broad, 2.1× as long as pedicel; scapal basin punctate on outer one-third, microridged on middle third; TFC partly broken, M-like (Fig. 3); malar space 2.8 MOD; subantennal space 1.8 MOD. Pronotum as long as scutellum, grooved in front; metanotum rounded, mesopleuron edentate, episternal and scrobal sulci moderately impressed; propodeal projection pointed, concave behind. Midline of T-II faint in anterior one-half; T-III saddled before low transverse prepit swelling, lateral margin a little convex, pit row well developed, distal margin notched medially between rounded teeth (Fig. 3), apicolateral corners broadly rounded; S-II spots long oval, widely separated.

Female holotype (PRETORIA-TM), SOUTH AFRICA: Cape Prov., Willowmore (Dr. Brauns). Paratypes, 3 females, same data as holotype (PRETORIA-TM, DAVIS).

DISCUSSION: This is related to *exsecata* Mocsáry on the basis of its laterally rounded and medially notched distal rim of T-III, M-like TFC, slender F-I, and medially microridged scapal basin. However, *capana* is a larger and more slender species, S-II spots much farther apart, TFC partial, F-I 4.3 rather than 3× as long as broad, and T-III finely rather than coarsely punctate (Fig. 3).

Chrysis capicola Bohart, new species

HOLOTYPE MALE: Length 6 mm. Body moderately slender, green, grading to purple in ocellar area, T-II medially, and T-III; F-I weakly green, wings lightly stained. Punctation moderate and close. F-I 2× as long as broad, F-II 1.2× and a little shorter than F-III which is 1.5× as long as broad (Fig. 4); scapal basin punctate in outer one-fourth, microridged with some punctures in middle half; TFC like a broad and rounded M; malar space 2.3 MOD; subantennal space 1.6 MOD. Pronotum a little shorter than scutellum, median groove well developed; metanotum rounded; mesopleuron edentate, episternal and scrobal sulci well developed; propodeal projection sharp, incurved behind. Midline of T-II-III faint; T-III with a low medial prepit swelling, lateral margin nearly straight, pits distinct in a shallow pit row groove, postpit area short, 4 short and obtuse distal teeth (Fig. 4); S-II spots long oval, 4.5 MOD apart.

FEMALE: About as in male; F-I 2.4× as long as broad, longer than F-II which is longer than F-III; subantennal space 1.8 MOD; TFC rather faint; one female mostly purple; T-III (Fig. 4).

Male holotype (GAINESVILLE-AI), SOUTH AFRICA: Cape Prov., Kirstenbosch, XI-25-70 (H. and M. Townes). Paratypes (SOUTH AFRICA, Cape Prov.), 5 males, some data as holotype (also DAVIS), 2 females, IX and I, Jonkersboek (H. and M. Townes, GAINESVILLE-AI; V. Whitehead, CAPE TOWN); female, Cape Nature Reserve, III-10-68 (P. Spangler, DAVIS).

DISCUSSION: The slightly short male F-II (Fig. 4) places this species in the *splendidula-senegalensis* group along with other African species: *laeta* Dahlbom, *senegalensis* Mocsáry, and *impudens* Edney. From all of these, *capicola* differs by its longer malar space (2.3 MOD vs. about 1.0). Also, T-III teeth are less sharp, and male F-III-X are dark. In the other 3 species these male articles tend to be reddish. In *kenyana* Bohart the malar space is 0.8 MOD and it has a distinctive pretegular hook.

Chrysis crenula Bohart, new species

HOLOTYPE MALE: Length 4.5 mm. Body slender, blue-green with some purplish, especially at base of T-II and on T-III, wings water clear. Punctation moderately coarse, punctures 0.5–1.0 PD apart and intervening space micropunctate, especially on terga. F-I 2.1× as long as broad, a little longer than F-II, which is equal to F-III; scapal basin mostly punctate and silver pubescent, narrowly polished medially; brow rough but without a TFC (Fig. 5); malar space 2.5 MOD; subantennal space 1.5 MOD. Pronotum shorter than scutellum, median groove weak; metanotum rounded; mesopleuron edentate, episternal and scrobal sulci weak; propodeal projection slender and sharp, incurved behind. Midline of T-II faint; T-III evenly convex before well developed pit row, lateral margin straight, 4 short distal teeth, middle pair close together (Fig. 5); S-II spots oval, separated by 2 MOD.

FEMALE: about as in male, T-III slightly saddled.

Male holotype (PRETORIA-NC), SOUTH AFRICA: Transvaal Prov., Roodenplaat, XII-1978 (C. D. Eardley). Paratypes, 2 females, same data as holotype (PRETORIA-NC, DAVIS); female, Natal Prov., Umfolozi Game Reserve, XI-20-78 (D. J. Brothers, C. F. J. Guillarmod, GRAHAMSTOWN).

DISCUSSION: This small slender species, with T-III notched apically is a little like *delicatula* but the moderately long F-I and absence of a TFC (Fig. 5) rule it out of that group. In addition the interpunctural microsculpture is distinctive.

Chrysis evexa Bohart, new species

HOLOTYPE FEMALE: Length 7 mm. Body medium slender, green, a little purple in midscutal area, F-I weakly green, tarsi light brown, wings slightly stained. Punctation of head, notum and T-I moderate to coarse (on scutum), interspaces partly microsculptured; T-II-III with small, somewhat spaced punctures with intervening microsculpture. F-I 2× as long as broad; scapal basin with fine, striatiform punctation; brow rough and partly obscuring TFC which is parenthesis-like (Fig. 6); malar space 1.6 MOD; subantennal space 1.0 MOD. Pronotum shorter than scutellum, median groove shallow, lateral margin (in dorsal view) expanded before middle; metanotum with a short, posteromedian, spoonlike projection; mesopleuron edentate, episternal and scrobal sulci deep, leaving 2 polished areolae at bottom of mesopleural side; propodeal projection sharp, incurved behind. Midline of F-I-II faint; T-III hardly saddled, no prepit bulge, lateral margin slightly concave except for a flattened lobe in basal one-fifth (Fig. 6), pit row shallow but pits distinct, 4 sharp distal teeth (Fig. 6); S-II spots medium large, oval, practically touching.

Female holotype (CAMBRIDGE), ZAIRE: Katanga, Lubumbashi, XI-23-20 (J. Bequaert). Female paratype, same data as holotype (DAVIS).

DISCUSSION: This species belongs to the *wahlbergi* group, all of which have some sort of basolateral projection on T-III. *C. evexa* is close to *hoplites* Mocsáry but in *evexa* the shape of T-III (Fig. 6), shorter metanotal projection, evenly incurved propodeal projection, and generally more slender body are distinctive.

Chrysis genosa Bohart, new species

HOLOTYPE FEMALE: Length 7 mm. Body slender, greenish-blue; purple on scutum medially, metanotum, T-II-III basolaterally; F-I-II blue in front; wings lightly stained. Punctation moderate and close on vertex and notum, a little spaced on T-II and on T-III prepit hump. F-I 2.6× as long as broad; scapal basin punctate in lateral two-fifths, microridged in middle one-fifth; TFC well developed, biconvex; face greatly widened at mandible base where it is nearly twice as broad as at TFC (Fig. 7); malar space 4 MOD; subantennal space 1.5 MOD; postocellar area unusually large. Pronotum about as long as scutellum, median groove present but weak; metanotum rounded; mesopleuron edentate, episternal and scrobal sulci moderately impressed; propodeal projection slender, sharp, incurved behind. T-I with subbasal humps unusually prominent; T-II midline faint; T-III slightly saddled, a median hump before pit row, lateral margin straight, pits deep, 4 distal teeth, lateral pair forming a right angle, middle pair closer together and sharp but short (Fig. 7); S-II spots long oval, 5 MOD apart.

Female holotype (PRETORIA-NC), SOUTH AFRICA: Transvaal Prov., Nylsvley Nature Reserve, XII-11-79 (W. A. Harrop). Paratype female, SOUTH AFRICA: Transvaal Prov., Entabeni Forest Reserve, Soutpansberg, XI-7-80 (M. W. Mansell, DAVIS).

DISCUSSION: The exceptionally broad face at the mandible base is distinctive for this medium-sized species (Fig. 7). This broadening also affects the interantennal and eye-genal carina spaces, which are greater than usual. The rather knobby T-I in front is reminiscent of the palearctic *subsinuata* group but the similarity is probably coincidental. In most respects *genosa* fits into the *delicatula* group, but discovery of the male will be needed to confirm this. Although *mandibularis* Buysson is considerably smaller, and its interpunctural areas are microsculptured, the laterally expanded face and other features are much like those of *genosa.*

Chrysis kenyana Bohart, new species

HOLOTYPE FEMALE: Length 6 mm. Body slender, green marked with purple in ocellar areas, most of midscutal area, T-II sublateral basal spots, T-III basally and postpit. F-I green in front; wings nearly clear; tarsi brownish yellow. Punctation moderate and close, coarse toward middle of T-II. F-I 1.3X as long as broad, about as long as pedicel, a little longer than F-II; scapal basin with sides nearly parallel (Fig. 8), finely punctate and faintly microridged medially; TFC M-like; midocellar area partly margined; malar space 0.8 MOD; subantennal space 1.8 MOD. Pronotum as long as scutellum, a shallow median groove; scutum with a strong pretegular hook; metanotum rounded; mesopleuron edentate, episternal and scrobal sulci well developed; propodeal projection sharp, incurved behind. Midline of T-II a flat median welt; T-III slightly saddled, a low transverse prepit swelling, lateral margin with a distinct obtuse angle at middle point (Fig. 8), pit row moderately impressed, pits relatively large, distal margin with 4 long, sharp teeth (Fig. 8); S-II spots oval, 2.5 MOD apart.

Female holotype (COPENHAGEN), KENYA: Tiwi Beach, IV-19-76 (H. Gonget). Paratype female, same locality as holotype, IV-14-76 (K. Gonget, DAVIS).

DISCUSSION: This species appears to be in the *splendidula-senegalensis* group, and is quite similar to *laeta*. However, the pretegular scutal hook of *kenyana,* as well as the prominent angle on the lateral T-III margin (Fig. 8) are distinctive.

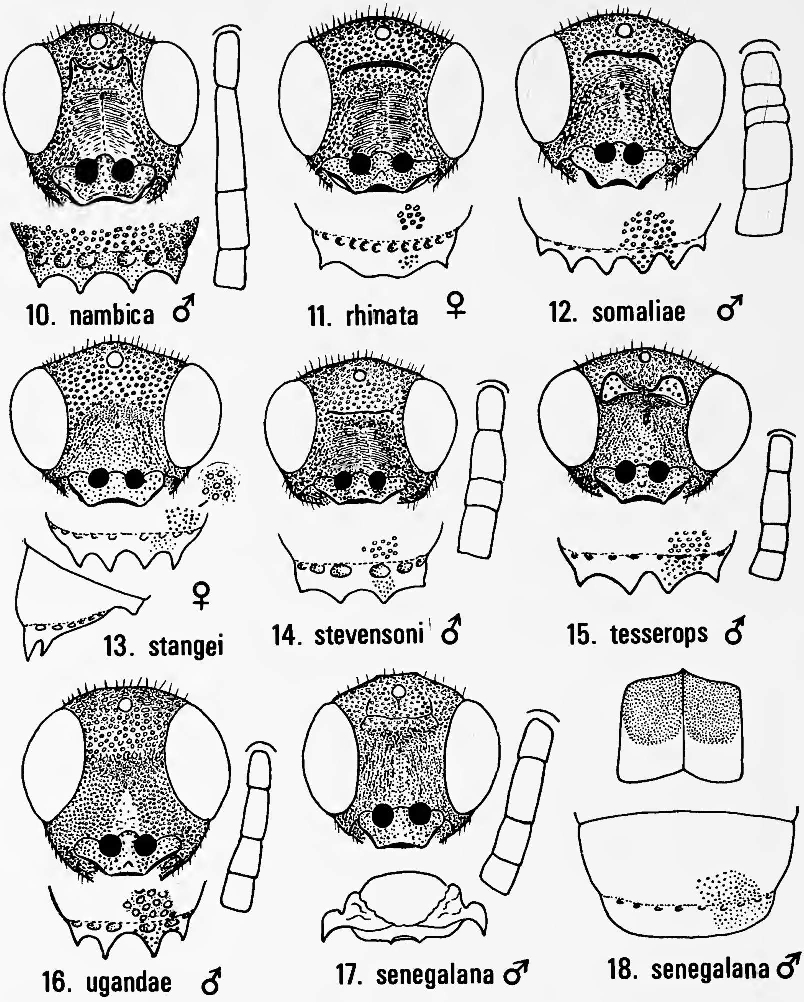
Chrysis krugerana Bohart, new species

HOLOTYPE MALE: Length 8.5 mm. Green with tinges of purple, T-III mostly purplish blue, F-I green in front, wings brown except toward apex. Punctation moderately coarse and close on vertex and notum, punctures of terga mostly 0.5 PD apart. F-I as broad as long and slightly longer than pedicel, F-II shorter, F-III a little longer than F-I (Fig. 9); scapal basin with close and somewhat transversely striatiform punctation, sparsely pubescent on outer one-third; TFC strong, weakly and irregularly biconvex (Fig. 9); midocellar area slightly indicated; malar and subantennal spaces each 1.7 MOD. Pronotum a little shorter than scutellum, median groove weak; metanotum rounded; mesopleuron edentate, scrobal and episternal sulci strong; propodeal projection sharp, concave behind. T-II midline a faint welt; T-III with a prominent rounded prepit bulge, lateral margin nearly straight, pit row moderately impessed, weakly divided medially, 4 obtuse distal teeth (Fig. 9), S-II spots ovoid, 3 MOD apart.

FEMALE: About as in male; F-I-II green in front, F-I 2× as long as broad; T-II purple basolaterally.

Male holotype (PRETORIA-NC), SOUTH AFRICA: Transvaal Prov., Kruger National Park, Pretoriuskop, I-17-85 (G. L. Princeloo). Paratypes (SOUTH AFRICA, Transvaal), male, female, Barberton, XI-11-78 (C. D. Eardley, G. L. Princeloo (PRETORIA-NC); male, Hectorspoint, XI-23-73 (A. Strydam, PRETORIA-TM); male, 2 females, Lapalala Nature Reserve, I-23-87 (R. B. Kimsey, DAVIS).

DISCUSSION: The form of the male antenna (Fig. 9) place this in the *cerastes* group where it is the only known South African species of this color and moderate size.



10. nambica ♂

11. rhinata ♀

12. somaliae ♂

13. stangei ♀

14. stevensoni ♂

15. tesserops ♂

16. ugandae ♂

17. senegalana ♂

18. senegalana ♂

Fig. 11, face and apex of T-III; 10, 12, 14, 15, 16, 17, also pedicel to T-III of antenna (enlarged). Fig. 13, face, T-III lateral and apex dorsal. Fig. 18, S-II and T-III apex.

Chrysis namibica Bohart, new species

HOLOTYPE MALE: Length 5 mm. Body slender, blue-green with green and purple tinges, a laterobasal purple spot on T-II, F-I weakly green, wings clear. Punctation moderate and close. F-I 3.4× as long as broad (Fig. 10). Scapal basin punctate and silver haired on lateral one-third, polished and microridged in central one-third; TFC M-like (Fig. 10); midocellus lidded; malar space 2.2 MOD; subantennal space 1 MOD. Pronotum a little shorter than scutellum, median groove weak; metanotum rounded, mesopleuron edentate, mesopleural and scrobal sulci shallow; propodeal projection sharp, incurved behind. Midline of T-II a faint welt; T-III evenly convex before moderately deep and large pit row, lateral margin straight, 4 sharp but short distal teeth (Fig. 10); S-II spots large, quadrate, practically touching.

FEMALE: About as in male. T-III saddled, slightly bent out mediolaterally, S-II spots small, nearly touching.

Male holotype (DAVIS), NAMIBIA: Namib Desert Park, Gobabeb, II-12-74 (M. E. Irwin). Paratype female, same data as holotype (L. Lyneborg, COPENHAGEN).

DISCUSSION: The long F-I, clear wings, polished and microridged middle of the scapal basin (Fig. 10), and lidded midocellus are distinctive for this slender species. The species group appears to be *comparata-scutellaris,* but the long and slender F-I is atypical (Fig. 10).

Chrysis rhinata Bohart, new species

HOLOTYPE FEMALE: Length 5.5 mm. Body moderately slender, greenish-blue with purple in ocellar area, midscutum and in sublateral basal spots on T-I-II; F-I-II green in front, wings lightly stained. Punctation moderately coarse and close. F-I 2.3× as long as broad; scapal basin punctate in outer two-fifths, microridged in middle one-fifth (Fig. 11); TFC a slightly irregular downcurved crescent; midocellus narrowly lidded; malar and subantennal space each about 1 MOD. Pronotum about as long as scutellum, median groove weak; metanotum rounded; mesopleuron edentate, scrobal and episternal sulci distinct; propodeal projection sharp, incurved behind. No midline on T-II; T-III nearly straight before pit row in lateral view, lateral margin slightly convex, pit row moderately deep, without a strong median division, distal margin with a pair of short but sharp lateral teeth, medial pair rounded and weakly divided, forming a broad nasiform projection (Fig. 11); S-II spots small, round, 1.5 MOD apart.

Female holotype (PRETORIA-NC), SOUTH AFRICA: Transvaal Prov., Kruger National Park, Pafuri, I-26-84 (C. D. Eardley). Paratype female, ZAIRE: Mulubulu (J. Bequaert, DAVIS); paratype female, NIGERIA: U-Ora Creek, XI-17-74 (J. T. Medler, DAVIS); paratype female, SOUTH AFRICA: Hluhlawe Game Reserve, XI-13-70 (H. and M. Townes, GAINESVILLE-AI).

DISCUSSION: The facial features, such as short malar and subantennal spaces, and crescentic TFC (Fig. 11) suggest that *rhinata* belongs in the *maculicornis* group. Discovery of the male will be needed for confirmation. The odd, nasiform look of the T-III apex is found elsewhere only in the *bihamata* group. However, in *rhinata* the scapal basin is microridged medially, and the subantennal space is shorter.

Chrysis senegalana Bohart, new species

HOLOTYPE MALE: Length 5 mm. Body moderately stout, blue-green, F-I dark, wings faintly stained. Punctation close, moderate on vertex and notum, small on terga, indistinct on T-III postpit. F-I 2X as long as broad (Fig. 17), lower frons nearly parallel-sided, quadrate, finely punctate and not crossridged; TFC a broad reverse U (Fig. 17), quite weak, strongest medially; malar space 0.6 MOD; subantennal space 2 MOD. Pronotum nearly as long as scutellum, hardly grooved; metanotum rounded, mesopleuron weakly bidentate below scrobal sulcus which is distinct and a little areolate, episternal sulcus linear; propodeal projection sharp, incurved behind (Fig. 17). Midline of T-II indistinct; T-III not saddled, lateral margin with a slight basal convexity; pit row sunken but well devloped, postpit area a prominent curved flange (Fig. 18); S-II spots large, quadrate, touching (Fig. 18).

FEMALE: About as in male.

Male holotype (LUND), SENEGAL: 3 km n. Tanaff, III-7-77 (Cederholm, Danielson, Larson). Paratypes, male, 7 females, same data as type (LUND, DAVIS, PRETORIA-TM).

DISCUSSION: The T-III distal flange is similar to that in some *Spintharina,* but the incurved propodeal projection (Fig. 17) rules out a close relationship. The weakly bidentate lower mesopleuron, quadrate lower frons, flanged T-III, and large S-II spots (Fig. 18) place *senegalana* in the *cuprata* group. It is the first species of the group recorded from the Afrotropical Region. The all green color, and large T-III postpit flange are distinctive.

Chrysis somaliae Bohart, new species

HOLOTYPE MALE: Length 7 mm. Body moderately stout, green, some purple in ocellar area, midscutum, and basolaterally on T-I-II; pedicel and flagellum dark, tarsi reddish brown, wings lightly stained. Punctation moderate to coarse, slightly spaced on terga. F-I broader than long and shorter than pedicel, F-II even shorter, F-I-II together shorter than F-III (Fig. 12), scapal basin with outer one-third punctate, upper middle one-third weakly microridged between punctures; TFC strong, crescentic (Fig. 12); malar space 2.0 MOD; subantennal space 2.0 MOD. Pronotum shorter than scutellum, median groove present but weak; metanotum rounded; mesopleuron edentate, episternal and scrobal sulci distinct; propodeal projection sharp, incurved behind. T-II midline a raised welt; T-III evenly convex before pit row which is obsolete, lateral margin slightly sinuate, 6 short but sharp distal teeth (Fig. 12), outermost pair shortest; S-II spots rather small, round, 2 MOD apart.

Male holotype (DAVIS), SOMALIA: Laga, XI-29-1894 (A. D. Smith).

DISCUSSION: This species does not seem to be related to any other African *Chrysis.* Especially notable are the extremely short F-I-II which separates it from all other 6-toothed *Chrysis* (Fig. 12). A few other species in the *smaragdula* group, and all of the *oculata* group have F-I short, but none have this condition in both F-I and F-II.

Chrysis stangei Bohart, new species

HOLOTYPE FEMALE: Length 5.5 mm. Body moderately stout, green, grading to blue on T-II-III, tegular purple, tarsi light brown, F-I green in front, wings nearly clear. Punctation moderately coarse and slightly spaced on vertex, notum, and T-I, interpunctural areas microsculptured; T-II-III punctures small, somewhat spaced, interspaces obviously microsculptured. F-I twice as long as broad, scapal basin punctate in outer one-third, weakly microridged in middle one-third; brow rough without indication of TFC (Fig. 13); malar space and subantennal space each about 1 MOD. Pronotum shorter than scutellum, median groove weak; metanotum with a posteromedian spoonlike projection extending about 1.5 MOD; mesopleuron edentate, episternal and scrobal sulci distinct, a large areole below latter; propodeal projection sharp, with a small convexity at middle of posterior edge. Midline of T-II indistinct; T-III evenly convex prepit, lateral margin concave except for a strong tooth in basal one-fifth (Fig. 13), pit row well impressed, pits large, 4 sharp distal teeth (Fig. 13); T-II spots long oval, close together, weakly pigmented (Fig. 13).

Female holotype (GAINESVILLE-FS) NAMIBIA: 68 km e. Karibib, II-4-83 (L. Stange, B. Miller). Paratype, female, ZAIRE: Urundi Kisenyi, May, 1955 (F. J. Francois, TERVUREN). Other paratypes (SOUTH AFRICA, Transvaal Prov.) female, Ellisras, XI-22-78 (D. J. Brothers, C. E. J. Guillarmod, GRAHAMSTOWN); female, Mogol Nature Reserve, XI-23-79 (S. J. van Tonder, PRETORIA-NC), female, Barberton, XI-11-78 (C. M. Eardley, PRETORIA-NC) female, Lapalala Nature Reserve, I-23-89 (R. B. Kimsey, DAVIS).

DISCUSSION: A close relative in the *wahlbergi* group is *hoplites* Mocsáry. Distinguishing features of *stangei* are the small size (length 5.5 mm vs. 8.0), absence of the TFC, shorter malar space (1 MOD vs 1.3), more distinctly toothlike projection basolaterally on T-III (Fig. 13), deeper pit row, and differently shaped propodeal projection (*hoplites* is notched basoposteriorly). The species is named for a collector of the holotype, my friend Lionel Stange.

Chrysis stevensoni Bohart, new species

HOLOTYPE MALE: Length 5 mm. Greenish blue, marked with purple in ocellar area, midscutum, T-II basolaterally, T-III basally; F-I green in front; wings nearly clear. Punctation moderate and close. F-I 1.3× as long as broad, as long as pedicel, longer than F-II, shorter than F-III (Fig. 14); scapal basin punctate and with silvery hair on lateral third, microridged otherwise; TFC nearly straight; malar space 1.8 MOD; subantennal space 1.2 MOD. Pronotum a little shorter than scutellum, hardly grooved medially; metanotum rounded; mesopleuron edentate, episternal sulcus strong, scrobal sulcus weak and incomplete; propodeal projection sharp, incurved behind. No T-II midline; T-III evenly convex before well-indented pitrow, lateral margin straight, 4 distal teeth of which outer pair are obtuse (Fig. 14), inner pair sharp but short; S-II spots oval, widely separated.

FEMALE: About as in male; F-I 2× as long as broad, F-I-II green in front; malar space 2 MOD.

Male holotype (GRAHAMSTOWN), SOUTH AFRICA: Cape Prov., Hilton, XI-9-75 (F. W. Gess). Paratypes, one male, 4 females, topotypical, X and XI (GRAHAMSTOWN, DAVIS); female, SOUTH AFRICA: Cape Prov., Rooiheuwell (R. H. Watmough, PRETORIA-NC), female, ZIMBABWE: Bulawayo, VIII-5-23 (R. Stevenson, CAPE TOWN).

DISCUSSION: Among the few known South African *cerastes* group species in which both male F-I and F-II are shorter than III (Fig. 14), *stevensoni* is distinguished by its blue to purple color, small size, weak TFC and faintly impressed scrobal sulcus. The species is named for R. Stevenson, who collected many Zimbabwan chrysidids.

Chrysis tesserops Bohart, new species

HOLOTYPE MALE: Length 6.5 mm. Body medium slender, blue-green with ocellar triangle and midscutum partly purple, F-I-II green in front, III-X reddish brown, tarsi light brown, wings nearly clear. Punctation moderately coarse, a little spaced. F-I twice as long as broad (Fig. 15), II 1.2× and in some views faintly shorter than III; scapal basin finely punctate in outer two-fifths, mostly polished in middle one-fifth; TFC prominent, recurved, spectacle-like, enclosed "eyes" punctate but brightly reflective (Fig. 15). Malar space 1.2 MOD (ocellus small); subantennal space 1.6 MOD. Pronotum shorter than scutellum, median groove well marked; metanotum rounded; mesopleuron edentate, scrobal and episternal sulci shallow but distinct; propodeal projection pointed, nearly straight behind. No T-II midline; T-III evenly curved before pit row, lateral margin straight, pit row hardly indented but pits distinct, 4 sharp distal teeth, outer pair obtuse, inner pair acute, median notch deeper than submedian (Fig. 15); S-II spots large, long oval, narrowly separated.

FEMALE: About as in male. F-I 2.3× as long as broad, III-X dark; tarsi brown; T-III saddled and with a low prepit convexity, pit row moderately deep.

Male holotype (GENOA), ETHIOPIA: Sagan-Omo, Cashel, VII-8-39, (M. E. Zavattari). Paratypes, female, ZAIRE: Parc national Garamba (H. De Saeger, TERVUREN); female, TANZANIA: East Usambara, Amani, II-3-77 (O. Lomholdt, COPENHAGEN); female, SOUTH AFRICA: Transvaal Prov., Acornhoek, XI-1918 (R. W. Tucker, DAVIS).

DISCUSSION: Although male F-II is only marginally shorter than F-III, other features indicate that *tesserops* is in the *splendidula-senegalensis* group. The outstanding feature of *tesserops* is the spectacle-like form of TFC (Fig. 15). This formation has been observed in other unrelated *Chrysis,* but nowhere so extreme. In other respects there is a resemblance to *senegalensis* Mocsáry, but that species has the scapal basin microridged medially.

Chrysis ugandae Bohart, new species

HOLOTYPE MALE: Length 4.5 mm. Body unusually slender, green to blue, notum and T-I-II apex with a faint coppery sheen, F-I green in front, wings nearly clear. Punctation moderate, slightly spaced, more so on scutum, intervals microsculptured. F-I 2.3× as long as broad; scapal basin finely punctate, narrowly polished medially (Fig. 16). TFC absent on broadly rounded brow, lateral acellus 1 MOD from eye, postocellar area unusually long; malar space 4 MOD, subantennal 1.3 MOD. Pronotum one-third longer than scutellum, median groove weak but present; metanotum rounded; mesopleuron edentate, episternal groove present, scrobal sulcus quite faint; propodeal projection short, pointed, slightly concave behind. T-II twice as long as T-III, midline evanescent; T-III evenly convex before pit row, lateral margin straight but concave near apex, pit row weakly impressed but pits relatively large, 4 distal teeth acute, sharp (Fig. 16) arranged in a rooflike curve; S-II spots large, long quadrate, narrowly separated.

FEMALE: About as in male. Length 5–6 mm. T-III median pair of teeth somewhat flaring, median emargination broader and shallower than lateral one.

Male holotype (BUDAPEST), UGANDA: Katona, Sept. 1913 (Mujenje coll.). Paratypes, 4 females, same data as holotype

(BUDAPEST, DAVIS); paratype female, ZAIRE: Parc National Garamba, III-2-50 (H. DeSaeger, TERVUREN).

DISCUSSION: This species clearly belongs to the *maindroni* group, and is closely related to *maindroni* Buysson. Both have the very slender body, moderately long male F-I, long malar space, rounded brow without a TFC, long postocular area, obsolete scrobal sulcus, sharp T-III teeth, and large S-II spots. However, in *ugandae* the middle of the scapal basin is polished instead of microridged (Fig. 16), and the outer pair of T-III teeth are not unusually large. In *longigena* Mocsáry, also related, the interpunctural areas of the scutum are not extensively microsculptured and the lateral ocellus is 2 MOD from the eye.

Chrysis whiteheadi Bohart, new species

HOLOTYPE FEMALE: Length 7 mm. Body moderately slender, greenish blue, grading to purple on vertex, midsection of scutum, terga except laterally and postpit area of T-III; F-I dark blue, wings lightly brownish. Punctation of head and thorax moderate and close, tergal punctures about a puncture diameter apart and intervening spaces microreticulate. F-I 3× as long as broad, scapal basin punctate in outer one-third, transversely microridged in depressed median one-third, TFC broadly M-like above extensive punctate area, fine posterior rami nearly enclosing midocellus; malar space 3.1 MOD; subantennal space 1.4 MOD; pronotum shorter than scutellum, median groove well developed; metanotum rounded; mesopleuron edentate, scrobal and episternal sulci distinct; propodeal projection sharp, incurved behind. No T-II midline; T-III saddled but with low prepit swelling, pit row not deep but pits distinct and a little longer than broad, distal rim evenly and broadly rounded; S-II spots moderately large, almost coalescent.

Female holotype (CAPE TOWN), SOUTH AFRICA: Cape Prov., Jonkershoek, near Stellenbosch, XII-27-70 (V. Whitehead). Paratype female, same data as holotype (DAVIS); paratype female, SOUTH AFRICA: Cape Prov., Hilton, XII-5-79 (F. W. and S. K. Gess, GRAHAMSTOWN).

DISCUSSION: The rounded distal rim of T-III, microreticulate interspaces between moderately large punctures on T-III, long malar space, and M-like TFC characterize the species. The T-III shape is similar to that in *capitalis* Dahlhom but in other respects *whiteheadi* is close to *exsecata* Mocsáry. The species is named for the collector of the holotype, my friend Vince Whitehead.

SUMMARY

Seventeen species of African *Chrysis* are described as new. Pertinent structural features are illustrated. Assignment to species groups has been made, when possible. New species are: *Chrysis aspredinis, brothersi, capana, capicola, crenula, evexa, genosa, kenyana, krugerana, namibica, rhinata, senegalana, somaliae, stangei, stevensoni, tesserops, ugandae,* and *whiteheadi.*

PUPA ACCEPTANCE BY SLAVES OF THE SOCIAL-PARASITIC ANT *POLYERGUS** (HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Slave-making ants of the formicine genus *Polygerus* are obligatory parasites of the genus *Formica.* To maintain a supply of slaves, *Polygerus* workers raid *Formica* colonies and capture brood, primarily pupae. Some of this brood survives to eclosion in raiders' nest, and these new workers perform their species-typical behaviors in the service of the slave-makers. Colonies of the eastern species *P. lucidus,* and of the western species, *P. breviceps,* contains only one species of slave, unlike related faculative slave-makers of the genus *Formica. P. lucidus* enslaves the subgenus *Neoformica,* while *P. breviceps* uses the *Formica fusca* species group (Creighton, 1950).

Formica slaves within a *Polygerus* nest rear through eclosion both the *Polygerus* brood and the brood retrieved from various *Formica* nests. An encounter between two *Formica* workers from different nests, either free-living or enslaved, is fiercely aggressive. Under laboratory conditions where mutual avoidance is impossible, injury or death usually result (Goodloe & Topoff, unpublished data). *Formica* workers may be able to perceive colony specific differences in pupae (Wilson, 1971). If slaves were inclined to ignore or destroy pupae from alien conspecific colonies, survival of captured brood would be threatened. For the myrmicine slave-maker *Harpagoxenus americanus,* Alloway (1982) has shown that the presence of the slave-makers enhances the pupae-acceptance behavior of the slaves (fewer pupae are eaten and therefore more are saved to eclose).

**Manuscript received by the editor May 30, 1987.*

This paper presents the results of three experiments designed to elucidate the relationship between enslavement and pupae acceptance in *Polygerus* and their *Formica* hosts. Experiment 1 explored the parameters of intraspecific pupae-acceptance of slave species in their free-living state. Experiment 2 considered whether association with the slave makers causes a change in the pupae-acceptance behavior of the slave species. Field studies by Talbot (1967), Cool-Kwait & Topoff (1984), and Topoff, LaMon, Goodloe, & Goldstein (1984), showed that much of the brood retrieved by the raiders is consumed. Since raiders obtain all food from their slaves, it is the slaves who are consuming the captured pupae.

The Long Island habitat of *P. lucidus* is unique in that it contains at least three slave species of *Formica.* In the nests of neighboring facultative raiders, it is common to find more than one slave species, while *P. lucidus* is found with only one. Previous research (Goodloe, Sanwald, & Topoff, 1987) has shown that a *P. lucidus* colony will almost exclusively raid colonies of the same slave species present in their nest. Another factor that might foster the host-specificity of *P. lucidus* would be differential consumption of captured pupae. If a species other than the slave species currently in residence is raided, brood from this raid might be more likely to be consumed. Experiment 3 examined whether pupae from different host species would be differentially consumed in *P. lucidus* colonies.

EXPERIMENT 1: INTRASPECIFIC PUPAE EXCHANGE (FREE-LIVING *FORMICA*)

Methods and materials

Seven free-living colonies of *F. schaufussi* (a slave species of *P. lucidus)* were collected near Rocky Point in Suffolk County, N.Y., during the summers of 1983 and 1984, and were maintained in the laboratory. The colonies were kept in 21.6 × 29.2 cm plastic boxes, with approximately 1 cm of fresh sand covering the bottom. The sides of the boxes were coated with polytetrafluorethylene to prevent the ants from escaping. Within each box, a 150 mm plastic petri dish, containing a white hydroset substrate of approximately 5 mm in depth to retain moisture, served as a nest. Honey, water, and *Tenebrio* larvae were provided ad libitum.

Table 1. Pupae acceptance by slave species workers *(F. schaufussi)*

Colony	# Workers	*Surviving Pupae* Same	Different
F23	250	25	24
F28	550	25	23
F16	200	22	25
F24	214	24	21
F36	354	25	25
F57	208	25	24
F55	300	25	22

Correlated groups t = 1.25; df = 6; NOT SIGNIFICANT

Prior to the experiment, the queen and most of the workers from each of the seven colonies were removed from the nest and placed in a fresh box and nest dish, with food and water. The experimental colonies ranged in size from 200 to 550 workers (Table 1). After 24 hr, the queen and workers in each of the seven new nests were presented with 25 pupae, either from their own colony ("same"), or from one of the other experimental colonies ("different"). Four colonies received the "different" condition first, while the remaining three began with the "same" condition. After five days, the surviving pupae and callows were removed and counted. After another 24 hr (to recover from these manipulations), each colony was presented with 25 pupae from the alternative condition to their first presentation, and a count was made five days later.

During the summer of 1986, eleven partial colonies of *F. gnava* (a slave species of *P. breviceps*) were collected in Cave Creek Canyon, Cochise County, Arizona. Eight of these contained no queen, one contained a single queen, and the rest contained multiple queens. Laboratory colony size ranged from 81 to 500 workers (Table 2). Colonies were kept under conditions nearly identical to those described above with the exception that 16 × 150 mm test tubes containing about 3 cm of water and plugged with cotton were substituted for the plastic petri nest dishes, and the plastic boxes in which they were contained were 20 × 15 cm. Two-to-four weeks after the colonies were collected, they were subjected to the experimental procedure described above.

Results

As shown in Tables 1 and 2, no significant difference was found between the mean number of pupae accepted from the "same" and

Table 2. Pupae acceptance by slave species workers *(F. gnava)*

Colony	# Workers	*Surviving Pupae* Same	Different
FG2	81	24	25
FG3	85	24	23
FG4	276	23	23
FG5	323	24	22
FG6	500	25	25
FG7	238	24	22
FG8	400	23	23
FG9	174	21	24
FG10	250	23	24
FG11	115	23	24
FG12	112	25	24

Correlated groups t = 0.19; df = 10; NOT SIGNIFICANT

"different" conditions for both species of *Formica* (t-test for correlated groups, *F. schaufussi:* t = 1.25, df = 6; *F. gnava:* t = 0.19, df = 10). Free-living *Formica* workers of these species treat alien conspecific pupae as their own. With the exception of *F. gnava* colony FG10, in which two pupae of the "same" condition were found in their "garbage" pile, pupae were not discarded intact from any nest and none became moldy. The number of pupae that disappeared was fairly constant in all groups despite differences in colony size. Possibly the lost pupae were defective or diseased, which might be expected to occur with a similar frequency in all groups.

EXPERIMENT 2: INTRASPECIFIC PUPAE EXCHANGE (FREE-LIVING VS. ENSLAVED *FORMICA*)

Methods and materials

Three laboratory colonies of *P. lucidus* with *F. schaufussi* slaves and six free-living laboratory colonies of *F. schaufussi* were used in this experiment, which was conducted in January and February of 1985. Each colony was handled as in the previous experiment, with queen and workers being placed in a new nest. P5, a large *P. lucidus* colony, was divided into two parts: P5(1), with a ratio of slaves to raiders of approximately 10:1, and a total of 459 ants; and P5(2), with a ratio of 1:1 and a total of 200 ants. After a 5-day period of isolation, 25 *F. schaufussi* pupae from different colonies were added to each. Five days later, the surviving pupae and callows were counted.

Results

Table 3 shows that the number of pupae surviving in the mixed nests was significantly less than the numbers surviving in the free-living *F. schaufussi* colonies ($t = 7.40$, $df = 8$, $p < .0005$). Since all colonies were on the same diet as those used in Experiment 1, and were satiated at the time of the experiment, these results suggest that captured pupae have a particular importance as a food source in the mixed colonies. Unlike the myrmicine raiders studied by Alloway (1982), the presence of these slave-makers appears to induce consumption of the alien pupae by the slaves.

EXPERIMENT 3: INTERSPECIFIC PUPAE EXCHANGE

Methods and materials

A large colony of *P. lucidus,* with *F. schaufussi* slaves, was collected during the summer of 1984 and subjected to two cooling induced cycles of reproduction. In March of 1985 the colony was divided into five smaller, queenless colonies: P5A contained 100 slaves and 26 raiders; P5B, 100 slaves and 12 raiders; P5C, 100 slaves and 25 raiders; P5D, 100 slaves and 50 raiders; and P5E, 100 slaves and 100 raiders. In addition, a colony (S) consisting of 200 workers from a freee-living *F. schaufussi* colony was used for comparison.

Table 3. Pupae acceptance: free vs. parasitized slave species colony

	Free Living			*Enslaved*	
Colony	# Workers	#Surviving Pupae	Colony	# Workers	#Surviving Pupae
F18	94	21	P3	150F* 120P**	5
F56D	82	23	P4	140F 40P	15
F76	110	24	P5(1)	415F 44P	9
F15	643	22	P5(2)	100F 100P	8
F32	781	23			
F70	100	21			
Mean		22.333			9.25

* F = *F. schaufussi* workers

** P = *P. lucidus* workers

$t = 7.40$; $df = 8$; $p < .0005$

As in the previous experiments, each group was placed in a fresh box with fresh nest dish. After 24 hours to recover from the move, all the experimental colonies, except P5A, were presented with 20 pupae from *F. nitidiventris* nests. P5A was presented with 20 pupae from *F. schaufussi* nests to check for a possible order effect. After five days, a count of surviving pupae was made in each group and all pupae were removed. Following a three-day recovery period, 20 pupae of the alternative slave species were presented to each colony. After five days another count was made and again three days were allowed for recovery. This cycle was repeated two more times, using 15 rather than 20 pupae (due to a decreasing laboratory supply), so that each colony received six presentations, three of pupae from each species for a total of 55 pupae from each.

Results

All experimental colonies consumed significantly more *F. nitidiventris* pupae than *F. schaufussi* pupae, including the group containing no *P. lucidus* workers (Table 4), suggesting that this is characteristic of *F. schaufussi* workers, whether free-living or enslaved. No correlation was found between the size of the colonies or the ratio of slaves to raiders and the amount of pupae consumed, although variability in both size and the ratio of slaves to slave-makers under natural conditions is much greater than that represented here. Previous research (Goodloe et al., 1987) showed that a *P. lucidus* raid on a host species other than the one already present in the nest is a rare event. Cool-Kwait & Topoff (1984) estimated that 75% of the brood retrieved by *P. lucidus* raiders is consumed. Considering the differential consumption of pupae according to species shown in this experiment, it seems unlikely that any pupae of a slave species, other than the resident one, would survive to eclose in a *P. lucidus* nest.

DISCUSSION

The first hypothesis concerning the origins of dulosis was Darwin's (1859) suggestion that slavery developed as a by-product of brood predation among related species. A second hypothesis (Wilson, 1971; Alloway, 1980; Stuart & Alloway, 1982; Topoff et al., 1984) focuses on territorial interactions, with opportunistic brood predation, as the main pathway to dulosis. Both hypotheses assume

Table 4. Consumption of pupae: same vs. alien slave species

Colony	# Slaves	#Raiders	Total F.N.* Pupae Consumed	Total F.S.** Pupae Consumed
P5A	100	25	15	3
P5B	100	12	33	0
P5C	100	25	32	2
P5D	100	50	12	0
P5E	100	100	35	3
S	200	0	33	2
Mean			26.667	1.667

* of 55 *F. nitidiventris* pupae

** of 55 *F. schaufussi* pupae

$t = 5.24$; $df = 5$; $p < .005$

that the interactions—either brood predation or territoriality—occurred between closely related species, which would increase the probability that captured brood might survive in the captors' nest.

Although Experiment 1 showed that unenslaved *F. schaufussi* colonies treat pupae from alien conspecific colonies as their own, no information was provided to determine whether the workers are able to discriminate such alien pupae from their own. Experiment 2, by contrast, showed that enslaved *F. schaufussi* workers consume large amounts of captured alien conspecific pupae. Since none of the colonies in Experiment 2 had larvae, and since colonies appeared to be satiated on the laboratory diet, consumption of protein-rich pupae is even more difficult to explain. Possibly in these slave-makers, unique dietary requirements led to brood predation in the ancestral slave-makers. It might seem equally parsimonious to assume that a previously established host-parasite association, possibly the result of territorial interactions, led to more specialized dietary needs in the slave-makers. However, in the *Neoformica* species enslaved by *P. lucidus,* and in the *F. fusca* group species enslaved by *P. breviceps,* considered (by way of Emery's Law) to be the closest relatives of these slave-makers (Wilson, 1971), there is no evidene to suggest a predisposition toward such territorial behaviors.

In Alloway's (1980) experiments with three *Leptothorax* slave species, both interspecific and intraspecific raids occurred. Some captured brood survived, resulting in both interspecific and intraspecific slavery. More important, however, were the findings from queenright colonies in the field, where each of the three species contained several workers of one of the other species and no evidence of slave-makers. Subsequent brood produced by these colonies was of the same species as the queen and the majority of workers in the colony. This suggests that facultative slave-making occurs among species which are normally enslaved by other species.

For *Formica,* by contrast, no mixed colonies of these slave species have ever been reported in the absence of slave-makers. Laboratory manipulations with *F. schaufussi* and *F. nitidiventris* (in which two conspecific colonies are connected and no emigration is possible) have shown that colony fusions often occur, with relatively little violence, with the exception that at least one queen is usually eliminated (Goodloe & Topoff, unpublished data). Workers of the eliminated queen might be considered "enslaved" by the others, but there is no evidence that such fusions occur in nature. Admittedly, such conspecific mixes would be almost impossible to detect in the field.

While the *Leptothorax* territorial encounters were marked by continuous violence (Alloway, 1980), *Neoformica* colony fusions were characterized by a curious lack of aggression. Although initial encounters with alien conspecifics resulted in fighting, this behavior often disappeared within a day, and subsequent encounters were impossible to distinguish from encounters with nestmates. This lack of aggression is not consistent with traditional concepts of territorial behavior.

The lack of discrimination in the care of pupae from alien conspecific colonies in *F. schaufussi* and *F. gnava* is not surprising since extra conspecific workers can be absorbed into the service of the queen present in the nest and might provide an adaptive advantage. However, it is difficult to speculate on selection pressures that might exist when there are no known interactions between free-living colonies of these species that would result in one colony coming into possession of a conspecific colony's brood.

Differential consumption of brood of another species is consistent with developmental studies (Jaisson, 1975; Le Moli & Passetti, 1977; Le Moli & Mori, 1982) which show that some *Formica* species imprint, during the days following eclosion, to the brood present in the nest. After that time, they will care for the brood of the species to which they were exposed, and treat the brood of other species as food. In *Raptiformica* colonies, it is common to find more than one species of slave present, and thus the slaves must accept pupae from more than one species. It would be interesting to track the fate of captured pupae from different species, with the species composition of several generations of slaves that had eclosed in the slave-makers nest.

Alloway (1982) speculated that the enhancement of pupae acceptance in *Leptothorax* slaves by the presence of the slave-makers is pheromonally mediated, with a substance either applied to the pupae themselves or transmitted trophallactically by the slave-makers. Possibly, the "deterioration" of pupae acceptance, or the switch to conspecific pupae as a food source by *F. schaufussi* in the presence of the slave-makers, is mediated the same way. As the above comparisons suggest, the evolution of dulosis has apparently proceeded along quite different pathways in myrmicine and formicine ants.

SUMMARY

Pupae acceptance behavior was studied in *Formica* species used as slaves by the slave-making ant genus *Polyergus*. Only one slave species is found in any single *Polyergus* nest. Pupae exchanges between different free-living colonies of *F. schaufussi* (enslaved by *P. lucidus*) and *F. gnava* (enslaved by *P. breviceps*) demonstrated that workers treat pupae of alien conspecific colonies as their own. However, in the presence of their slave makers, enslaved *F. schaufussi* workers consume a greater proportion of alien conspecific pupae than their free-living sisters. Also, enslaved *F. schaufussi* workers consume more pupae of a different slave species of *P. lucidus (F. nitidiventris)* than of the resident slave species. Comparisons with studies of pupae acceptance in slave species of myrmicine slave makers suggest they may have followed a different evolutionary pathway to dulosis.

ACKNOWLEDGMENTS

This study was supported by NSF Grant BNS-8402041, and by PSC-CUNY Grant 6-66346. We thank Stefan Cover for reading the manuscript.

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YOUNG LARVAE OF *VEROMESSOR PERGANDEI* (HYMENOPTERA: FORMICIDAE: MYRMICINAE)

By George C. Wheeler and Jeanette Wheeler

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Time was when it seemed every myrmecologist wanted to work on *Veromessor pergandei,* but we can find no mention of it in the last eight years of *Zoological Record.* When we lived with it in Death Valley and southern Nevada it became one of our favorite ants.

To differentiate instars we would like the following specimens: a first instar inside an egg; a second instar inside a first instar that is ready to moult; a third instar inside a second ready to moult; etc.; a mature larva; a prepupa. Fortunately our *V. pergandei* material meets all the requirements, except the first. *V. pergandei* is polymorphic, which presents another problem: when does subcaste differentiation begin? How can one tell whether a small larva is the young of a major or a mature of a minim; or whether a medium-sized larva is the mature of an intermediate worker or the half-grown larva of a major? In *V. pergandei* subcaste differences apparently begin in the fourth instar and are manifested only in size.

V. pergandei presents another problem: there are two body shapes for mature worker larvae. We have no explanation for this.

Vermessor pergandei (Mayr)
Figures 1–6.

Egg. Figure 1. About 0.32 × 0.52 mm.

First Instar. Figure 2. Length (through spiracles) about 0.48 mm. Entire larva feebly sclerotized. Body sac-like; head on anterior end and greater in diameter then thoracic somites. Spiracles about 0.006 mm in diameter. No spinules nor hairs on body. Cranium subcircular in anterior view. Antennae represented by 2 sensilla. About 20 head hairs, 0.013–0.025 mm long, unbranched. Mouth parts small. Labrum with a ventrolateral swelling on each half of anterior surface; 2 or 3 sensilla on each half of ventral surface. Mandibles subtriangular; apical tooth straight and sharp-pointed;

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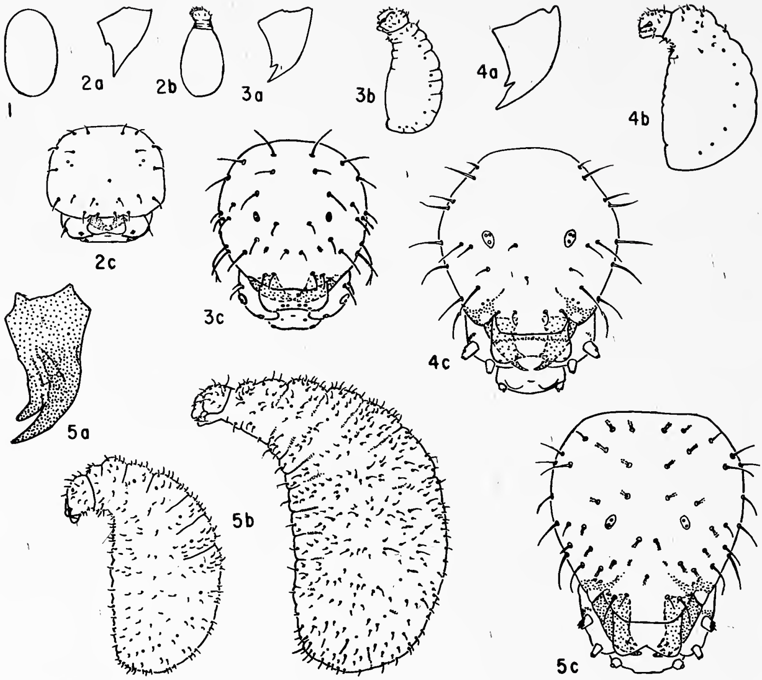
Manuscript received by the editor June 4, 1987



Figures 1–5. Left mandible in anterior view, ×185; larva in side view and egg, ×19; head in anterior view, ×76. 1. Egg. 2. First Instar. 2a, Mandible; 2b, profile; 2c, head. 3. Second Instar. 3a, Mandible; 3b, profile; 3c, head. 4. Third instar. 4a, Mandible; 4b, profile; 4c, head. 5. Fourth Instar. 5a, Mandible; 5b, profiles of two sizes of larvae; 5c, head.

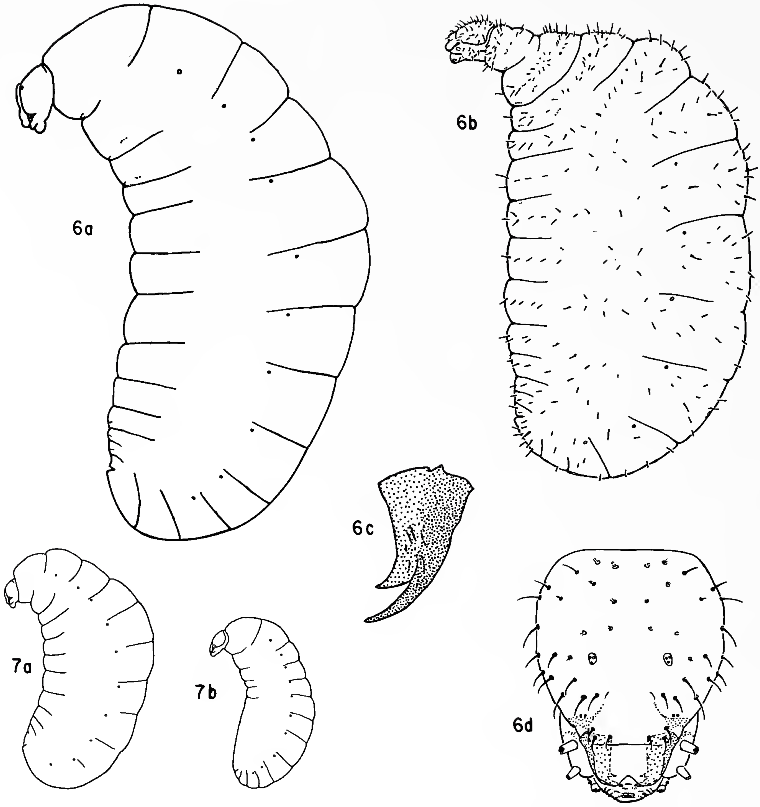
medial border with a small projection. Maxillary palp with 5 sensilla on a slight elevation; galea represented by 2 sensilla. Labium short and wide; palp represented by 5 (?) sensilla.

Second Instar. Figure 3. Length (through spiracles) about 1.6 mm. Dorsal profile of body feebly C-shaped, ventral feebly sigmoid; T1–T3 nearly same diameter; AIII–AIV widest, tapering slightly to anterior end and more rapidly to posterior end; head and anus ventral; anus with a small posterior lip. Spiracle diameter about 0.008 mm. Integument with minute spinules in short rows on venter of thorax and all surfaces of AVIII–AX. Body hairs on T1 only; 0.006–0.018 mm long, slightly curved and with frayed tip. Cranium oval, narrowed ventrally; length subequal to width. Antennae with 3 sensilla each. Head hairs few (about 35); 0.006–0.018 mm long, with short frayed tip. Labrum feebly bilobed; anterior surface of each lobe with a few sensilla near and on ventral surface. Mandible feebly sclerotized. Maxillary palp represented by a cluster of 5 sensilla; galea a slight elevation with 2 sensilla. Labial palp represented by a cluster of 5 sensilla.

Third Instar. Figure 4. Length (through spiracles) 2.4–2.8 mm. Similar to second instar except as follows: Body widest at AIII, venter nearly straight; dorsal profile long and C-shaped. Spiracles about 0.019 mm in diameter. Entire integument with minute spinules in short arcuate rows. Body hairs very few; on thorax only; 0.013–0.028 mm long, with very short-bifid tip. Cranium subhexagonal in anterior view; width and length subequal. About 30 head hairs; 0.013–0.058 mm long, with short 2- or 3-branched tip. Labrum bilobed; each lobe with 2 sensilla on anterior surface; ventral surface with 3 sensilla on each half; posterior surface with 3 sensilla near ventral border of each lobe and with a cluster of 3 sensilla near middle; with small patches of isolated spinules dorsally and near middle. Maxilla with round-pointed apex and with a few short rows of minute spinules; palp a short frustum with 5 sensilla; galea a low rounded knob with 2 sensilla. Labium with small patches of spinules dorsally near middle, the spinules isolated or in short rows; palp a slightly elevated cluster of 5 sensilla; an isolated sensillum between each palp and the opening of the sericteries; the latter a short transverse slit. Hypopharynx with a few minute spinules in short transverse rows.

Fourth Instar. Figure 5. Length (through spiracles) about 3.0–4.9 mm. Similar to third instar except as follows: Body hairs sparse, generally distributed; 0.013–0.1 mm long; with slightly curved shaft and short-frayed tip. About 45 head hairs; 0.012–0.05 mm long. Posterior surface of labrum with rather coarse spinules, isolated or in short rows dorsally. Mandible moderately sclerotized; apical tooth long, narrow and sharp-pointed; subapical tooth shorter and less pointed. Maxillary palp and galea more elevated. Labial palp a low knob with 5 sensilla. Hypopharynx with numerous short transverse rows of minute spinules; upper portion with numerous short ridges [furrows?] converging into pharynx.

Fifth Instar (Mature Larva). Figure 6. Length (through spiracles) 4.3–6.8 mm. Similar to fourth instar except as follows: Body profile pogonomyrmecoid but of two different shapes: (1) stout, with AII and AIII swollen dorsally; (2) abdomen swollen and sac-



Figures 6–7. Fifth Instar (Mature Larva). 6a (hairs omitted) and 6b, profiles, ×19; 6c, left mandible in anterior view, ×185; 6d, head in anterior view, ×76. 7. Profiles of mature larvae to show size range (hairs omitted), ×8. 7a, Major worker; 7b, minor worker.

like, thorax narrowed abruptly and turned ventrally, T1 about same diameter as head length. Otherwise larvae with different profiles similar. Anus with small lips. Leg, wing and gonopod vestiges present. Body hairs with bifid or frayed tip. Antennae small, each with 3 sensilla; at midlength of cranium. Head hairs with slightly curved shaft and 2- or 3-branched tip. Mandibles ectatommoid; heavily sclerotized; apical tooth long and narrowed to a sharp point; subapical tooth at end of medial blade, with stout base and sharp apex. Maxillary palp paxilliform with 5 (4 apical and 1 lateral) sensilla; galea stout and digitiform with 2 apical sensilla. Labium with minute spinules in short to long arcuate rows which are arranged in subtransverse rows; opening of sericteries a moderately long transverse slit.

Material studied: numerous larvae from Death Valley National Monument, California and Boulder City, Nevada.

In studying the living larvae the following characters will be most useful in distinguishing instars: First instar. Lacks hairs on body. Head hairs few (about 20). Second Instar. Body hairs very few, confined to T1 only. Head hairs few (about 35). Third Instar. Body hairs very few, some on each thoracic somite. Fourth Instar. Body profile lacks distinct neck. Entire integument covered with spinules and hairs, the hairs with short frayed tips. Fifth Instar (Mature Larva). Body profile pogonomyrmecoid. Length 4.3–6.8 mm. Body hairs with short 2- or 3-branched tip.

SUMMARY

The larva of each of five instars of *Veromessor pergandei* is described in detail and illustrated. In the fifth instar there are two types of body profiles. The instars of living larvae may be differentiated by a few easily observed characters.

BRODIOPTERA STRICKLANI N. SP. (MEGASECOPTERA: BRODIOPTERIDAE), A NEW FOSSIL INSECT FROM THE UPPER MANNING CANYON SHALE FORMATION, UTAH (LOWERMOST NAMURIAN B)

By C. Riley Nelson[1] and William D. Tidwell[2]

The insect described in this report was collected from the uppermost units of the time-transgressive unit—the Manning Canyon Shale Formation, in central Utah. This formation of Late Mississippian to Early Pennsylvanian (Namurian A and B) age consists predominately of shales with interbedded limestones, orthoquartzites and some siltstones. A flora has been described from the upper portion of this formation at and near the collecting site for this insect. The flora from the upper Manning Canyon Shale, as presently defined, contains 43 genera and 103 species (Tidwell, 1967; Tidwell et al., 1974; Webster et al., 1984). Thus, it represents the most diversified flora of Carboniferous age presently known in western North America. Plant fossils from this formation consist of fern or fern-like foliage, lycopods, species with calamitean affinities, various seed types, cordaitean taxa and several forms related to microsporangiate structures. These plants indicate that the area was a swampy, moist lowland with perpetual summer-like conditions (Tidwell, 1975).

The Manning Canyon Shale is the oldest horizon reported to be insect-bearing in western North America (Durden, 1984). The age of the uppermost Manning Canyon Shale Formation remains uncertain. Many paleontologists and geologists consider the formation to be entirely Mississippian (Upper Namurian A: Bissell, 1959; Gordon and Duncan, 1970; and Webster et al., 1984). Others (Chamberlain and Clark, 1973; Sando, 1985) place the base of the formation in Upper Mississippian and the upper portion in the Lower Pennsylvanian (Namurian B and C). The majority of the fossil plants from the upper shales of this formation are encountered only in the Penn-

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Manuscript received by the editor June 10, 1987.

sylvanian, whereas a small number of species are typically Mississippian. Therefore, we consider this upper flora, as well as the insect, to be lowermost Namurian B in age.

The insect specimen described in this paper is a compression fossil consisting of the body, four wings, cerci, legs, and antennae. It is assigned to *Brodioptera* of the paleopterous order Megasecoptera, which is related to the orders Diaphaneropterodea and Paleodictyoptera. All of these Paleozoic orders had sucking beaks and probably fed by sucking the contents of fructifications and cones of lycopods, cordaiteans, and pteridosperms (Kukalová-Peck, 1983, 1985).

The oldest North American pterygote insect known so far is *Metropator pusillus* Handlirsch collected near "Altamount Colliery" in the Anthracite coal region of Pennsylvania (Carpenter, 1965). It is of historical note that there were two Altamount Collieries both near Frackville, Pennsylvania. Coal mined at the Altamount Colliery #1 was in the Tumbling Run Member of the Pottsville Formation which is Morrowan (Late Namurian) in age and coal mined at the Altamount Colliery #2 was in The Sharp Mountain Member of this same formation. The latter member is of Atokan (partly Westphalian B and partly Westphalian C) age. Since the coals for the Altamount Colliery are not older than the Tumbling Run Member, then the oldest this insect can be is Namurian B.

A rich Namurian entomofauna has been described from Europe, including Poland, Czechoslovakia, Belgium, and numerous specimens from the Ruhr Valley of West Germany. Further, two very well preserved and almost complete wings of Protodonata were reported from Namurian strata of Argentina in South America by Riek and Kukalova-Peck (1984).

The order Megasecoptera occurs from Upper Carboniferous to Upper Permian (Brues, Melander, and Carpenter, 1954). The numerous families composing this order have been separated mainly on differences in their venation. Most members of this order have been named on the basis of single wings. Because of its completeness, the specimen from the Manning Canyon Shale is a significant contribution.

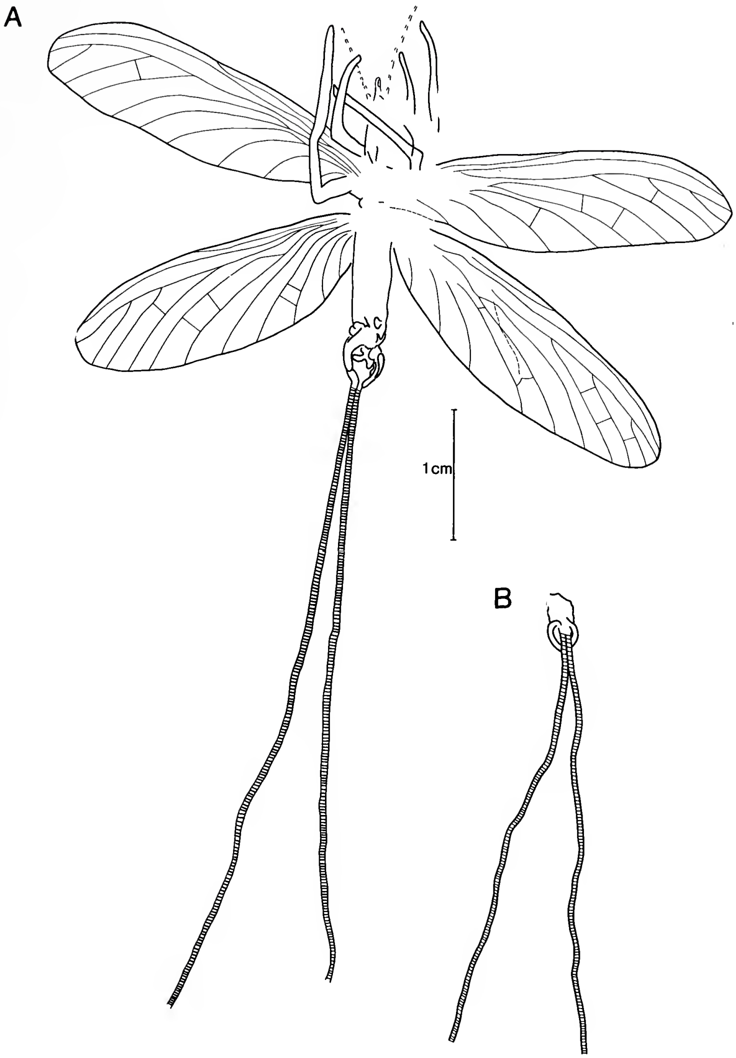

Fig. 1. A. Habitus of ***Brodioptera stricklani*** n. sp., holotype. B. Drawing of ***Brodioptera stricklani*** n. sp. BYU 3243, dorsal view of the male terminalia.

Megasecoptera

Brodiopteridae Carpenter, 1963

Brodioptera Copeland, 1957

Brodioptera stricklani n. sp.

Figs. 1–2

HOLOTYPE. Male, UTAH, Utah Co., 1.5 miles East of highway 73 at point 4.3 miles west of Lehi (Sec. 9 T5S R1W, Utah County, Utah in Jordan Narrows Quadrangle; 40°23′30″N 111°57′30″W) in clay pits of the Manning Canyon Shale Formation of lowermost Pennsylvanian (lowermost Namurian B) age. Deposited in Brigham Young University paleontological collection as specimen #3160.

DESCRIPTION. Male, length from head to distal portion of genitalia 26 mm; expanse measured between apices of forewings of complete specimen 57 mm; head with vaguely preserved mouthparts; antennae filiform, incomplete right remnant 9 mm in length, left remnant 40 mm; legs poorly preserved, three on left side, two on right; length of each forewing 28 mm, width of each forewing measured at apex of Sc 8 mm; length of right hindwing 25 mm, not flat during preservation, length of left hindwing 28 mm, width of each hindwing 8 mm measured at apex of Sc. Wings as in Figs. 2a–d; Sc joining C near midlength of each wing; R_1 and Rs forking in basal quarter, Rs with four branches; MA and MP forking at 1/3 wing length, MA arching anteriorly near fork with MP to nearly contact Rs; CuA and CuP forking in basal 1/3; anal veins composed of three branches with A_3 seen only in right hind wing (Fig. 2d); crossveins few but straight and irregularly placed. Abdomen with faint indication of segmentation; genitalia 4.8 mm in length, composed of lateral claspers and medial gonapophyses, neither claspers nor gonapophyses with annulations; cerci long and filiform more than 54 mm in length.

PRESERVATION. The specimen of *B. stricklani* consists of a part and counterpart with characters better preserved on one rather than the other of the faces. The specimen is lying ventral side up. In this position, the basal portions of the wings are covered from view with the legs lying over parts of the specimen. Details of the head as well as the thorax including attachments of the legs and wings cannot be observed. The specimen is a compression fossil with concavities and convexities of the wings not apparent. Many of the structures of the specimen are indicated by hematitic material; however, the legs and

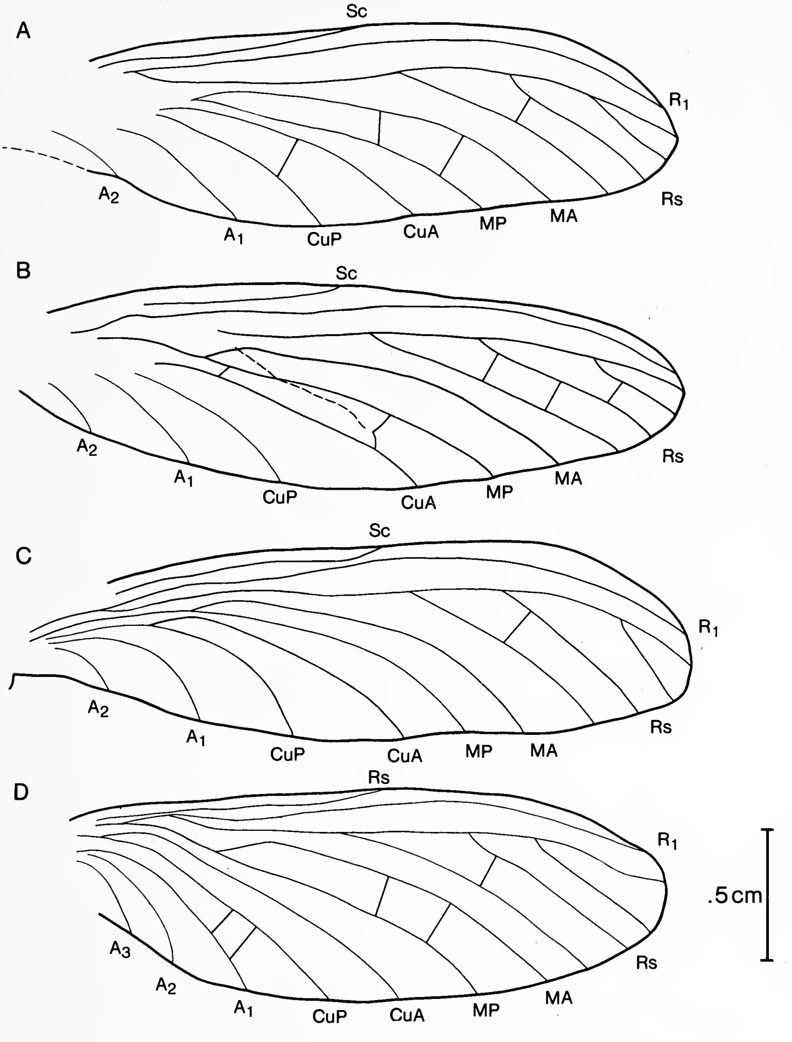

Fig. 2. A–D. Wings of *Brodioptera stricklani* n. sp., holotype; A. left forewing; B. right forewing. C. left hindwing; D. right hindwing.

some of the veins are raised areas or impressions depending on which face is viewed. Vague outlines of the head and sucking beak are indicated near the basal end of the antennae.

DIAGNOSIS. *Brodioptera stricklani* is closely related to *B. cumberlandensis* Copeland 1957. Comparison of the wing of *B. cumberlandensis* (Carpenter, 1963) reveals that it more closely resembles the forewing of *B. stricklani* than the hindwing. The two may be separated on the basis of details of forking patterns of the veins. The shorter subcosta of *B. stricklani* joins the costa at about the midpoint of the wing while that of *B. cumberlandensis* joins the costa well beyond the midpoint. The radial sector, media, and cubitus all fork more distally in *B. stricklani* than in *B. cumberlandensis.* Both the fore and hind wings of *B. stricklani* have a relatively broader anal region than does *B. cumberlandensis.* Further, the MA in *B. stricklani* does not curve forward as sharply as in *B. cumberlandensis.*

ETYMOLOGY. This species is named in honor of Mr. Dave Stricklan of Provo, Utah, who donated the holotype specimen for this study.

DISCUSSION. The well-spread wings of *B. stricklani* give supplementary support to the concept that Megasecoptera were unable to fold their wings over the dorsum of the abdomen and, therefore, that Carpenter (1963) was correct in placing *Brodioptera* in Megasecoptera. Further, the adequately preserved genitalia of this specimen closely resemble those of extant Ephemeroptera (Edmunds, et al., 1976) and should provide valuable information for future phylogenetic and evolutionary studies. It is interesting to note, as did Carpenter (1963), that such apparently apomorphic reduction in venation is present in an insect found so near the age (Namurian) in which the oldest winged insects have been discovered.

ADDITIONAL MATERIAL. A second specimen consisting of genitalia and cerci has been collected near the same locality as the holotype. The specimen is considerably smaller than the holotype but has a similar genitalic structure. This specimen consists of both the part and counterpart that reveal the dorsum of the specimen including the dorsal attachment of the cerci to the abdomen. This second specimen is tentatively assigned to *B. stricklani* and is deposited as figured specimen #3243 in BYU paleontological collection.

ACKNOWLEDGMENTS

We thank Dave Stricklan for the generous donation of the holotype specimen as well as Victor Call for the second specimen. Many thanks are given to Dr. J. Kukalová-Peck of Carleton University for valuable information and numerous suggestions that greatly improved this paper and to Dr. A. T. Cross of Michigan State University for his assistance with stratigraphic problems. Additional thanks are extended to J. Chandler for help with literature searches and to N. Hebbert for inking the illustrations.

SUMMARY

A fossil megasecopteran of the family Brodiopteridae, *Brodioptera stricklani* n. sp., is described. This is the first report of a nearly complete specimen of the family and is the first insect recorded from the transitional Mississippian-Pennsylvanian (Namurian A and B) Manning Canyon Shale Formation of Utah in western North America.

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OBSERVATIONS OF *XENORHYNCHIUM NITIDULUM* (FABRICIUS) (HYMENOPTERA, EUMENINAE), A PRIMITIVELY SOCIAL WASP

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Introduction

Until recently primitively social wasps, with more than one female sharing a nest but without a reproductive division of labor, were considered rare. For many years, the only such wasps known were the five species cited by Wheeler (1928) in his classic book on the social insects. More primitively social wasps are now known (for a partial list see West-Eberhard, 1979). It is clear, however, that many more remain to be discovered, and information on the biology of primitively social species is still scarce. It therefore seems worthwhile to report the following brief notes on *Xenorynchium nitidulum* (Fabricius), a primitively social wasp found in India. The observations reported here were made on nests collected in the village of Janla, Puri District, Orissa (about 20 degrees N.Latitude) in November, 1979. *X. nitidulum* is widely distributed in India. Vecht (1963 p. 112) cites Dover and Rao (1922) as recording this species from Calcutta, Pusa, Bangalore, Lucknow, Kashmir, and Lahore (Punjab).

Nest Structure and Contents

Xenorhynchium nitidulum builds a nest consisting of several barrel-shaped mud cells coated with an amber-colored substance that is sticky when fresh, and that later forms a hard lumpy coating. This coating strengthens the rather fragile mud walls of the cells which are only 0.25–0.5 mm thick. It may also afford some protection against insect predators and parasitoids, as further discussed below. Horne (1870) and Dutt (1912) report that the gummy substance comes from the trees *Ficus religiosa* and *Acacia catechu.*

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Manuscript received by the editor September 25, 1987.

The largest recorded nest of *X. nitidulum* contained 25 cells (Dutt, 1912). Two inhabited nests collected in Janla (N1, N2) contained 14 and 2 cells, respectively. Cells are 17.0–22.0 mm long and 12.0 mm wide at the center, with the mouth 5.0–7.0 mm in diameter. The cells are arranged in a cluster, with the foundations of the first three or four cells usually attached to the underside of a horizontal surface, such as the ceiling of a man-made structure. The first cells are inclined with their axes at about 80° from the attachment surface, and additional cells are aligned parallel to them, but with their foundations displaced slightly so as to be free of the substrate. All of the cell entrances face in the same direction; they open upward when the nests are attached to a wall.

The two inhabited nests were located on the ceiling of a dark room. Abandoned nests were found in similar sheltered situations, e.g., in the rooms and stairways of an abandoned house in the same village. The species had evidently been common in ancient abandoned Jain caves at Udayagiri, near Bhubaneshwar, but the walls and ceilings of the caves had recently been cleaned, leaving only gummy outlines of where the bases of cells had been attached. While searching the caves for nests, I noted several black female wasps the size of *X. nitidulum* sitting inside mud and gum-lined holes in the cave walls, facing outward as does this species in the cells of the nest (see below). Several such holes were sealed with mud and a gummy substance. This species thus may sometimes inhabit pre-existing holes; but I was unable to collect specimens of the hole-occupying wasps for certain identification.

When collected on 24 November nest N1 contained 11 closed cells (sealed with mud overlain with gum) and three open cells. One open cell was empty, and a day later I found the two other open cells contained a single lepidopterous larva, 7.5 mm long, without an egg; and a mature wasp larva in the process of spinning a cocoon within the cell. N2 consis~~ted of~~ two cells, one of them empty but lined with a silky material as if it had already produced an adult, and the other incomplete (in the process of construction). These two nests were only about two feet from each other in the same room. I kept nest N1 in a jar to see what would emerge from the eleven sealed cells. They produced four female and three male *X. nitidulum* adults, and three males of the cleptoparasitic wasp *Stilbum cyanurum splendidum* (Chrysididae). The three parasites, and one male and one female *X. nitidulum* emerged before 26 December. The remaining

X. nitidulum adults emerged in the following order (with time elapsed since nest collection given in parentheses): male (32 days), female (42 days), female (52 days), male (60 days), female (61 days). When one of the closed cells produced nothing after more than three months I opened it and found that it contained two desiccated objects that appeared to be caterpillars but that were in such poor condition that they could not be identified.

An abandoned nest (N3) was also collected. It consisted of 11 cells, six of them sealed with mud and gum prior to abandonment. Two sealed cells contained chalcid parasites (five in one cell and seven in the other). A small larva was found in each of two open cells, and a large larva was in a sealed cell with three prey. Of the remaining cells, two were damaged by collection and the contents lost; two had been secondarily occupied by some other species (one was sealed with a thick mud plug, and one contained a vacated puparium); one contained a nearly mature male; and one open cell contained a desiccated adult male.

N1 was inhabited by two adult females when captured. A third female caught entering the room with prey was probably associated with N1 which had the only cells in the room containing prey or larvae. It is also possible that this female was carrying the first prey to the empty cell of N2. Thus N1 was attended by at least two and probably three females. Another female, netted as she entered the room with mud, was probably building the incomplete cell of N2, since it was the only cell of the two nests present containing freshly applied mud. A fifth female, collected later by the owner of the room, was reported by him to be associated with the site of N2, but the two nests were so close together that this was difficult to confirm.

The five females associated with these two nests were dissected. All of them had sperm in the spermathecae (were mated). The spermatheca of one of the females known to be associated with N1 was brownish in color, and her ovary contained many yellow bodies—both often characteristics of old female wasps. The female sitting in the empty cell of N1 when it was collected had two well developed eggs in her ovary (measuring 2.5 mm and 2.0 mm in length). This was the most developed ovary of the five females. Three of the females had just one large egg each; and one, evidently a young female judging by the light color of her abdominal apodemes (see Richards, 1971), had undeveloped ovaries (no visible oocytes).

THE BEHAVIOR OF THE ADULTS

Adults of both sexes sit facing outward in empty cells on the nest. It is not known if they likewise sit in cells containing immatures or prey, but seems likely that they do. There is no doubt that the female wasps defend the cells in which they sit. When I touched nest N1 while preparing to collect it to my great surprise I was immediately stung by a female sitting in a cell. Close examination of the position assumed by such females revealed that they sit curved in the shape of a letter "C," so that both head and abdomen point outward at the mouth of the cell. When approached, the head is slightly retracted and the abdomen thrust forward to sting. I know of no published records of defensive stinging by Eumeninae or other solitary aculeate wasps. I have been stung by airborne females of *Zethus miniatus* while tampering with their nests, but those females, which also sit facing out of brood cells, withdraw into the cells when threatened rather than coming forward to sting. One *X. nitidulum* female also stung me readily when accidentally touched in the collecting net.

Another unusual feature is that these wasps either sometimes begin provisioning before ovipositing, or they store prey in empty cells, as evidenced by the broodless cells containing prey on N1. All vespoid wasps oviposit in an empty cell and begin provisioning later, often after the egg hatches (Evans and West-Eberhard, 1970). However, Isely (1913) found that some Kansas eumenines deposit a few prey in the cell prior to oviposition. This point merits further study in the case of *X. nitidulum,* since I saw only one (eggless) cell being provisioned.

The contents of N1 suggest that vacated cells are reused. The three cells of N1 that were open when collected were among the older (uppermost) cells of the nest; one was being provisioned, and one contained brood. Females may reuse vacated cells when they are available, and build new cells only when they are not. On N1 and N2 there were five adult females and only four vacated empty cells; in that situation one new cell had been initiated.

The fact that a large larva was found in an open cell may indicate progressive provisioning of the young. However, one of the closed cells of the abandoned nest (N3) contained the remains of a large larva and three uneaten prey. Perhaps *X. nitidulum,* like the primitively social eumenine *Zethus miniatus* (personal observation), engages in what Evans (1966) calls "truncated progressive provisioning," in which several prey are brought to the cell in quick succession when the larva is nearly grown, and the cell is then sealed.

The chrysidid wasp, *Stilbum cyanurum,* probably opens an oviposition hole in the cell wall after the host cells are sealed (see Bequaert, 1918; Iwata, 1976, p. 57). The sticky covering of *X. nitidulum* nests may provide some protection against the attacks of such intruders.

Even though brief, these observations show that *Xenorynchium nitudulum* should be classified as at least "primitively social," defined as nest-sharing without a reproductive division of labor. Of the five females associated with the two inhabited nests of this study, all were mated, and all except a very young (probably recently emerged) individual had developed ovaries. Of the five females, three were known to be active caretakers of the nests; one was observed provisioning, one carrying mud, and one defending the nest by stinging an intruder. The combination of dissection and behavioral data indicates that the females associated with the nests were not simply resting there, but active residents of shared nests.

A male which emerged in captivity attempted copulation on the nest with a female which emerged a day later. Each time the male's gentalia were extruded he placed his mouthparts just behind the female's head and bit at her mildly. When mounted the male periodically fanned his wings and while doing so lowered his antennae against those of the female, as in *Polistes* and some other vespoid wasps (see West-Eberhard, 1969 and references therein). Intromission was not observed. These two adult wasps fed on raisins and water, and survived for several days in the jar containing the nest. Although they wandered about the jar during the daytime, at night the female always sat inside one of the empty cells (not always the same one) facing out. The male was less consistent in his sleeping habits, sometimes sitting in a cell facing inward, once facing outward. He usually spent the night sitting on the surface of the nest rather than in a cell.

FOLKLORE

Xenorhynchium nitidulum is a common wasp in Orissa and other parts of India (see Vecht, 1963). Because of its habit of building nests on human habitations, it is familiar to the residents of the region. Mrs. Rukmini Patnaik, whose family is from a village near

Janla, informed me that *X. nitidulum* is known in the Oriya language as "lakha bhanra" ("the lacquer bee"), and is popularly distinguished from species building plain mud nests ("matti bhanra," or "mud bees"). Some people believe that pregnant women in homes inhabited by "lacquer bees" are destined to give birth to boys, whereas "mud bees" forecast the birth of a girl.

SUMMARY

The Indian eumenine wasp *Xenorynchium nitidulum* is at least sometimes "primitively social" in that more than one adult female participates in brood-rearing on a single nest. Examination of nest contents and dissection of females indicate that cells are reused and larvae are progressively provisioned, at least in the early larval stage. Females sit facing outward in uncapped cells and sting defensively by bringing the tip of the abdomen forward without coming out of the cell. The gummy coating of the outside of the thin mud cell walls may provide some protection against the parasitoid *Stilbum cyanurum splendidum* (Chrisydidae), which emerged from collected nests. Courtship behavior was observed in the laboratory. *X. nitidulum* is known as "the lacquer bee" in Orissa, and is popularly believed to be useful in predicting the sex of unborn children.

ACKNOWLEDGMENTS

Fieldwork in India was made possible by a grant from the Smithsonian Institution Special Foreign Currency Program. While in Orissa I was a guest at Utkal University. I thank my hosts, Zoology Department chairman Dr. B. K. Behura, and especially Dr. P. Mohanty-Hejmadi. Work in Janla was arranged by Dr. Mohanty-Hejmadi and her student, Miss K. Samantray. I am indebted to Miss Samantray and her parents, Mr. and Mrs. K. C. Samantray for their hospitality in Janla and for help in locating nests. Dr. Sushil Dutta also kindly assisted in the field. Drs. K. V. Krombein and J. van der Vecht identified specimens of Hymenoptera. Voucher specimens are deposited in the U.S. National Museum. William G. Eberhard made helpful suggestions on the manuscript.

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COMPETITION FOR PREY BETWEEN ANTS AND BURYING BEETLES (*NICROPHORUS* SPP): DIFFERENCES BETWEEN NORTHERN AND SOUTHERN TEMPERATE SITES.

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Introduction

Burying beetles (Silphidae: *Nicrophorus*) utilize small vertebrate carcasses which can be quickly buried or rolled down a hole and concealed. Because carrion is also used by other invertebrates and vertebrates, burying beetles may be in competition with species of a wide variety of taxa for access to carcasses. For example, calliphorid flies are often first to oviposit on carrion and if the eggs are not detected and destroyed by *Nicrophorus* the carcass may be consumed by developing fly larvae, causing the beetles to abandon the resource.

One aspect of resource competition in *Nicrophorus* that has not been examined concerns interactions between burying beetles and ants (Arnett 1946). Ants are abundant, omnivorous scavengers in many habitats; ant colony size is often large and many species have swift recruitment systems that would allow them to occupy and defend small vertebrate prey. Ant species diversity and abundance are known to follow a latitudinal gradient (Kusnezov 1957, Wilson 1971, Jeanne 1979), and therefore the predatory or scavenging habits of ants may exert different effects on the ability of northern and southern temperate *Nicrophorus* species to control small vertebrate carrion. In this paper we report on the results of a study examining competitive interactions between burying beetles and ants at northern and southern sites in North America.

Materials and Methods

The natural history of burying beetles (*Nicrophorus* spp.) and their ecological relationships have been well described (Pukowski

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**Revised manuscript received by the editor September 10, 1987.*

1933, Milne and Milne 1976, Anderson 1982, Wilson 1983, Wilson et al. 1984, Wilson and Knollenberg 1984, Wilson and Fudge 1984). Males and females are attracted to carrion, and intrasexual competition occurs within each sex until usually only one male and female remain. The pair may then move the corpse; both sexes dig beneath to bury it, remove the fur or feathers of the carcass, and roll it into a ball treated by both male and female with anal and oral secretions. Following burial, the female's ovaries rapidly complete development (Scott and Traniello 1987) and she lays approximately thirty eggs in the soil nearby which hatch into altricial larvae that are fed regurgitated food by both parents. The larvae are soon capable of feeding from the corpse directly, but may also receive food from their parents throughout development. About two weeks after burial, the larvae leave the burial chamber and pupate in the soil nearby. Usually, at least one parent remains with the brood until larval dispersal.

Ant and burying beetle competition was studied in a mixed hardwood (maple/birch/beech) and softwood (pine/hemlock/spruce) forest at Jaffrey, New Hampshire (Cheshire County) and in a pine/oak forest and two field sites at Wimauma, Florida (Hillsborough County). *Nicrophorus sayi, N. orbicollis, N. defodiens,* and *N. tomentosus* are common at the northern site, and *N. orbicollis* and *N. carolinus* were trapped in Florida. In order to study abundance and diversity of ants and burying beetles, a transect of 10–25 pitfall traps (0.95 liter jars) located 10 m apart was set out on each site. In New Hampshire these were baited with aged beef kidney and in Florida with previously frozen whole chicks (*Gallus gallus*) which did not dry out in the heat and were more effective in attracting all invertebrates. Pitfall traps were censused after 24 h. To examine competition between ants and beetles for the utilization of small vertebrate carrion, previously frozen mice (*Mus musculus*), 8–60 g, or chicks, 45–55 g, were placed over 0.95 liter jars or 11.4 liter pots filled with potting soil and sunk into the ground at 25-m intervals. These traps were censused every 24 h and the ultimate fate of each carcass (buried by beetles, overrun by ants until the carcass was consumed or was no longer attractive, removed by vertebrates, or utilized primarily by flies) was recorded. The traps containing carcasses buried by beetles were retained and adults leaving the brood chamber, and either eclosing flies or teneral beetles were captured. Studies were conducted June–August 1984, 1985 in New Hampshire and May–July 1986 in Florida.

RESULTS

Burying beetles were readily caught in pitfall traps at both locations. In New Hampshire, 662 beetles of all four above-mentioned common species were trapped in 525 trap-nights in 1984 and 457 beetles were trapped in 525 trap-nights in 1985. Ants (*Camponotus novaboracensis, Acanthomyops* sp. and *Aphaenogaster* spp) were found in less than 2% of the pitfall traps and always in low numbers (less than 10). At the southern site 441 beetles were trapped in 794 trap-nights. Ninety-five percent of these were *N. carolinus* which were trapped in equal numbers in the forest and in the field. *N. orbicollis* were captured primarily in the forest. Ant/burying beetle interactions were related to habitat also, reflecting the primarily open-field distribution of the imported fire ant *Solenopsis invicta.* In the forest *S. invicta* was found in 33% of the pitfalls and other ant species in 9% (N = 360); in the field 61% of the pitfalls were occupied by fire ants and 6% by other ant species (N = 434). Information on ant abundance from the pitfall traps at the two study sites similarly indicates a greater potential for ant interference at the Florida site. When ants were present in pitfalls, 94% of traps contained more than approximately 100 workers. Other ant species (*Camponotus abdominalis floridanus, Crematogaster clara*) were found in pitfall traps in small numbers (less than 10). *Pheidole dentata, P. moerens, Crematogaster ashmeadi* and *Conomyrma* sp. were found at baits in the same habitat but not in the pitfall traps.

There were striking differences between sites in New Hampshire and Florida in the percentage of mice or chicks available that were successfully buried by *Nicrophorus* spp. (42% vs 10%, N = 172 and 48, respectively, $t_s = 4.70$, $P < 0.001$, angular transformation test for the equality of two percentages). In New Hampshire, *N. orbicollis* was the dominant species and accounted for 55% of the carrion buried. In Florida, only *N. carolinus* successfully buried prey items experimentally offered. Only 12% of all prey were ultimately utilized by ants at the northern site. Generally, only a few ants were present at a time with the exception of two or three small prey which were completely overrun with *Acanthomyops.* In contrast, significantly more (77%) of the prey at the southern site were utilized by ants, primarily *Solenopsis* ($t_s = 8.79$, $P < 0.001$). Other ant species collected in pitfall traps were not observed on these prey placed on the surface, perhaps due to displacement by fire ants. Flies were more successful in utilizing prey in New Hampshire ($t_s = 7.23$, $P < 0.001$) perhaps also due to displacement by fire ants in Florida.

At both sites, prey size affected its ultimate utilization. In New Hampshire, ants were significantly more successful at utilizing small prey (< 30 g, $t_s = 5.34$, $P < 0.001$) and flies were significantly more successful utilizing large prey ($t_s = 5.45$, $P < 0.001$). In Florida, beetles were less successful in burying small prey ($t_s = 2.30$, $P < 0.02$) but ants were equally successful with large or small prey ($t_s = 0.96$, $P = 0.33$; Table 1).

DISCUSSION

The wide range of feeding habits of ants produce considerable dietary overlap with members of other, unrelated taxa utilizing the same resources (see for example Brown and Davidson 1976). Because many ant species are opportunistic and scavenge for a wide variety of sizes and types of animal prey, it is not unusual that carrion may be used as a food source when available. Such a large, concentrated resource will induce an extraordinary recruitment response from a colony, perhaps exhausting all foragers within the nest. Although the sensitive chemoreceptors of *Nicrophorus* permit them to locate carrion over long distances, the high density of foragers of ant species with well-developed trail communication and chemical or aggressive defense of resources may bring burying beetles and ants into competition for small vertebrate carcasses. Even if prey are first found by *Nicrophorus,* the time during which intrasexual competition occurs and burial is completed could increase the time period in which the carcass might be located by ants and thus increase the probability that they would displace the beetles. In the present study the lack of success of Florida *Nicrophorus* on carcasses was apparently due to interference from fire ants rather than to a lack of beetles in the study area because 416 *N. carolinus* were collected from pitfall traps but only five prey (N = 48) were buried. The nocturnal activity of some *Nicrophorus* species might favor early detection of carcasses and successful utilization, but this advantage would depend upon the temporal pattern of vertebrate mortality. Carcasses could also be lost to ants following burial, as

Table 1. Ultimate use of prey of different sizes in New Hampshire and Florida. Prey unaccounted for in the table (17%, 12%, 33%, and 5% for small and large prey, NH and FL, respectively) disappeared and were presumed to have been taken by vertebrates. N = sample size.

	Prey size (grams)	N	Use by: beetles	ants	flies
New Hampshire	8–29	69	45%	28%	10%
	30–60	103	41%	2%	46%
Florida	20–25	12	0	67%	0
	45–55	36	14%	81%	0

many species have subterranean as well as epigaeic foraging habits.

In addition to loss to ants, *Nicrophorus* will abandon carcasses that are infested with fly larvae. The mutualism between burying beetles and *Poecilius* mites that are predators of fly eggs appears to have evolved in the context of reducing competition with dipterans (Wilson 1983). Also, the cooperative burial shown by the diurnal *Nicrophorus tomentosus* may function in accelerating carcass concealment, thereby reducing prey availability to flies during the warmer periods of the day when fly activity is greater (unpublished data). We observed no behaviors in *Nicrophorus* that could be interpreted as specific to ant/beetle competition, although their coordinated carcass movement (Pukowski 1933, Milne and Milne 1976) could have the effect of decreasing the chance of ant utilization. Moving the carcass to a site suitable for burial might involve selection of appropriate soil conditions and lower ant abundance. The few direct interactions we observed between ant and burying beetles were characterized in New Hampshire (between one beetle and less than 10 ants) by indifference or removal of the ant which had come in contact with the beetle's leg. In Florida, however, *Nicrophorus* avoided carcasses occupied by ants.

There are 85 species of *Nicrophorus* worldwide, most being European and Asian in distribution, and there is a decrease in species diversity at southern latitudes in both the Old and New World (Peck and Anderson 1985). In the New World, fifteen species occur in the United States and Canada, nine in Latin America, three of which are endemic to South America and two endemic to Central America (Anderson and Peck 1985). The biogeography of silphids in general indicates that they are less prominent members of tropical carrion-feeding insect guilds than in temperate regions (Carnaby 1974, Jirón and Cartin 1981). It has been suggested that their lower abundance in the tropics is due to the increased loss of carrion to bacteria, fly larvae, carrion-scavenging vertebrates and ants (Arnett 1946, Peck and Anderson 1985). It would be tempting to assume that the inverse correlation between ant and burying beetle species diversity is a causal factor in the distribution of silphids. However, our limited study of competition between ants and burying beetles allows us to conclude only that ants may exert at least a strong, local effect on the ability of burying beetles to secure carrion. This effect does not appear dependent only on interactions with the imported species *Solenopsis invicta;* the native *S. geminata* also dominates carrion placed out at other sites in Florida (Lloyd Davis, pers. comm.). Although there is a difference in ant species diversity between the two sites in our study (approximately twelve species total in New Hampshire and sixteen to thirty in Florida; Jeanne 1976, Calabi 1986, Trager, pers. comm., Traniello, pers. obs.), we cannot conclude that there is a direct cause-and-effect relationship between ant diversity and the ability of ants to control prey potentially available to burying beetles. In fact Jeanne's (1979) data show that predation rate by ants was higher on the ground than on vegetation although ant species diversity was higher in the latter microhabitat. Although very little is known about the use of small vertebrate carrion in the tropics, such resources may be exploited by ants, and the presence of only a few dominant ground species may reduce burying beetle reproductive success. Given the information available on the patterns of distribution and abundance of ants, it can be inferred that carrion may be approached more frequently by ants in the tropics than in the temperate zone. A relatively small number of omnivorous genera having species with large colony size and rapid recruitment communication may effectively restrict the use of carrion by burying beetles, perhaps producing patterns in the tropics similar to what we have described in Florida. In New Hampshire and Florida the relative importance of ants in *Nicrophorus* ecology seems dramatically different, but the relative importance of the distribution of ants, flies, and microbes in the biology of burying beetles remains to be determined.

SUMMARY

By sampling the diversity and abundance of burying beetles and ant species utilizing small vertebrate carcasses with pitfall and burial traps and recording the success of *Nicrophorus* spp. in securing carrion for reproduction, we found that ant interference was more prevalent in a population in central Florida than in southern New Hampshire. Carrion placed along transects in central Florida was occupied by the imported fire ant *Solenopsis invicta,* and although burying beetles were abundant in the area, few prey were successfully utilized. It is concluded that some ground-dwelling ant species may have a significant local impact on burying beetle reproductive ecology.

ACKNOWLEDGMENTS

We thank Dr. James Trager for identifying ants at the Florida site and Dr. Lloyd Davis for comments on the manuscript. Funds for this research were provided by Grant GRS 805 BI from the Graduate School of Boston University, by a grant from the Boston University chapter of Sigma Xi to I.F., and by NSF grant BNS 82 16702 to J.F.A.T., and by a Science Scholars Fellowship from the Mary Ingraham Bunting Institute of Radcliffe College sponsored by the Office of Naval Research to M.P.S.

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AN UNUSUAL NEW GENUS OF CHRYSIDIDAE FROM OMAN (HYMENOPTERA)

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The chrysidid tribe Elampini comprises a diverse group of genera. There are a number of small (1–3 species) highly derived genera in this group. Nearly all of these occur in 2 regions, southwestern North America and the area comprising the Middle East, southern USSR and North Africa. The small North American genera are *Hedychreides* Bohart, *Microchridium* Bohart, *Minymischa* Kimsey, *Pseudolopyga* Bodenstein and *Xerochrum* Bohart. Those in the latter region include: *Haba* Semenov, *Prochridium* Linsenmaier and the new genus, *Adelopyga,* described below. One genus, *Muesebeckidium* Krombein, occurs in both North and South America.

The following abbreviations are used: F = flagellomere, MOD = midocellus diameter, PD = puncture diameter, Rs = forewing radial sector, and S = gastral sternum.

Adelopyga Kimsey, new genus.

Type species: *Adelopyga huberi* Kimsey, new species.
Etymology: *Adelo* - "obscure", *pyga* - "tail", taken from *Holopyga,* f., Grk.

Diagnosis. Scapal basin smooth with large punctures laterally and slightly rugose medially; F-I shorter than II, and pedicel; mandible with 1 subapical tooth; mesopleuron rounded, with distinct scrobe and oblique scrobal sulcus; female foretarsal claws edentate, mid and hindtarsal claws with single subparallel tooth; apical female fore and midtarsomeres curled, appearing prehensile; hindcoxa without dorsobasal carina; forewing Rs tiny, less than one-sixth stigmal length, stigma apically rounded and medial vein straight;

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Manuscript received by the editor April 7, 1987

propodeum irregularly sculptured and punctate, without carinae, lateral angles small and broadly triangular; abdominal terga narrow and shallowly convex, sterna flat or shallowly convex; body with pale markings on mandibles and legs.

Discussion. In the Palearctic Region *Adelopyga* appears to be most closely related to *Haba* and *Prochridium.* It can be distinguished from both by the edentate female foretarsomeres and dentate mid and hindtarsomeres, the curled fore and midtarsi, very short Rs vein, straight medial vein, apically rounded stigma and narrow terga. The nearctic genus *Minymischa* is also similar to *Adelopyga,* particularly in the wing venation and coiled female fore and midtarsomeres. However, *Adelopyga* differs from *Minymischa* in the tarsal claw dentition, narrow terga, absence of a lateral pronotal carina and the short F-I.

It should be noted that the type and paratype specimens were preserved in alcohol and then critical point dried. The convexity of the abdominal sternum may be due to this treatment. If the sternum is actually flat or somewhat concave the abdomen would be very thin in profile.

Adelopyga huberi Kimsey, new species.

Holotype female. Body length 2 mm. Face convex with depressed scapal basin and with large shallow punctures laterally 0.1–0.4 PD apart; scapal basin polished, smooth and impunctate; malar space 1 MOD long; frons and vertex with large, irregular shallow punctures, 0.2–2.0 PD apart; F-I 0.9× as long as broad, 0.6× as long as pedicel, 0.9× as long as F-II; F-II and V as long as broad; mandible with 1 subapical tooth; pronotum shorter than head length in dorsal view, with shallow scattered punctures 0.2–2.0 PD apart, somewhat wrinkled laterally; scutal punctation same as pronotum, with fine transverse scratches particularly between parapsides and notauli; scutellum smooth with punctures 1.0–1.5 PD apart; mesopleuron with faint indication of oblique mesopleural carina, and about 8 large shallow punctures above scrobal sulcus, finely and densely scratched below scrobe; metanotum with punctures clumped along anterior half, impunctate posteriorly; propodeum irregularly sculptured and punctate, appearing roughened, without carinae on posterior surface, lateral angles small and broadly triangular; gastral terga shiny, with tiny, shallow punctures,

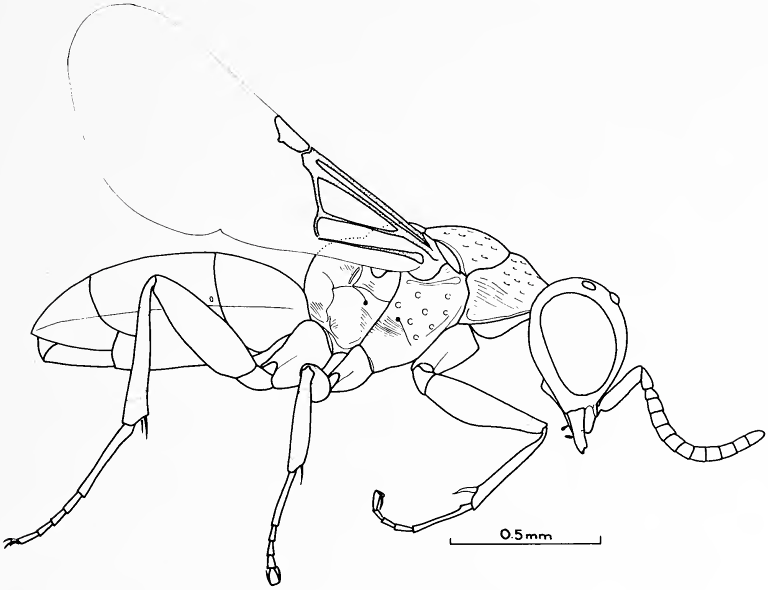

Fig. 1. Lateral view of female holotype of *Adelopyga huberi.*

1–4 PD apart or more. Head, thorax, tegula and terga shiny green; mandible basally green, medially off-white, apically red; femora green with nonmetallic yellow apex; foretibia and tarsi yellow; mid and hindtibia green medially, otherwise yellow; mid and hindtarsi yellow; wing veins pale yellow, membrane water clear; abdominal sterna brown, with small green medial spot on S-I and II.

Male unknown.

Holotype female—OMAN: Al Mintirib, n. end Wahiba sands, 26 February 1986, J. T. Huber. Paratype female, same data as type (DAVIS).

Discussion. The tiny size and coloration of this species make it quite distinctive and easily recognizable. This species is named in honor of the collector and fellow hymenopterist, John Huber.

SUMMARY

The new chrysidid genus *Adelopyga* is described from Oman based on the new species *huberi.*

NEOCLYSTOPSENELLA (BETHYLIDAE) A SYNONYM OF *TAPINOMA* (FORMICIDAE)

By William L. Brown, Jr.

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I followed up Dr. Karl Krombein's suggestion that Kurian's species *Neoclystopsenella luffae* might be an ant, and not a bethylid as originally described. The type place of deposit is unknown, but a reading of the original paper convinces me that the description, although vague and incomplete, fits well the current concept of male *Tapinoma* in the subfamily Dolichoderinae. The specific identity of ***Tapinoma luffae*** NEW COMBINATION remains obscure, but judging from the small size given, "2.4 mm," and the wing venation as figured by Kurian, it may be close to or the same as *T. melanocephalum* or one of its relatives in "subgenus Micromyrma."

Tapinoma

Tapinoma Foerster, 1850: 43, worker, queen (not male). Type: Tapinoma collina Foerster = Tapinoma erraticum, monobasic.

Neoclystopsenella Kurian 1955: 133, male. Type: *Neoclystopsenella luffae* Kurian, by original designation, monobasic (described in Bethylidae). New synonym.

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A SUBSTITUTE NAME FOR THE EXTINCT GENUS *STENELYTRON* KUKALOVÁ (PROTELYTROPTERA)

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In 1966 I described a new species of the extinct order Protelytroptera belonging to a new genus, *Stenelytron,* and representing a new family, Stenelytridae. Having recently learned from Professor F. M. Carpenter that the name *Stenelytron* is preoccupied, I am herein proposing a replacement name, as follows:

Labidelytron, *nomen novum pro Stenelytron* Kukalová, 1966, p. 102, *non* Handlirsch, 1906, p. 451. The type species, *Stenelytron enervatum* Kukalová, 1966, original designation, becomes *Labidelytron enervatum* (Kukalová), new combination. The genus is known only from the Permian of New South Wales, Australia.

The family name, Stenelytridae Kukalová, 1966, p. 102, is herein replaced by Labidelytridae. The genus *Xenelytron* (Kukalová), 1966, p. 105, also from the Permian of New South Wales, is the only other genus known in the family.

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WORKER LONGEVITY IN HARVESTER ANTS (*POGONOMYRMEX*)

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Most studies of worker longevity in ants have been made in the laboratory (Haskins and Haskins 1980; Porter and Tschinkel 1982). In the field, increased energy expenditures, predation, and environmental fluctuations may all contribute to shorten the life of a worker ant. In the few existing studies of worker longevity conducted in the field, the lifespan of exterior workers was found to be extremely short. For example, Schmid-Hempel and Schmid-Hempel (1984) found that the half-life of *Cataglyphis* foragers, after they were marked, was only 6 days.

In harvester ants of the genus *Pogonomyrmex,* the only existing field study of worker longevity demonstrated that the average life expectancy of foragers and defenders (ants emerging from the nest in response to a disturbance) of *P. owyheei* is 14 days (Porter & Jorgensen 1981). Here we show that these results for *P. owyheei* cannot necessarily be generalized to other species in the genus, and that longevity results for the exterior workers engaged in one activity, such as foraging, may not apply to exterior workers that do other tasks.

METHODS

P. barbatus

Longevity data were collected near Rodeo, New Mexico in July–August 1987, in the course of other studies of polyethism in *P. barbatus* (Gordon, in prep.). Ants from 38 mature colonies were marked. In each colony, 50–100 workers were marked from each of the activities under study. Foragers were collected while travelling towards the nest on a trail carrying a food item; patrollers were collected while circling the nest area in a characteristic, zig-zag fashion, and after contacting at least 2 other workers with antenna;

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*Current address: Centre for Mathematical Biology, University of Oxford, 24-29 St. Giles', Oxford OX1 3LB, England midden workers while sorting or repiling the colony refuse pile; and nest maintenance workers after they had come out of the nest entrance with a piece of sand, put it down, and turned to go back into the nest (see Gordon 1986 for detailed description of the four activity types). Individuals were marked in the field using Pactra "hot fuel-proof" model airplane paint; ants of each activity were marked with a unique color. In the course of the field season, a total of 3521 individuals were marked: 307 midden workers, 1169 foragers, 895 patrollers, and 1150 nest maintenance workers. Colonies were checked once daily, usually between 8 and 8:30 a.m., for the presence of marked ants.

P. rugosus

Observations were made near Rodeo, New Mexico in July–August 1986. In one colony, 173 foragers were collected on the foraging trail, and marked in the field using Testors PLA paint. On 27 subsequent days, the colony was checked twice daily for marked ants, once between 700 and 1000 and once between 1600 and 1800.

RESULTS

Table 1 shows the numbers of marked ants observed each day subsequent to marking. Exterior workers survive up to 33 days after marking (nest maintenance worker, *P. barbatus*).

Figure 1 shows the longevity data for *P. barbatus* according to activity when marked. As a result, the number of colonies observed and the total numbers of marked ants both varied as a function of number of days since marking. The data in Figure 1 are normalized to take this variation into account. Shown are the ratios of numbers of ants observed to the numbers of marked ants theoretically available to be observed on that day. For example, there were 12 colonies that were observed 11 days after marking, and these colonies contained a total of 819 marked foragers. A total of 10 marked foragers were observed on the eleventh day after marking. The number shown in Figure 1 is 10/819, or 0.0122, that is, the proportion of all ants marked that were observed. It appears that marked nest maintenance workers outlasted marked foragers, which outlasted marked patrollers.

Table 1. Numbers of marked ants observed as a function of days elapsed since ants were marked. M = midden workers, PT = patrollers, F = foragers, NM = nest maintenance workers.

Days since marking	*P. barbatus*				*P. rugosus* F	
	M	PT	F	NM	a.m.	p.m.
1	–	–	–	–	6	2
2	–	–	–	–	7	4
3	–	–	–	–	–	3
4	7	7	4	6	1	4
5	4	7	12	14	2	7
6		4	7	12	3	3
7	0	4	12	5	3	4
8	2	4	3	3	–	4
9	2	1	6	4	1	0
10	7	2	17	13	3	–
11	4	1	10	17	2	1
12	3	3	6	16	8	2
13	0	3	3	8	–	0
14	0	9	2	15	3	3
15	0	1	6	7	0	4
16	1	2	3	3	0	0
17	1	1	3	7	5	6
18	0	1	0	8	3	–
19	2	0	2	6	–	0
20	0	1	0	1	1	4
21	0	2	0	4	–	5
22	0	1	0	0	–	3
23	1	0	1	0	2	6
24	0	2	2	0	–	4
25	0	3	2	0	0	3
26	0	0	0	2	–	1
27	0	0	0	0	2	4
.						
.						
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33	0	0	0	1	–	–

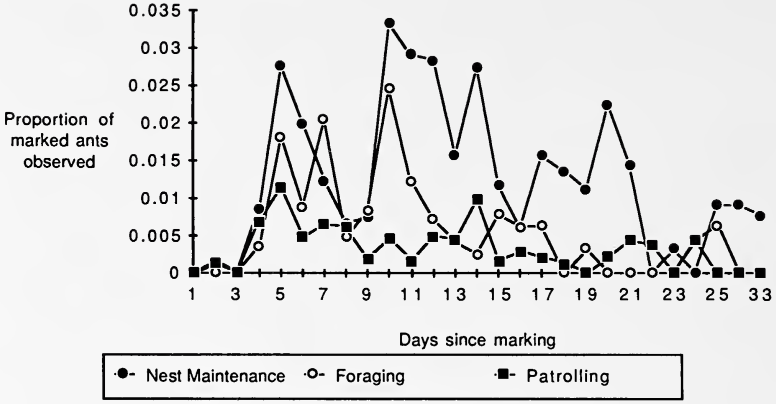

Figure 1. The abscissa shows number of days since ants in a particular activity were marked. The ordinate is the ratio of numbers of marked ants observed to total numbers of ants marked in the colonies under observation on that day (see text for explanation).

DISCUSSION

The main result of this study is to extend the known lower limits on how long a *Pogonomyrmex* worker can live. The results show that in *P. barbatus* and *P. rugosus,* exterior workers can clearly live longer than 14 days after marking.

Figure 1 suggests that activities may be ranked as follows in the order of decreasing longevity: nest maintenance, foraging, and patrolling. Other results indicate that at a given time in a mature *P. barbatus,* there are three distinct groups of workers: one group of individuals that do nest maintenance, one that does foraging, and one that does both midden work and patrolling (Gordon, in prep.; also Gordon, 1984 for *P. badius*). Marked patrollers may disappear the most quickly because they lead the most dangerous lives; it is the patrollers that respond most actively to intrusions by other workers, and the numbers of patrollers increase when artificial disturbances are created (Gordon 1987). Patrollers as defined here probably correspond to the "first defenders" described by Porter & Jorgensen (1981) to be longer-lived than foragers. The latter authors elicited defenders by experimental perturbations, while in the present study patrollers were observed in undisturbed colonies.

Foragers are less likely to engage in confrontations than patrollers are, but they are subject to predation by horned lizards (*Phrynosoma* spp.). Nest maintenance workers, which appear to be the longest-lived, stay closest to the nest. Their task is in some sense the safest of the three. In addition, nest maintenance workers may be younger than the others, if this species adheres to the usual sequence of age polyethism in ants, in which younger ants work inside the nest and then move on to exterior tasks. Nest maintenance workers may be in transition from interior tasks to exterior ones such as patrolling and foraging.

There are two important sources of uncertainty in this study: the paint used for marking can wear off, and marked individuals may still be alive inside the nest. Both these factors would lead us to underestimate worker longevity. More extensive studies are needed to determine how the expected lifespan of a harvester ant worker depends on its task, and how mortality rates vary in different *Pogonomyrmex* species.

SUMMARY

Exterior workers were marked in the field, in colonies of the harvester ants *Pogonomyrmex barbatus* and *P. rugosus*. Some marked workers survived up to about 30 days after marking. These results extend the known limits on how long an exterior *Pogonomyrmex* worker can live. It appears that longevity may depend on worker task, with the following tasks in order of decreasing longevity: nest maintenance workers, foragers, and patrollers.

ACKNOWLEDGMENTS

B. Cuevas, K. Roth, M. Allinei and H. Graham provided invaluable assistance in the field. We thank N. Carlin for comments on the manuscript. The work was supported by National Science Foundation grants BNS-8701480 to D. M. Gordon, and BNS 8521575 to B. Hölldobler.

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MACROHABITAT SELECTION BY THE ORB WEAVING SPIDER, *MICRATHENA GRACILIS*.

By Margaret A. Hodge*

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Introduction

Animals often do not occupy all potential habitats even when they are capable of dispersing into unoccupied areas. This may reflect a "choice" by individuals not to live in certain habitats. In theory, habitat selection behaviors may evolve when large differences between habitats result in differential survival and reproduction rates. If an animal cannot survive and reproduce everywhere, natural selection will favor recognition of suitable habitats (Levins 1968; Krebs 1985).

The mobility and activity patterns of many animals make them difficult subjects for studies of habitat selection. Web building spiders, however, are an exception. Web conspicuousness and the relative ease of marking and following individuals makes them ideal subjects for studying the behavioral mechanisms involved in habitat choice. *Micrathena gracilis* (Walckenaer) (Araneae: Araneidae), an orb weaving spider, characteristically builds webs which span wide spaces in shady deciduous forests, and rarely occur in adjacent successional areas (Elliot 1930; Uetz et al., 1978; Biere & Uetz 1981; Hartsock 1983; Hodge 1985). In this study, release experiments were conducted to determine whether *M. gracilis* actively selects deciduous forests, and if so, what environmental variables influence this choice.

Methods and Materials

Study organism

Members of the Neotropical genus *Micrathena* are mostly diurnal, forest dwelling, orb weaving spiders. Although most species are

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Manuscript received by the editor July 24, 1987. Publication delayed on request of author.

tropical, *M. gracilis* ranges into temperate North American deciduous forests east of the Rocky Mountains (Levi 1985). This spider builds an orb web within a rectangular or triangular silk frame which is typically located 1–3 m high and spans large open spaces in the forest understory. The orb portion of the web is removed in the evening and rebuilt at dawn. The frame, however, may persist at the same site for many days. In the southeastern United States *M. gracilis* reaches maturity by mid-to-late July. There is extreme sexual dimorphism, and upon reaching maturity males cease building webs. Therefore, adult females were used in this study, since they maintain webs throughout the summer, and these webs are crucial to survival and egg production.

Release experiments

This study was conducted during July and August 1983 in a forested area which included a transition zone from an open pine stand to a deciduous forest. The privately-owned site was located in Griffen, Georgia (4.5 miles W. of the Spalding Co./Butts Co. line). Canopy tree species in the deciduous section were *Quercus velutina* Lam., *Q. nigra* L., *Acer rubrum* L., and *Pinus taeda* L. The pine stand consisted of mature *P. taeda,* young *P. taeda* (< 2m tall), *Q. nigra* and *Rubus* sp. (both < 1m tall). The pine stand was bordered on one side by the deciduous area; the opposite side was bordered by a row of small pine trees, beyond which was a grape arbor; a dry ditch and a paved road ran along one side, and opposite this was continuation of pine forest. The deciduous forest area was also bordered by the road, and the two other sides were a continuation of deciduous habitat.

Release experiments were conducted in a 32 × 32 m plot encompassing both pine and deciduous forest. Each square meter of the study plot was assigned a number corresponding to numbered flags which bordered the area at 1 m intervals. Prior to initiation of spider manipulations, the height of all vegetation in each square meter of the study plot was measured, and the presence or absence of pine canopy and deciduous canopy was recorded.

All of the adult female *M. gracilis* present were collected from the study plot and the surrounding area ($n = 24$). Spiders were marked by affixing newsprint letters to the dorsal surface of the abdomen with clear nail polish, providing each with a unique letter identity, and retained for 12 hours in one-dram plastic vials at room temperature to ascertain that there were no detrimental effects due to the marking procedure. At 0700 hours on 21 July, the 24 marked spiders were released into randomly chosen quadrats (using numbers selected sequentially from a random number table), resulting in 15 spiders being released into the pine stand, and 9 into the deciduous forest. I censused spider locations and distance moved (if any) each morning between 0800 and 0900 hours, from 22 July through 2 August. Web sites were marked with flags placed in the ground below the web, and the letter identity of the spider was written on the flag with waterproof ink.

In order to clarify whether the movement patterns of spiders in the two habitats were different, I repeated the experiments using a different release protocol. I recollected the 14 spiders remaining in the study area on 18 August and released them into randomly chosen quadrats within the pine stand on 19 August. Seventeen additional spiders, collected from adjacent woods, were marked and released at random points within the deciduous area on 24 August. All spiders were censused from the time of release through 9 September (see Table 1).

Table 1. Canopy cover at spider release points and endpoints within each habitat.

	Canopy type release point	Canopy type end point	% total released (N = 19)
Deciduous stand	Open	Open	5%
	Open	Deciduous	16%
	Mixed	Deciduous	5%
	Deciduous	Open	21%
	Deciduous	Deciduous	53%
PINE STAND	Open	Open	53%
	Open	Deciduous	17%
	Pine	Open	5%
	Pine	Deciduous	10%
	Mixed	Deciduous	5%
	Deciduous	Deciduous	10%

*15% of these spiders did not build webs

Environmental measurements

Over a five-day-period during the final release experiments, some of the environmental factors which may have caused spiders to relocate were monitored in the two habitats. In both the deciduous forest area and the pine stand, temperature and humidity were recorded every three hours from 0900 through 1800 hours, at two randomly chosen quadrats. Humidity was measured using a Mason's hygrometer (Taylor Instruments, Arden, N.C.) and temperature readings were obtained from the dry bulb of this instrument. Sticky traps were set out at these same sites to estimate prey availability in the two habitats. These traps consisted of a 20 cm diameter embroidery hoop covered with a double layer of cheese cloth. The cheese cloth was coated with Stickem Special (Seabright Enterprises, Emeryville, Calif.), an insect trapping compound. The traps were suspended one meter above the ground (which approximates the average height of a *M. gracilis* web; (Hodge 1985)). I set these out at 0700 and retrieved them at 1800 hours. Trapped insects were removed and identified to order and their body lengths were measured to the nearest mm. During this five-day-period, all webs in the study area were visited every three hours and thermoregulatory positioning by the spider and web condition (damaged or undamaged) were recorded.

RESULTS

I was able to follow 19 of the 23 spiders released into the pine stand, and 19 of the 32 released into the deciduous forest. Residence times at web sites for spiders released into each habitat were significantly different (t-test, $p < 0.01$; Fig. 1). The mean residence time at a given site by spiders in the deciduous forest was 8 days (S.D. = 4), whereas spiders in the pine stand only stayed an average of 1 day (S.D. = 2) at a web site. By September 9, the last census day, almost all spiders released into the pine stand had, through successive web relocations, moved into the deciduous forest or had disappeared from the area (Fig. 2). Exceptions included three spiders that did not build webs over the six days that they were observed before they disappeared. Three other spiders successfully maintained webs in the pine stand, but all were near the transition zone to the deciduous section (Fig. 2). None of the spiders released into the deciduous forest was ever observed to have moved into the pine stand (Fig. 3). Spiders released within the deciduous woods usually moved from a site of deciduous canopy to similar sites, but sometimes moved to quadrats with no canopy (Table 1).

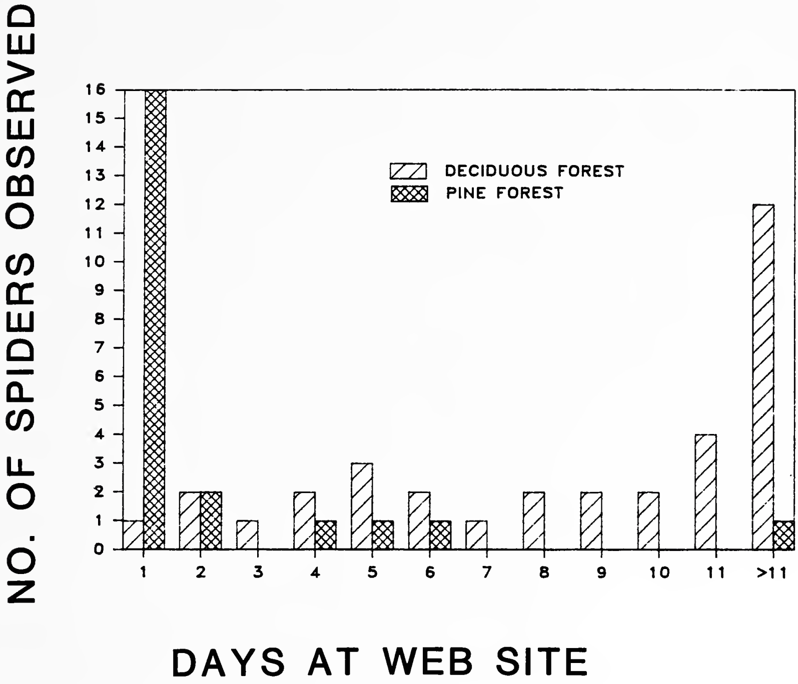

Figure 1. Comparison of web site residence times of spiders released into the pine forest and the deciduous forest (significantly different, $p < 0.01$).

If spider web site relocations occur at random, then the expected distribution of time intervals between relocations should follow a negative exponential distribution, which describes random events over a time-course (Bailey 1964; Ross 1970). Spider residence times in each habitat were compared to values expected from a fitted negative exponential distribution. There was no significant difference between the observed residence times and those expected for the pine stand ($0.01 < 0.05$; Fig. 4), supporting a random movement hypothesis. In contrast, observed and expected residence times in the deciduous woods were highly significantly different ($p < 0.001$; Fig. 5).

A much higher percentage of quadrats had no canopy in the pine stand than in the deciduous woods; the deciduous area had a higher percentage of canopy than did the pine stand (Table 2). The quantity of vegetation below 1 m in each quadrat of the pine versus the deciduous area was not significantly different (t-test, $p > 0.05$).

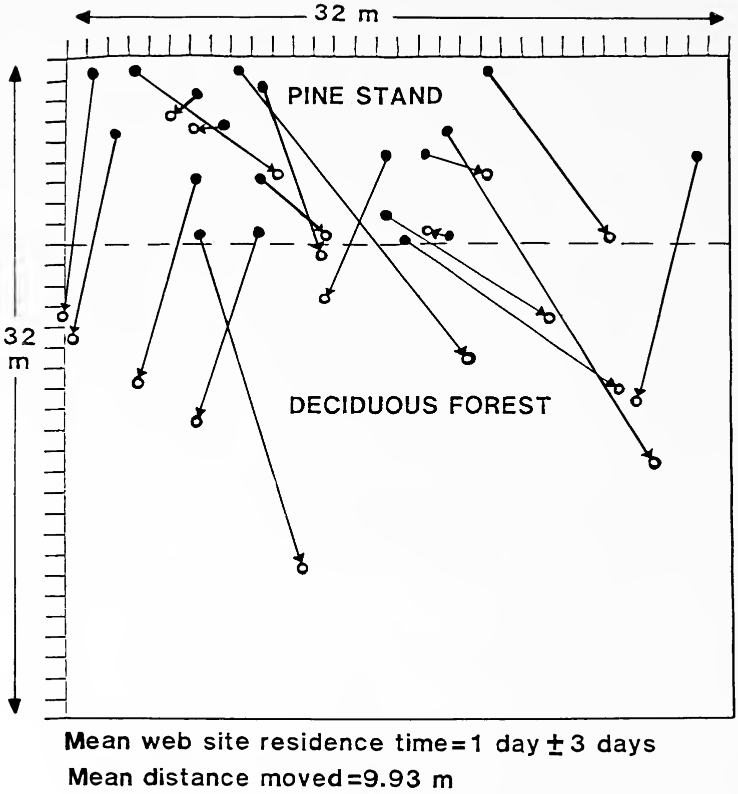

Figure 2. Release points and end points of spiders released into the open pine stand (solid circles indicate release point, open circles indicate where the spider was seen last).

However, a significant difference did exist in the amount of vegetation between 1–3 m high and over 3 m, with the deciduous area having more of this taller vegetation than the pine stand (t-test, $p < 0.01$). Of the other environmental parameters measured, only insect length showed a significant difference between habitats (Table 3). A Mann-Whitney U test indicates that no significant difference existed in humidity or ambient temperature levels between the deciduous forest and the pine stand ($p > 0.01$). Likewise, a Mann-Whitney U test on the number of insects caught each day at each sticky trap indicates no difference between habitats ($p > 0.01$).

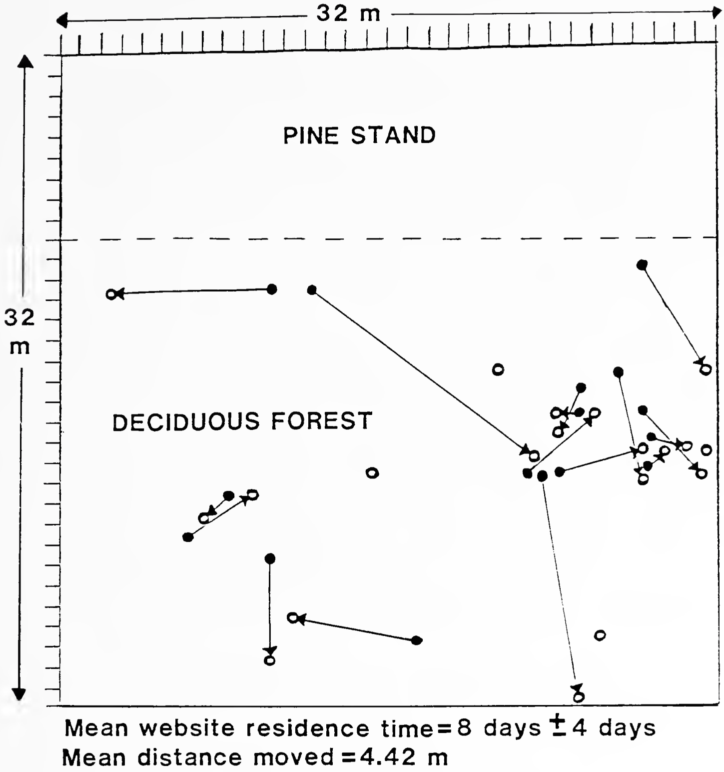

Figure 3. Release points and end points of spiders released into the deciduous forest (solid circles indicate release point, open circles indicate where the spider was seen last).

Several observations of spider behavior and web condition suggest additional environmental differences between pine and deciduous forests that may affect web site tenacity. Spiders under heat stress hang on the web in such a way as to minimize the amount of body surface area exposed to the direct rays of the sun (Krakauer 1972; Carrel 1978; Robinson & Robinson 1974, 1979; Biere 1977; Biere & Uetz 1981). Five days of observations made at 3 hour intervals revealed that by 1200 hours, all spiders in the pine stand were assuming this thermoregulatory position. None of the spiders in the deciduous forest were ever observed to posture in this manner. This

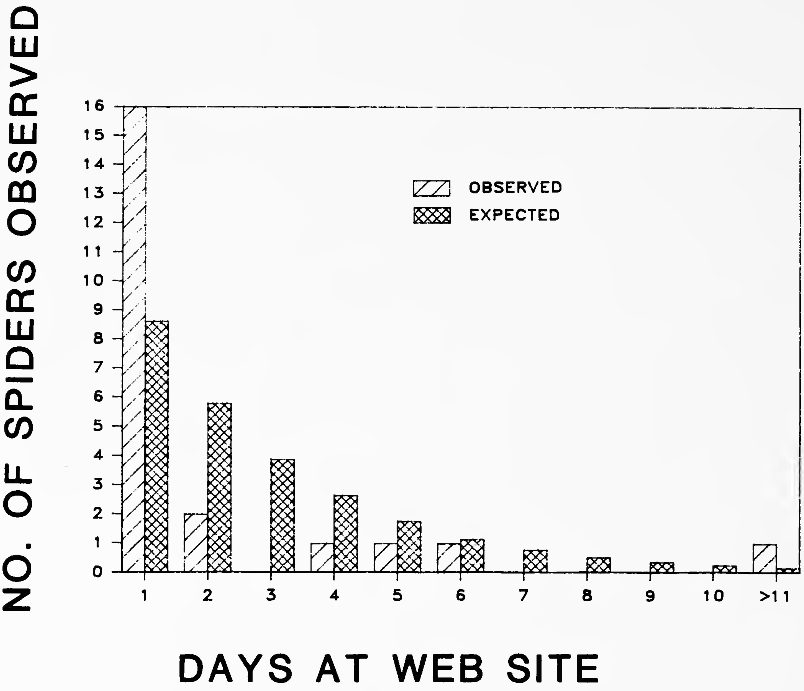

Figure 4. Comparison of distribution of residence times of spiders released into the pine stand with that expected from a random movement hypothesis (no significant difference, $0.01 < p < 0.05$).

may be directly related to the differences in canopy cover between the two habitats (Table 2). Over this same five-day-period, only 4% of the observations of webs in the deciduous forest noted web destruction ($n = 66$), in contrast to 22% noted in the pine stand ($n = 59$). Such collapsed webs may have been caused by occasional strong breezes, large insects flying through, or predation attempts by birds or wasps.

Discussion

Field experiments demonstrating active habitat selection are relatively uncommon. Wecker (1963) and Douglas (1976) used release experiments which revealed habitat preference in rodents. Among insects, the occurrence of discriminating habitat selection has been shown for digger wasps (Brockmann 1979), honeybees (Lindauer

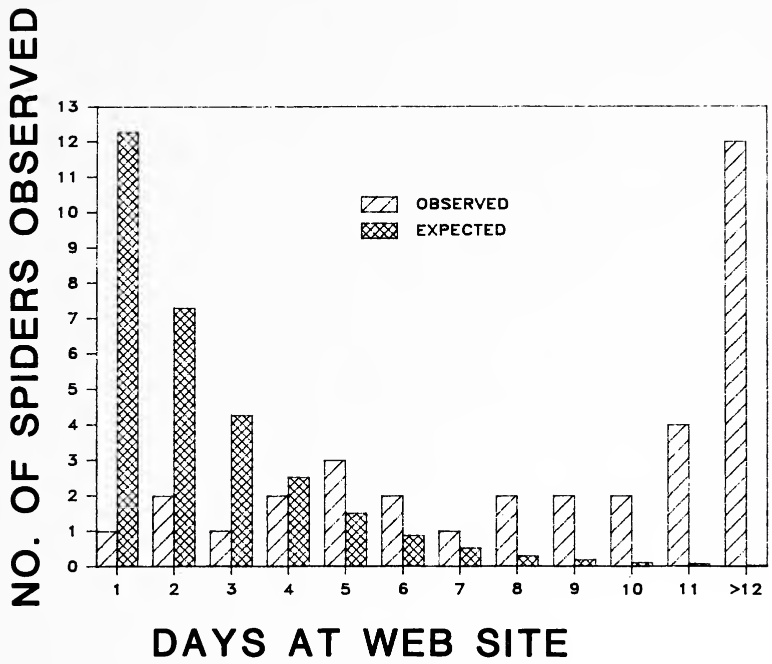

Figure 5. Comparison of distribution of residence times of spiders released into the deciduous forest with that expected from a random movement hypothesis (significantly different, $p < 0.001$).

1961) and aphids (Whitham 1979). Enders (1972) found that field-dwelling orb weavers (*Argiope* spp.) released into wooded habitats did not remain in the wooded area, but successively relocated their webs until they came to a field situation. This is similar to the behavior observed in this experiment. The observation that spiders released into the pine stand moved into the deciduous forest, whereas spiders released into the deciduous forest remained there, suggests that *M. gracilis* prefers that particular type of habitat. Further evidence of habitat preference is suggested by the significantly shorter residence times at pine stand web sites compared to those in the deciduous forest area.

Although five days is a relatively short period of time, weather conditions at the time of environmental data collection were representative of those present throughout the entire study, during which weather conditions were very constant. The results presented here

Table 2. Distribution of canopy types in each of the two habitats (% area covered).

Canopy type	Pine Stand	Deciduous Stand
Open	64%	33%
Pine	30%	5%
Mixed	2%	5%
Deciduous	4%	57%

indicate no difference in humidity or ambient temperature between the deciduous forest area and the pine stand. It would therefore seem that if habitat selection was based on ambient temperature or humidity, spiders would have been equally likely to move from the deciduous forest to the pine stand.

Prey availability, if different between the two macrohabitats, might provide a basis for macrohabitat selection. The sticky trap data indicate a significant difference in insect lengths between the habitats, suggesting that more biomass may be available in the deciduous forest. In addition, the higher frequency of web destruction in the pine stand may have reduced the time available on the web (which reduces the time available for intercepting prey). However, these data may not accurately reflect the prey which the spiders actually sampled, as the precision with which sticky traps represent prey intercepted by webs and captured by spiders is questionable (Castillo & Eberhard 1983).

Habitat preferences based on structural characteristics are a factor limiting the distribution of some spider species (Eberhard 1971; Colebourn 1974; Enders 1976). Hartsock (1983) suggests that such preferences may explain the different distributions of *M. gracilis* and *Verrucosa arenata* (Walckenaer) within the forest. The importance of structural properties in construction and maintenance of webs may be similarly involved in this study. The length and position of the bridge thread, which is the basic foundation of the web, is controlled by the spatial distribution of attachment sites (vegetation). Suitable attachment sites are vegetation between 1–3 m tall, or taller. This type of vegetation was significantly less abundant in the pine stand. The deciduous forest provided more attachment sites plus amelioration of destructive air currents (as seen by the lower percentage of web destruction in the deciduous area).

Several studies have demonstrated that solar radiation can have profound effects on the behavior of orb weaving spiders (Krakauer

Table 3. Mean and standard-deviation (S.D.) of environmental parameters measured in each habitat.

Parameter	Pine Stand	Deciduous Stand
Relative humidity		
Mean	53%	54%
S.D.	20%	30%
Temperature		
Mean	33° C	32° C
S.D.	5° C	3° C
Prey/Sticky Trap/Day		
Mean	7.2	4.6
S.D.	2.4	2.7
Prey size (mm)		
Mean	2.4**	4.6**
S.D.	1.4	2.9
Attachment points <1 m		
Mean	1.78	0.70
S.D.	0.92	1.05
Attachment points 1–3 m		
Mean	0.29**	0.45**
S.D.	0.54	0.62
Attachment points >3 m		
Mean	0.05*	0.39*
S.D.	0.23	0.59

*significantly different; t-test, $p < 0.01$
**significantly different; t-test, $p < 0.001$

1972; Robinson & Robinson 1974; Tolbert 1976; Carrel 1978). Differences in the canopy of pine and deciduous forests may affect the intensity of solar radiation reaching spiders in webs below. The deciduous woods had a much higher percentage of deciduous canopy, which is more effective than pine canopy in providing shade. Biere and Uetz (1981) have shown that even within the forest, *M. gracilis* adjusts the orientation of the web to minimize intense solar radiation in open patches. They also found that spider body temperature was positively correlated with the amount of solar radiation striking the animal. It is therefore possible that heat stress (as indicated by thermoregulatory posturing) in the pine stand contributed to web relocation. Experiments with *Micrathena schreibersi* (Perty) by Robinson and Robinson (1974) showed that sunlight which was redirected with a mirror down the plane of the web onto the ventral surface of the spider (similar to the sun's rays at noon) caused the spider to assume a posture which minimized the body surface exposed to the light/heat source. In similar experiments, Biere (1977) redirected the sun's rays so that the light was directly striking individual *M. gracilis.* He maintained this light/heat source until the spiders retreated from the hub to the upper bridge-thread attachment point. Seven of 12 individuals thus treated abandoned their former web sites the following day. The relocation response observed in this study may be similar to that observed by Biere (1977). Exposure to insolation is sporadic in deciduous forests, and can usually be dealt with using web orientation and/or thermoregulatory postures. It may be that in the pine stand, these behaviors were not effective in relieving the effects of prolonged exposure to direct sunlight. An additional light-related variable which was not measured in this study, yet which could serve as a proximate cue, is the difference in light intensity between the two habitats. However, Enders (1972) demonstrated that certain forest-dwelling orb weavers showed no preference for any particular level of light. Similar experiments are needed to clarify whether *M. gracilis* uses light-levels as a cue in its macrohabitat selection process.

Events which occur with a constant probability over time intervals as short as one day follow a negative exponential distribution (Bailey 1964; Ross 1970). Such events may be stimuli such as disturbance due to climatic factors, or cues from vegetation structure (Janetos 1982). The distribution of residence times in the pine stand followed a negative exponential distribution. This is indirect support that vegetation structure and climatic factors influenced the frequent relocation in the pine stand. In contrast, the probability of moving increased with the number of days at a web site in the deciduous forest. In a subsequent study, I have found that this nonrandom distribution of residence times in the forest is related to hunger, a stimulus that has a cumulative rather than a constant probability over time (Hodge 1988).

Reichert & Gillespie (1986) have identified three components of habitat selection by spiders: 1) the incentive to move; 2) movement curtailed upon encountering a favorable new environment; and 3) active search for a specific microhabitat. In *M. gracilis,* the incentive to move persists in the pine stand, as indicated by the short residence times. In the deciduous forest, spiders relocate much less frequently. This cessation of movement phase corresponds with the spider's entrance into a structurally and thermally favorable environment. Further studies of *M. gracilis* have shown that movement within the deciduous forest reflects the process of microhabitat selection, which only occurs after a suitable macrohabitat has been found (Hodge 1988).

SUMMARY

Release experiments were conducted to determine whether habitat selection is involved in producing the characteristic distribution of *Micrathena gracilis,* a forest-dwelling orb weaving spider. Marked spiders were released into a study area which included a deciduous forest habitat and an adjacent open pine habitat where spiders were previously never seen. Daily censusing and recording of movements revealed that spiders in the pine habitat spent significantly less time at web sites than did those released into the deciduous forest. Almost all of the spiders released into the pine stand, through successive web relocations, moved into the deciduous area, while none of the spiders released into the deciduous area was ever observed to enter the pine stand. Differences in prey availability, solar radiation and structural properties of the two habitats are suggested as factors involved in the observed macrohabitat choice.

ACKNOWLEDGMENTS

I would like to thank Drs. R. W. Matthews and J. O. Howell for providing me with the financial support and the opportunity to conduct this research. Dr. J. Arnold gave statistical advice, and Drs. A. Rypstra and G. W. Uetz offered valuable editorial assistance. I am especially grateful for the inspiration and support of Drs. J. Martyniuk, G. Morrison, G. W. Uetz, and R. S. Wilcox. This research was supported by the University of Georgia, Department of Entomology, Athens, Georgia, and the Georgia Experiment Station, Experiment, Georgia.

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FACTORS INFLUENCING WEB SITE RESIDENCE TIME OF THE ORB WEAVING SPIDER, *MICRATHENA GRACILIS.*

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Introduction

The word "habitat" may be used with varying degrees of precision. When describing the finer details of where an animal lives, the term microhabitat is often used to distinguish this from the particular community or ecosystem. Examination of microhabitat selection involves determining the factors which influence preference for a certain site. Many factors have been shown to affect the length of time that spiders will spend at a particular web site. Physical settings providing protection against web destruction by wind or rain may be important (Eberhard 1971; Enders 1976; LeSar & Unzicker 1978; Marson 1974). Prey abundance, as well as factors relating to prey detection and capture sucess, are also important in microhabitat selection (Riechert & Tracy 1975; Riechert 1976). Because food resources have been demonstrated to have a large impact on individual fitness in several spider species (Deevey 1949; Turnbull 1965; Miyashita 1969; Hagstrum 1970; Kessler 1973; Greenstone 1978; Kajak 1978; Morse & Fritz 1982; Wise 1975) web site selection should be expected to be strongly linked to food supply. Studies which have examined the dynamics of prey availability have implicated web site relocation as a proximate mechanism for food supply enhancement (Turnbull 1964; Riechert 1978; Olive 1982; Janetos 1982).

Micrathena gracilis (Walckenaer) is an orb weaving spider common to deciduous forests throughout northeastern North America. These spiders characteristically build webs spanning large open areas between vegetation (90–250 cm). Certain individuals may

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Manuscript received by the editor July 24, 1987.

occupy a web site for many days, and even weeks, whereas others relocate frequently. Since web site relocation requires a greater energy expenditure than does remaining at a site, the decision to leave may be related to the quality of the web site. This study used residence time at a particular web site as an indicator of microhabitat suitability and examined the relative contributions of feeding rates, web destruction, and sun-exposure (heat stress) to the tendency of a spider to remain at a web site.

Methods

This study was conducted in an approximately one-acre area of deciduous forest on the University of Georgia campus, Athens, Georgia (Clarke County). A thick understory of *Rubus* sp. (blackberry) and *Rhus radicans* (poison-ivy) and a canopy of *Quercus alba* constituted the major plant species of the study site.

One 12 July 1984, 25 *M. gracilis* were collected from the study site and from the University of Georgia Botanical Gardens. Only penultimate and mature females were collected. Spiders were marked with fast-drying enamel paint, using the positioned dots technique (Walker & Wineriter 1980). Ten spines on the abdomen of *M. gracilis* made convenient locations for different combinations of paint marks, giving each spider a unique identity. This paint mark identity was assigned a number to simplify data collection. Blue, green, white and black paint were used on the rationale that these colors would have the least effect in making the spider more conspicuous to vertebrate predators (though Rypstra (1984) has found that such paint marks may have very little effect on predation rates). Spiders were retained for 24 hours to assure that they would survive the marking procedure (which involved no anesthesia).

Spiders were released at random locations (using the wandering quadrant technique of Catana (1955)) at 1800 hrs on 13 July, and allowed 6 days to establish a web site. Observations were initiated on 20 July. The position of each spider was marked with a flag bearing its number identity, placed in the ground below the web. Unmarked spiders were marked in the field as they were discovered. Each day the distance (if any) moved by each spider was measured with a tape measure and recorded. Each web was checked hourly from 1000 hours until 1700–1900 hours. The following information was recorded at each hourly check: if the spider was feeding, was in direct sunlight and/or assuming a thermoregulatory position (Robinson & Robinson 1979), and the condition of the web (extent of damage, if any). These observations were made from approximately 1 m from the web, to avoid disturbing the spider. Thus it was not possible to measure prey lengths. However, if a spider captured a large prey item it was likely to feed for 2–3 hours (personal observation). This was recorded as 2–3 observations of feeding in the hourly censuses. Therefore, the feeding rate, equal to the number of feeding observations, is an estimate of the prey consumed by a spider at a particular web site. Other information, such as molting, mating activity, predation, and intra- or interspecific interactions were also recorded. The study was terminated on 11 August, 1984.

RESULTS

The average web site residence time was 6.7 days (S.D. = 5.29 days). Residence times were compared to values expected from a negative exponential distribution, which indicates random processes in time (Bailey 1964; Ross 1970). The distribution of observed residence times was significantly different from that expected by a random process ($\chi^2 = 1889$; $p \ll 0.001$; Fig. 1).

A total of 2131 web observations were made by checking spiders at hourly intervals. Of this total, there were few observations of sun-exposure or thermoregulation, and of these, few were followed by web site relocation (Table 1). A much greater percentage of the total number of relocations occurred following web destruction and/or were preceded by days of scarce prey (Table 1). There were 36 web site relocations during the study, and 34 of these were preceded by a day of either zero or one feeding observation, and/or web destruction by wind or rain. Only two relocations were not associated with either of these variables. Eighteen of the web relocations were preceded by web destruction. Thirteen of these 18 were simultaneously associated with low feeding rates. Sixteen relocations were associated with low feeding rates alone. A Chi-square test for independence led to acceptance of the null hypothesis that web relocation was not differentially influenced by either low prey levels (0–1 prey observations/day) or web destruction, or even by a combination of the two (Table 1; $\chi^2 = 2.16$, $p > 0.50$), i.e., both factors seemed to have a similar contribution to the decision to move. A feeding rate, equal to the number of feeding observations divided by

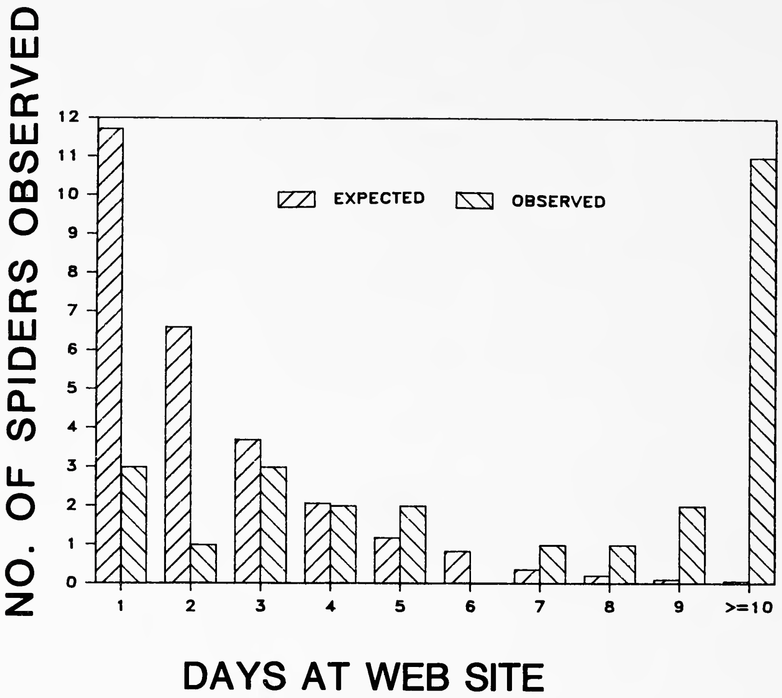

Figure 1. Distribution of observed residence times compared to that expected by a random process (significantly different, $p < 0.001$).

the residence time (days) at the site, was calculated for each web site occupied. There was a significant difference ($t = 2.55$; $p < 0.05$) between the feeding rates of spiders staying 1–5 days ($\overline{x} = 0.89$; $\sigma^2 = 0.59$) versus those staying for 6 days or longer at a site ($\overline{x} = 1.5$; $\sigma^2 = .53$).

DISCUSSION

Since the web is the only means an orb weaving spider has of encountering prey, web site selection has important consequences with respect to the spider's fitness. Physiological studies have shown that finding a web site and building a web are energetically costly activities for orb weaving spiders (Witt et al., 1968; Peakall & Witt 1976; Prestwich 1977). If behaviors associated with web site choice and tenacity have been selected for, then these choices should be

Table 1. Number of spiders relocating after exposure to various environmental factors.

Environmental Factor	Spider Relocation	% of total relocations	No spider relocation
Exposure to direct sunlight	3	8%	45
Thermoregulatory posture	1	3%	3
Courtship attempts	3	8%	15
Web destruction alone	5	15%	39
Low prey levels alone	16	47%	63
Both low prey and web destruction*	13	38%	82

*Chi-square test for independence indicates no differential influence of web destruction alone, low prey levels alone, or a combination of these factors on relocation; $\chi^2 = 2.16$, $p > 0.50$.

significantly correlated with the animal's energy gain, and therefore its fitness. Though a correlation between energy gain and fitness has not been shown for *M. gracilis,* it has been for many spider species (Deevey 1949; Turnbull 1962, 1965; Miyashita 1969; Hagstrum 1970; Kessler 1973; Greenstone 1978; Kajak 1967, 1978; Wise 1975, 1983). Morse & Fritz (1982) found that female crab spiders gain 7/8 of their biomass during the adult stage, which was the stage of most of the spiders observed in this study. Since biomass accumulation is crucial for egg production, it seems that web site residence time should be related to the energetic costs and benefits of moving versus staying. Factors such as web destruction (reduction of feeding time; cost of rebuilding) or low feeding rates may lead to a threshold hunger level which stimulates the spider to move.

The fact that 33 of 34 web relocations were preceeded by a day of low prey levels (0–1 feeding observations/day) and/or web destruction seems strong evidence that these factors are involved in the decision to move. However, most occurrences of low feeding rates and/or web destruction did not result in relocation (Table 1). The only conclusions that can be made from these data are that, although these two factors are almost always associated with web relocation, their occurrence alone is not enough to cause the spider to move. Some undetected environmental and/or physiological factors must contribute to the decision to relocate.

The two categories of residence times used in comparison of feeding rates were based on the average residence time of 6.7 days. Spiders staying at web sites for longer periods than six days had significantly higher feeding rates than those staying at web sites for five days or less. Olive (1982) has similarly shown that *Argiope* spp. moved more often when current feeding levels were decreased, and Vollrath (1985) observed that *Nephila clavipes* in poor environments changed sites more often than spiders in rich environments. Martyniuk (1983) found that filmy-dome spiders (Linyphiidae) which were moved to previously abandoned web sites of low prey availability and were provided with supplemental prey, remained at those sites.

Janetos (1982) has designated sheet-web weavers as "sit-and-wait" predators and orb weavers as "active" foragers. He assumed that orb webs could be put nearly anywhere, resulting in high variance in payoffs. Therefore, he predicted that orb weavers would do better by moving frequently among sites to find potential "hot spots." The assumption that orb webs can be put anywhere may not be correct. Several studies have shown that *M. gracilis* requires specific structural characteristics for web construction (Biere 1977; Hartsock 1983; Hodge 1985). Neither does *M. gracilis* follow Janetos's (1982) prediction of frequent movement among sites. Studies of *M. gracilis* and *M. schreibersi* (Perty) (Shelly 1984; Hodge 1985) have shown that these spiders often remain at web sites for 15 days or more. This contests the generalization that orb weavers are "active" foragers.

If spider web site relocations occur at random, then the expected distribution of intervals between relocations will follow a negative exponential distribution, which is a Poisson process (Bailey 1964; Ross 1970). If so, then the stimuli that induce a spider to leave a web site occur with a constant small probability in any short period of time. Such stimuli could be physical disturbance of the web due to climatic factors, or predation attempts (Janetos 1982). Comparison of the actual distribution of residence times with that expected from the random movement hypothesis indicates that *M. gracilis* does not move at random. A previous study of macrohabitat selection by *M. gracilis* found that spiders moved with a random pattern until they encountered a macrohabitat where environmental factors are ameliorated (Hodge 1988). This macrohabitat was a deciduous forest similar to the area in the present study. The distribution of residence times in these deciduous forest areas is almost identical, and both are significantly different from that predicted by the negative exponential. An interpretation of these distributions may be as follows. If each successive interval of nonperformance of a behavior depletes the animal's energy reserves, performance of the behavior (i.e., web site relocation) becomes more beneficial as the time elapsed since the last performance increases (Fagan & Young 1978). This applies to *M. gracilis* in that if a spider at a certain web site experiences a reduction in prey capture due to web destruction and/or low feeding rates, then the time between relocations (time spent at that site) results in a certain depletion of the spider's energy reserves. This may culminate in some energy-related cue, perhaps a threshold hunger level, which stimulates the spider to perform the behavior of web site relocation.

SUMMARY

This study examined the factors influencing web site residence time of the orb weaving spider *Micrathena gracilis*. Residence time at a particular site was used as an indicator of microhabitat quality. When spider residence times were compared to a negative exponential distribution, the distribution of observed residence times was significantly different from that expected from a random movement hypothesis. The relative contributions of prey consumption, web destruction, and sun-exposure (heat stress) were monitored by hourly census checks of marked spiders over a 22 day period. Thirty-four of 36 web site relocations were preceded by a day of either zero or one feeding observation, and/or web destruction by wind or rain. There were few observations of sun-exposure accompanied by thermoregulatory posturing, and of these, few were followed by web site relocation. Web destruction and low prey levels are suggested as contributing to a threshold hunger level which stimulates spiders to seek new web sites.

ACKNOWLEDGMENTS

I would like to thank Drs. R. W. Matthews and J. O. Howell for providing the financial support and the opportunity to conduct this study. Drs. J. Arnold and G. Morrison provided statistical advice and Drs. G. W. Uetz and A. L. Rypstra offered valuable editorial comments. I am especially grateful for the support of J. Pettis and D. Willer during this study. This research was funded by the University of Georgia, Department of Entomology, Athens, Georgia, and the Georgia Experiment Station, Experiment, Georgia.

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REVIEW OF THE EXTINCT FAMILY SYNTONOPTERIDAE (ORDER UNCERTAIN)*

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The family Syntonopteridae was named by Handlirsch in 1911 for a new genus and species, *Syntonoptera schucherti,* from the Upper Carboniferous of Mazon Creek, Illinois. Although the unique specimen on which the species was based consisted of only a wing fragment, the presence of several intercalary, triad veins was of unusual interest. During the 75 years that have passed since then, only six additional specimens of the family have been found (Carpenter, 1938, 1944; Richardson, 1956), all of them in the Mazon Creek beds. The latest of these specimens was sent to me for study by Dr. E. S. Richardson, Jr., a few months before his death, and I have only recently had the opportunity to study it and prepare illustrations. While working on this fossil, I decided to reexamine at the same time the other five specimens in the family known to me. A review of these specimens is included here, followed by revised diagnoses of the family and of the two known genera.

Genus *Syntonoptera* Handlirsch, 1911, p. 299.

Type species: *S. schucherti* Handlirsch, 1911. Type specimen, no. PM0019, Peabody Museum, Yale University.

This genus was based on a single specimen consisting of the reverse half of an incomplete fore wing (Fig. 1). As preserved, the specimen is 80 mm long but the complete wing was probably nearly 100 mm long. It lacks the proximal and distal areas of the wing, as is often the case with insects preserved in concretions. It does show clearly, however, the triad branching of MA, MP, and CUA. The distal part of RS, which presumably had a triad also, is not preserved. Handlirsch's figure (1911, p. 3) is correct in most respects

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*Research supported by National Science Foundation Grant DEB 8205398, F. M. Carpenter, Principal Investigator.

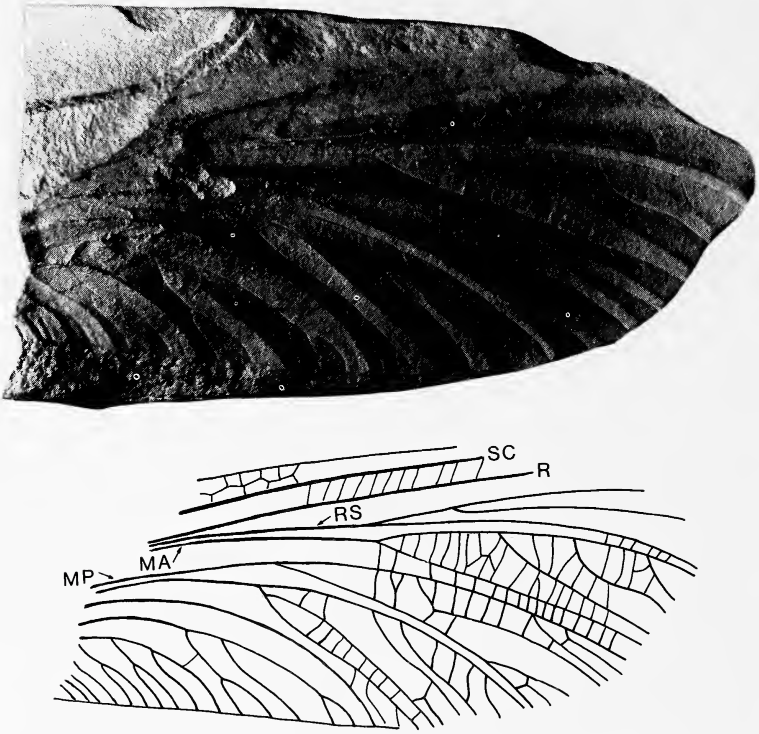

Fig. 1. *Syntonoptera schucherti* Handlirsch, fore wing. Upper figure: photograph of holotype, No. YPM19, Peabody Museum, Yale University. Length of wing fragment, 80 mm. Lower figure, venational pattern of holotype.

but it does depict the stem of MA as close to the stem of MP. These two veins are, in fact, widely separated, MA being very close to RS, and MP being close to CUA, which is a generic trait of the fore wings.

A second fragment of a fore wing of *Syntonoptera* (presumably *schucherti*) was found in the Langford collection (specimen no. 14881) of the Illinois State Museum, at Springfield (Carpenter, 1944). This specimen is nearly the size of the type and includes about the same area of the wing, but it is not so well preserved. In my figure of the specimen I represented with dotted lines the probable

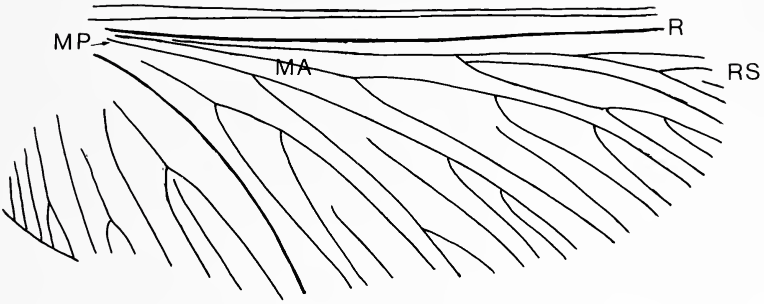

Fig. 2. *Syntonoptera schucherti* Handlirsch, hind wing. Venational pattern of specimen in Fig. 3b.

basal segment of MA diverging from MP to R, since that area was damaged in the fossil. I now think that the divergence probably occurred nearer the wing base. The wide area between MA and MP is like that of the type of *schucherti.*

The specimen that Dr. Richardson sent me a few years ago is in the collection of the Field Museum of Natural History, Chicago. It was found by Ida Thompson at Pit 11, Will County, Illinois, in 1928, and has the catalogue number PE16216. It consists of a nearly complete wing, lacking some of the base and a little of the apex. (Fig. 3). It is 100 mm long, as preserved, and probably had an original length of 110 mm. Since the size and venation are consistent with those of the type of *schucherti,* I consider this to be the hind wing of that species. Although more of the wing area is preserved than in the other two specimens, the preservation is not as good as that of the type. Only vague indications of the cross veins can be seen. The costal area, as usual in hind wings, is narrow, only about a third as wide as the subcostal area. (Fig. 2). The stem of RS is very close to the base of R but its actual origin has broken away. The base of MA is also very close to RS but, in contrast to the fore wing, MP is very near MA, indicating that the basal piece of MA, diverging from M, must have been very short. CUA and CUP are essentially as in the fore wing except that CUA, a very strong vein, is more oblique and curved. The anal veins are similar to those of the fore wing but with a difference of inclination because of the broad anal area.

Fig. 3a. *Syntonoptera schucherti,* hind wing. Specimen No. 16216, Field Museum of Natural History, Chicago. Length of wing as preserved, 100 mm. Photograph of obverse half.

Fig. 3b. *Syntonoptera schucherti,* hind wing. Same specimen as in Fig. 2a. Photograph of reverse half.

Genus *Lithoneura* Carpenter, 1938, p. 446.

Type species: *L. lameerei* Carpenter, 1938. Type specimen: no. 24537, Museum of Comparative Zoology, Harvard University.

This genus was based on a species known only by the type, consisting of a dorso-ventral view of the insect, with its four wings spread (Fig. 4). It is an interesting and important specimen, since it shows at least portions of fore and hind wings, as well as a few details of body structure. The wings are well preserved, except for the apical areas, which are not included in the concretion. The fore wing (Fig. 5, upper), which is 32 mm long as preserved, has a distinctly curved anterior margin, as least as far as the level of the midwing. The basal part of RS, although close to stem R, is independent of it. M is separate from RS basally but at about one-fourth the wing length from the base MA diverges anteriorly and merges with RS before diverging posteriorly as an independent vein; RS, MA, MP, and CUA have the triad, intercalary veins as in *Syntonoptera.* The hind wing (Fig. 5, lower) of *lameerei* has a very distinctive shape, being unusually broad in the anal, cubital, and medial areas. As in the fore wing, RS is independent of R basally. However, the stem of M is coalesced with the stem of CUA, and M divides into MA and MP, shortly after its divergence from CUA. MA is coalesced with RS as in the fore wing, and RS, MA, MP, and CUA have the intercalary, triad branches.

The body structures preserved in the type of *lameerei* are very limited (Fig. 6). These include the general thoracic area, part of the abdomen, and what appear to be parts of the head. In my original account of this specimen (Carpenter, 1938, p. 445) I stated that prothoracic lobes were “present, though small.” In the light of fifty years of additional experience with fossil insects, I am not as confident now as I was then that the prothoracic lobes are, in fact, present; a slight, local differentiation in the texture of the rock matrix might be misleading.

In this connection, I should mention that Dr. Kukalová-Peck has published an account of her observations on the structure of the type of *lameerei.* I find that her figure (Kukalová-Peck, 1985, fig. 11) is more in the nature of a reconstruction than a record of what is actually preserved. She states in her account: “The head is a composite impression of the dorsal and ventral head structures; the eyes

Fig. 4. *Lithoneura lameerei* Carpenter. Photograph of holotype, No. 24537, Museum of Comparative Zoology, Harvard University. Fore wing, 32 mm long as preserved.

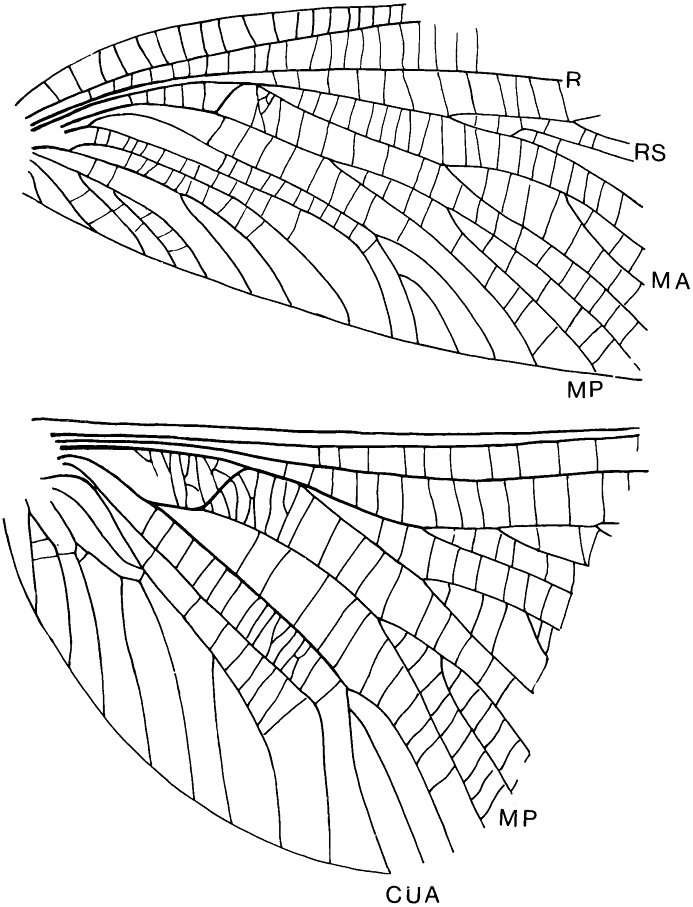

Fig. 5. *Lithoneura lameerei* Carpenter. Venational pattern of fore wing (upper figure) and hind wing (lower figure).

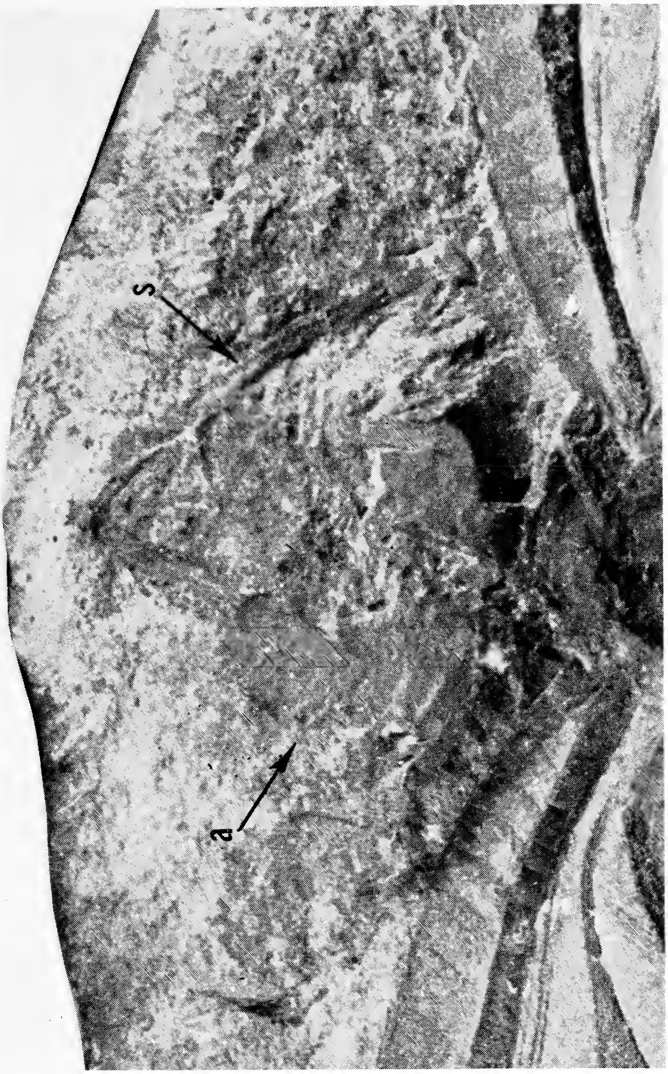

Fig. 6. *Lithoneura lameerei* Carpenter. Photograph of head and prothoracic regions of holotype; a, probable prothoracic lobe; s, plant shoot.

are very large and bulging; and the antennae are long, multisegmented, and relatively thick; the prothorax carried two large prothoracic wings, which were previously noted by (Carpenter 1938)." The head and thoracic area of the insect can be seen in the accompanying photographs (Figs. 4 and 6) at different magnifications. As shown in these figures, there seems to be a small prothoracic lobe (a) on the left side of the prothorax, noted in my original account of the specimen. This is only 2 mm wide. Anterior to it, on the same side, Kukalová-Peck has drawn a large, bulging eye. I had assumed in my account that the prothoracic lobe included that area, making the lobe about 5 mm long. I do not see anything on either side of the head resembling the two large eyes she has drawn. She has also included in her figure a pair of "pleisiomorphic" antennae, with numerous segments, arising from the head. I did not refer to those structures in my 1938 paper because I was convinced they were of plant origin. I recently brought the fossil to Professor Andrew H. Knoll, Curator of the Paleobotanical Collection at the Harvard University Herbaria, for his examination. He subsequently reported to me that the structures were without question the shoots of vascular plants (Fig. 6). The numerous segments, shown in Kukalová-Peck's figure, are not present in the fossil [See figures 4 and 6]. Also, I am unable to see any indication of the segmented piece of the antenna shown in her figure as arising from the right side of the head. There is one "joint" on a shoot near the front margin of the right wing, but this is typical of the "joints" that occur on shoots of many Carboniferous plants, especially among the Arthrophyta and other articulates. We do not yet know the nature of the antennae of *Lithoneura.*

In 1944 I described *Lithoneura mirifica,* a second species of the genus, based on a well-preserved, though wrinkled, hind wing (Fig. 7), the only complete wing so far known in the family. The holotype, no. 14880ab, is in the Langford collection of the Illinois State Museum, at Springfield. The wing is 85 mm long, about twice the size of *lameerei.* It is differently shaped from the hind wing of *lameerei,* being more nearly oval, and having a convex anterior margin and a broader anal area. The venation is close to that of *lameerei,* so far as the latter is known.

A third species of the genus, *carpenteri,* was named by Richardson in 1956 (Fig. 8). The holotype, no. 45248AB in the Walker

Fig. 7. *Lithoneura mirifica* Carpenter, hind wing. Photograph of holotype, No. 14880, Illinois State Museum. Length, 85 mm.

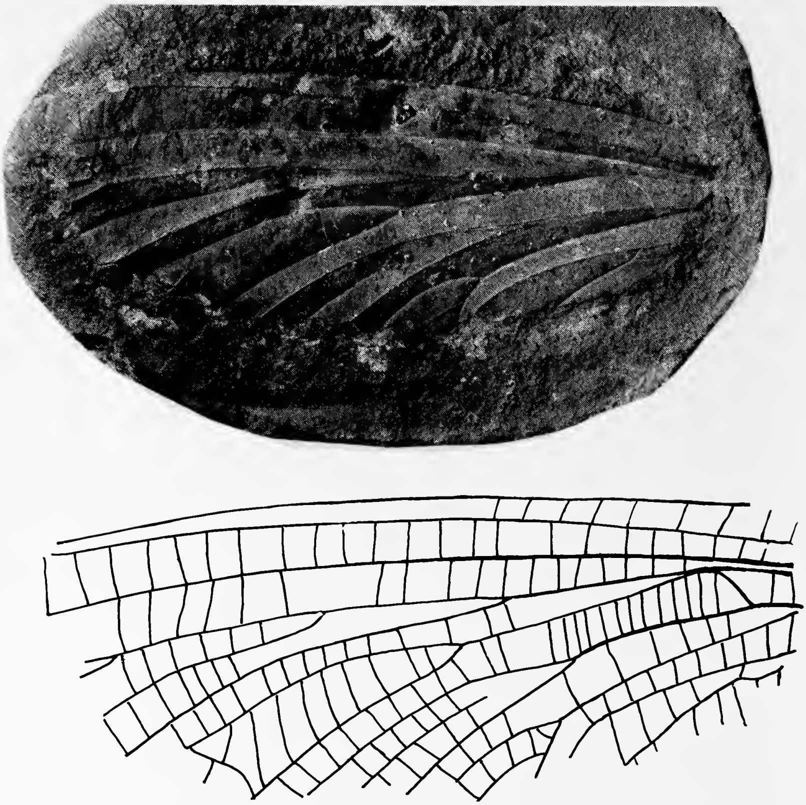

Fig. 8. *Lithoneura carpenteri* Richardson, fore wing. Holotype, No. 45248, Walker Museum, University of Chicago. Length of fragment, 55 mm. Upper figure, photograph of type; lower figure, venational pattern.

Museum, University of Chicago, consists of an incomplete fore wing, about 55 mm long. The original wing was probably about the same size as *mirifica.* This is almost certainly the same as *mirifica*; allowing for the difference in wing shape, the venation is virtually the same in the two holotypes.

Finally, the fourth specimen, no. 299 in the collection of Mr. and Mrs. Frank Wolff, was found in 1968 and has not previously been reported. It consists of a small basal fragment of a hind wing of *mirifica,* about 28 mm long. The costal area is not preserved but the fossil does show very well the separation of R and RS basally (Fig. 9).

Fig. 9. *Lithoneura mirifica* Carpenter, hind wing. No. 299, Wolff Collection. Length of fragment, 28 mm.

DIAGNOSIS OF FAMILY SYNTONOPTERIDAE

Medium-sized to large insects. Fore wing (incompletely known): costal area relatively broad proximally, very narrow distally; R without branches; stem of RS independent of stem R; stem of MA either close to RS or coalesced with it for brief interval; RS, MA, MP, and CUA with intercalary, triad branches; cross veins numerous, but rarely branched. Hind wing: broader than fore wing basally; venation essentially as in fore wing, but slightly modified by wing shape. Body: little known. Pronotum apparently with small lateral lobes. Antennae, mouthparts, legs, and cerci unknown.

Genus *Syntonoptera*

Fore wings: costal area with at least some reticulate cross veins; stem of MA very close to stem of RS; stem of MP remote from stem MA. Hind wing: venation as in fore wing but stem of MP very close to stem of MA.

Genus *Lithoneura*

Fore wing: cross veins in costal area without branches; stem of M remote from RS near wing base but then abruptly diverging anteriorly to RS and coalescing with it for a short interval. Hind wing:

stem of M coalesced with stem of CUA basally; anal, cubital, and medial areas very broad.

DISCUSSION

In the article cited above (1985), Kukalová-Peck described two specimens of nymphs, *Lithoneura piecko* and *L. clagesi,* from the Mazon Creek deposit, placing them in the order Ephemeroptera, family Syntonopteridae. Since the nymphs have a median caudal process, as well as the cerci, I agree that they are Ephemeroptera. Both of these nymphs had, in fact, been sent to me for study by Dr. Richardson many years ago. In a preliminary manuscript on them, I placed them in the Carboniferous genus *Triplosoba* Brongniart, family Triplosobidae, from Commentry, France. The type species of *Triplosoba, pulchella* Brongniart, is known by a single specimen, an imago having the three caudal appendages as well as an ephemeropterous venation, and is the only Carboniferous insect that has been consistently placed in the order Ephemeroptera. Since the two Mazon Creek nymphs showed no significant venation, I discontinued working on them, with the hope that better preserved nymphs might be found. However, in my opinion the assignment of these nymphs to the Syntonopteridae is very questionable, since the latter family is not, with certainty, a member of the order Ephemeroptera. It is quite possible that the two nymphs belong to the family Triplosobidae. In this connection, it is worth noting that several genera of insects are found in *both* the Commentry shales and the Mazon Creek beds. One of these, *Mischoptera,* of the order Megasecoptera, is represented by several imagoes in the Commentry deposit, although no nymphs of the genus have been found there; on the other hand, several specimens of nymphs, with the same venation and body structure, have been found in the Mazon Creek concretions (Carpenter & Richardson, 1968).

The precise affinities of the family Syntonopteridae are uncertain. Handlirsch (1911, 1919, 1922) placed it in the order Palaeodictyoptera, but of course he knew the family only by a small wing fragment, the holotype of *S. schucherti.* In 1938 and 1944, following my study of the specimens of *Lithoneura,* I suggested that the family may have been intermediate between the Palaeodictyoptera and the Ephemeroptera. A few years later, Edmunds and Travers (1954), linking the Syntonopteridae with both orders, proposed that the

Palaeodictyoptera might have been derived from the order Ephemeroptera. These ideas, however, were suggested before it was generally known that the Palaeodictyoptera had long, haustellate beaks. That had actually been shown by Laurentiaux in 1952, but there was some delay before its significance was fully appreciated. The following year, Laurentiaux (1953) designated a new order, Syntonopterodea, for the family. He did not, however, indicate any characters that would separate the new order from all others. More recently, Kukalová-Peck (1983) has placed the family Syntonopteridae in the order Ephemeroptera. In my opinion, we do not yet know enough about the body structure of the Syntonopteridae, including the mouth-parts and the terminal appendages of the abdomen, to justify that decision. As pointed out by Edmunds and Traver (1954), the Syntonopteridae may prove to have had two cerci plus a median caudal filament like the Ephemeroptera, when sufficiently well-preserved specimens are found. In that case, and provided they do not have haustellate mouthparts, their assignment to the Ephemeroptera would be justified. Until then, I prefer to place the Syntonopteridae in the category of Palaeoptera, Order Uncertain.

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PSYCHE

A Journal of Entomology

Volume 94

1987

Published Quarterly by the Cambridge Entomological Club
Editorial Office: Biological Laboratories
16 Divinity Avenue
Cambridge, Massachusetts, U.S.A.

The numbers of PSYCHE issued during the past year were mailed on the following dates:

Vol. 93, no. 3–4, March 17, 1987
Vol. 94, nos. 1–2, October 6, 1987

PSYCHE

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