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PSYCHE

Vol. 92 1985 No. 1

ANTS OF THE DOMINICAN AMBER (HYMENOPTERA: FORMICIDAE).
1. TWO NEW MYRMICINE GENERA AND AN ABERRANT *PHEIDOLE*

By Edward O. Wilson
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Ants rival dipterans as the most abundant fossils in the Dominican Republic amber. Since they are also phylogenetically compact and relatively easily identified, these insects offer an excellent opportunity to study dispersal and evolution in a Tertiary West Indian fauna.

The age of the Dominican amber has not yet been determined, but combined stratigraphic and foraminiferan analyses of its matrix suggest an origin at least as far back as the early Miocene (Saunders in Baroni Urbani and Saunders, 1982). I am inclined to favor this minimal age (about 20 million years) or at most a late Oligocene origin, for the following reason. In a sample of 596 amber pieces containing an estimated 1,248 ants that I recently examined (439 now deposited in the Museum of Comparative Zoology), I found 36 genera and well-defined subgenera, to which may be added one other, *Trachymyrmex,* reported earlier by Baroni Urbani (1980a). Of these 37 taxa only three, or 8%, are unknown from the living world fauna (see Table 1). The relative contemporaneity of the Dominican amber ants contrasts with that of the Baltic amber, which is Eocene to early Oligocene in age (Larsson, 1978) and possesses 44% extinct genera; that is, 19 of the 43 genera recorded by Wheeler (1914) are unknown among living ants. The Dominican amber ants also differ to a similar degree from those of the Florissant, Colorado, shales, which are upper Oligocene in age and contain 8 of 20, or 40%, extinct genera (Carpenter, 1930).

Table 1. List of ant genera and well-defined subgenera known from the Dominican amber. CBU: recorded by Baroni Urbani (1980a–d) and Baroni Urbani and Saunders (1982). CBU/EOW: recorded independently by both Baroni Urbani (1980a–d; and with Saunders, 1982) and E. O. Wilson (hitherto unpublished). Generic names without accompanying initials represent determinations by the author and are recorded here for the first time. (*) unknown in modern faunas.

Subfamily Ponerinae
Anochetus (CBU/EOW)
Cylindromyrmex
Gnamptogenys (CBU/EOW)
Hypoponera
Odontomachus
Paraponera
Platythyrea
Prionopelta
Trachymesopus

Subfamily Dorylinae
Neivamyrmex

Subfamily Pseudomyrmecinae
Pseudomyrmex (CBU/EOW)

Subfamily Myrmicinae
Aphaenogaster
Crematogaster (*Acrocoelia*)
Crematogaster (*Orthocrema*)
Cyphomyrmex
Erebomyrma
**Ilemomyrmex*, new genus
Leptothorax (*Macromischa*)
Leptothorax (*Nesomyrmex*)
Octostruma
Oligomyrmex
**Oxyidris*, new genus
Paracryptocerus (CBU/EOW)
Pheidole
New genus, near *Rogeria*
Smithistruma
Solenopsis (*Solenopsis*)
Solenopsis (*Diplorhoptrum*)
Trachymyrmex (CBU)
[*Zacryptocerus*: see *Paracryptocerus*]

Subfamily Dolichoderinae
Azteca
Dolichoderus
Hypoclinea
Iridomyrmex
[*Leptomyrmex* = *Camponotus*?, CBU/EOW]
Monacis (CBU/EOW)
Tapinoma

Subfamily Formicinae
Camponotus
Paratrechina
Prenolepis

The purpose of this first article of a planned series on the Dominican fauna is to describe the three most distinctive new species encountered in any collection known to me: two new myrmicine genera (*Ilemomyrmex*, *Oxyidris*) and a remarkable pheidoline which I have provisionally placed in the genus *Pheidole*.

Ilemomyrmex, new genus

Diagnosis (*worker*). Small, eyeless myrmicine possessing the following distinctive combination of features: large, flaring frontal lobes that are raised well above the antennal insertions and cover most of the clypeus in full-face view; shallow antennal scrobes with posterior margins curving laterally to embrace the ends of the scapes; paired clypeal carinae close together and projecting beyond the remainder of the anterior clypeal margin to form a short concavity between them; narrow, 3- or 4-toothed mandibles (apical region indistinct in the single specimen available); and 12-segmented antennae with 3-jointed clubs.

Queen (*tentative association*): Overall similar to worker, except that frontal lobes extend only part way over clypeus; mandibles are 5-toothed; and eyes and ocelli are well developed. (From Gr. *eilema,* envelope; and Gr. *myrmex,* ant).

Type species: Ilemomyrmex caecus.

Ilemomyrmex caecus, new species

(Figs. 1, 2)

Diagnosis (*worker*). Distinguished from all other known ant species by the combination of traits cited above for *Ilemomyrmex.* In addition, possessing a robust alitrunk with thick, triangular propodeal spines; and short, thick petiole and postpetiole, the latter with an acute, forward-projecting ventral spine.

Holotype worker. Head Width 0.51 mm, Head Length 0.58 mm, Scape Length 0.44 mm. Head coarsely rugoreticulate and completely opaque, the rugae near the rims of the antennal scrobes parallel to one another and following the contours of the rims. Entire alitrunk and waist similarly rugoreticulate and opaque, but the gaster is nearly smooth and is feebly shining to subopaque. Color (which may not have remained true in the fossil state) dark reddish brown.

Queen (*tentative association*). Winged. Differing from worker as described in generic diagnosis. Head Width (across and including eyes) 0.52 mm, Head Length 0.54 mm, Eye Length 0.16 mm.

Based on a single (holotype) worker and one alate queen in separate pieces of Dominican amber; no further locality data. Both specimens have been deposited in the Museum of Comparative Zoology.

Ilemomyrmex resembles the Old World, principally African genera *Calyptomyrmex* and *Dicroaspis* in antennal form and the peculiar shape of the frontal lobes. However, it differs from them in the following important respects: its mandibles are narrower, with fewer teeth (5 or more in *Calyptomyrmex* and *Dicroaspis*); its antennal scrobe is much shallower; its subpostpetiolar process is better developed; its head is narrower and overall less modified from the primi-

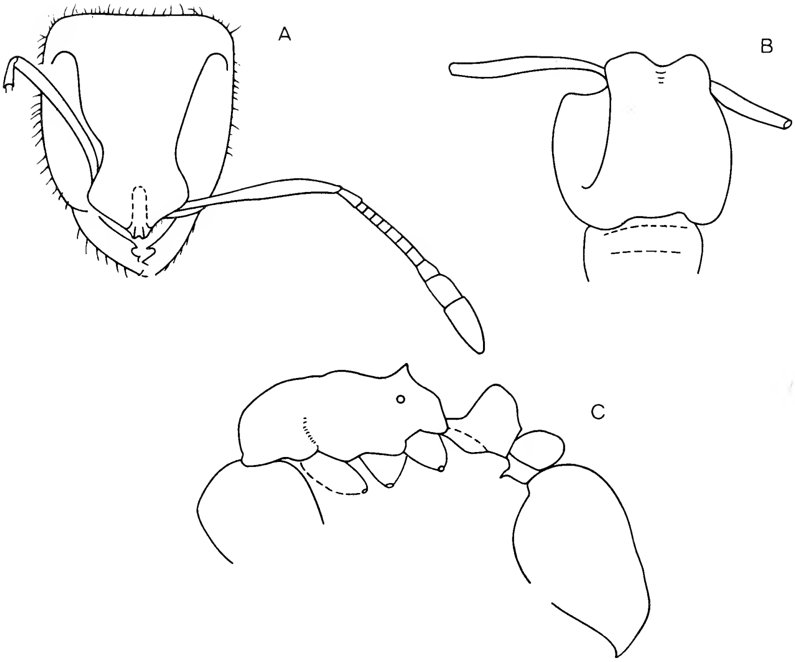

Fig. 1. *Ilemomyrmex caecus*. Holotype worker: A, frontal view of head; B, oblique rear view of head; C, side view of body.

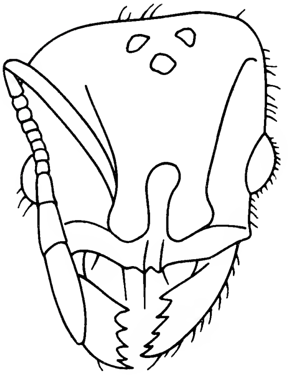

Fig. 2. *Ilemomyrmex caecus*. Frontal view of head of queen provisionally placed in this species.

tive myrmicine shape; and its hairs are thinner and less uniform and regularly distributed (furthermore, in *Calyptomyrmex* and *Dicroaspis* the hairs are blunt-tipped or, in the case of most species, spatulate or scale-shaped). In addition, *Dicroaspis* has 11-segmented antennae. I am inclined to regard the resemblance in frontal lobe shape between *Ilemomyrmex* and the two African genera as having arisen by convergent evolution.

Oxyidris, new genus

Diagnosis (*worker*). A very small myrmicine with closest overall resemblance to the South American genus *Oxyepoecus,* particularly in the general form of the antenna and waist; but differing in its lack of eyes, its 12-segmented antennae (11 in *Oxyepoecus*), in its 3 (possibly 4) mandibular teeth (4–5 in *Oxyepoecus*), and in its unarmed propodeum (angular or spinous in *Oxyepoecus).* (From Gr. *oxys,* sharp, acute; and Gr. *idris,* wise one; also to note resemblance to *Oxyepoecus*).

Type species: Oxyidris antillana.

Oxyidris antillana, new species

(Fig. 3)

Diagnosis (*worker*). Distinguished from all known ant species by the combination of traits just described for *Oxyidris.*

Holotype worker. Head Width 0.36 mm, Head Length 0.45 mm, Scape Length 0.30 mm. Antenna 12-segmented with 3-jointed club. Head densely and evenly rugulo-punctate (rugulae with longitudinal orientation) and opaque. Alitrunk and waist densely and uniformly punctate, and opaque. Gaster shagreened, subopaque. Color (which may be altered in the fossil state) light reddish brown.

Dominican Republic: Palo Quemado Mine, Santiago Province.

Paratype workers. Six additional workers, one each in 6 amber pieces from Palo Quemado Mine.

Holotype and paratypes deposited in the Museum of Comparative Zoology.

Pheidole tethepa, new species

(Figs. 4, 5)

Diagnosis (*minor worker*). An unusual pheidoline tentatively placed in *Pheidole,* differing from all known species of that genus by

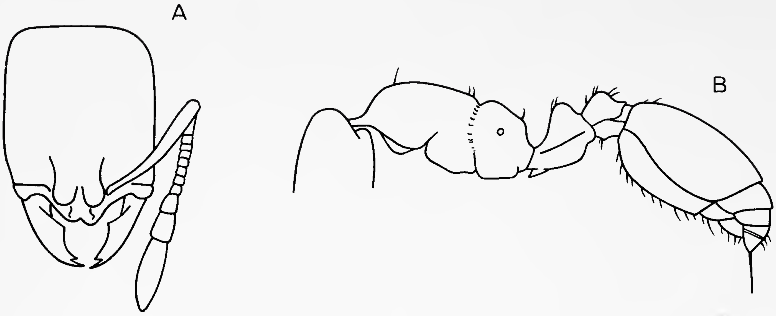

Fig. 3. *Oxyidris antillana.* Holotype worker: A, frontal view of head; B, side view of body.

the bulging, more-than-hemispherical eyes, and proportionately very large mandibles. Pronotum armed with two well-developed spines, a trait shared with members of the Old World *P. quadrispina* group but not with any known living New World *Pheidole* species. (Gr. *tethepa,* amazed; referring to the eyes).

Holotype minor worker. Head Width exclusive of eyes 0.76 mm, Pronotal Width 0.43 mm. Eyes with approximately 30 ommatidia. Head sparsely rugose to rugoreticulate with predominantly longitudinal orientation. Pronotum with several transverse rugae. Rest of dorsal surface of alitrunk evenly shagreened and subopaque.

Paratype minor workers. Two individuals poorly preserved but clearly sharing the diagnostic traits of the holotype.

Holotype and paratypes in a single amber piece from La Toca Mine, Dominican Republic.

DISCUSSION

Are *Ilemomyrmex* and *Oxyidris* really extinct? If so, they are extreme exceptions in the generic ranks of the Dominican amber ants. It may be significant that both are small, eyeless, and possess narrow, sharp-toothed mandibles. In addition, *Ilemomyrmex* is distinguished by expanded frontal lobes and scrobes that together can mostly cover the antennae. In the living fauna these traits are characteristic of cryptobiotic, often scarce myrmicine ants that are among the last to be collected and recognized. Examples of such living genera that have been recently discovered or at least recognized as

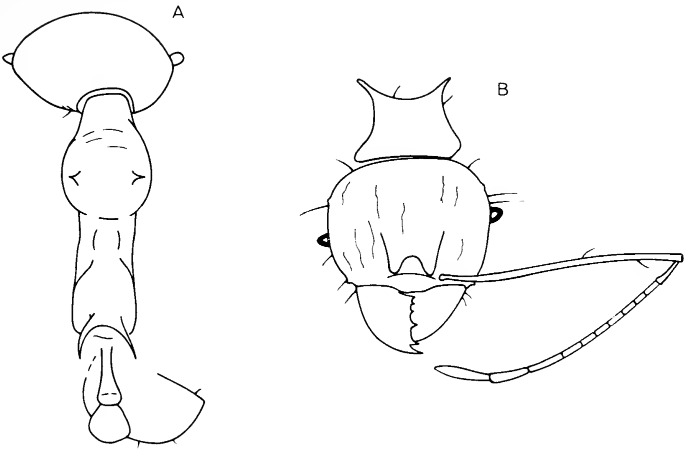

Fig. 4. *Pheidole tethepa.* Holotype worker: A, dorsal view of head and body; B, frontal view of head and pronotum.

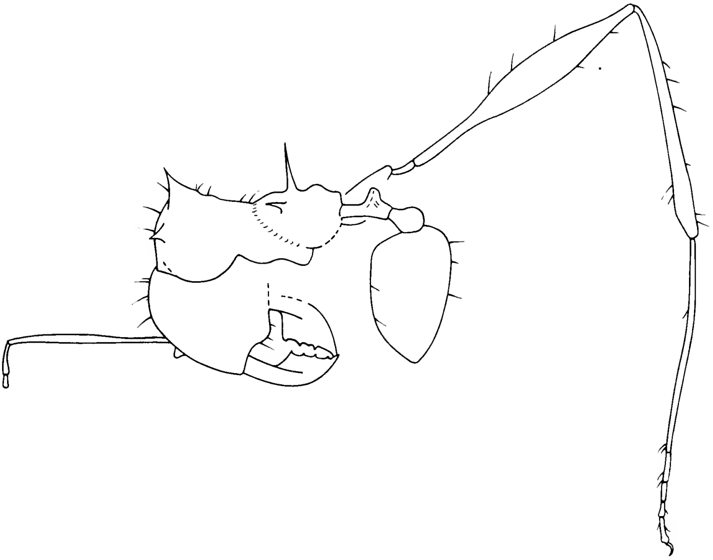

Fig. 5. *Pheidole tethepa.* Paratype worker from holotype amber piece, showing different view of body and head.

higher taxa in the New World tropics are *Creightonidris* (1949), *Dorisidris* (1948), *Phalacromyrmex* (1960), *Protalaridris* (1980), and *Tatuidris* (1967). Hence it is entirely possible that contemporaneous species of *Ilemomyrmex* and *Oxyidris* may yet be discovered, although not necessarily in the West Indies.

Pheidole tethepa has been placed in the genus *Pheidole* as a provisional measure. It may well represent a phyletic line sufficiently divergent from other members of the tribe Pheidolini to justify generic rank. The exophthalmic eyes and proportionately large mandibles are unique within *Pheidole* on a worldwide basis, while the pronotal spines were almost certainly derived independently from the Old World *P. quadrispina* group. More material is clearly needed to resolve the matter. In particular, the demonstration of a large-headed major caste (if one exists) would give added reason to retain *tethepa* in *Pheidole*.

ACKNOWLEDGMENTS

I am grateful to Cesare Baroni Urbani, Barry Bolton, and William L. Brown for their advice on the three new species described here. The research was supported by National Science Foundation grant no. BSR 81-19350.

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ANTS OF THE DOMINICAN AMBER (HYMENOPTERA: FORMICIDAE).
2. THE FIRST FOSSIL ARMY ANTS

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Despite the local abundance of the contemporary army ants, comprising about 105 species in the Old World Dorylinae and 147 species in the New World Ecitoninae (Gotwald, 1979), no fossil remains have hitherto been recovered. In the course of studying a large collection of Dominican amber ants newly assembled in the Museum of Comparative Zoology (see also Wilson, 1985), I encountered two well-preserved workers of an apparently extinct species belonging to the New World genus *Neivamyrmex.* Their status as the first ecitonine fossils, extending the history of the subfamily back at least as far as the early Miocene, deserves special notice. The discovery also has potential biogeographic significance, because no living species of *Neivamyrmex* or any other ecitonine is known from the Greater Antilles.

Neivamyrmex ectopus Wilson, new species
(Figs. 1, 2)

Diagnosis (based principally on the holotype). A medium-sized species (Head Width 0.4–0.6 mm) characterized uniquely by the following combination of traits: sides of head parallel or nearly so for most of their length; antennal scapes relatively slender (thicker in the paratype), approaching the occipital angles to within a distance a little less than the maximum scape width; occipital border moderately concave, the lateral angles well defined; dorsal and posterior (declivitous) borders of propodeum forming a small, strongly convex but not angulate juncture; petiolar node symmetric, with a well-defined anterior peduncle; the subpetiolar process small, limited to the anterior petiolar border, and projecting forward; body mostly covered with comparatively sparse, semierect pilosity. Head, petiolar node, legs, scapes, and gaster smooth to weakly shagreened and feebly shining. Color dark reddish brown, although this may be an artifact of preservation.

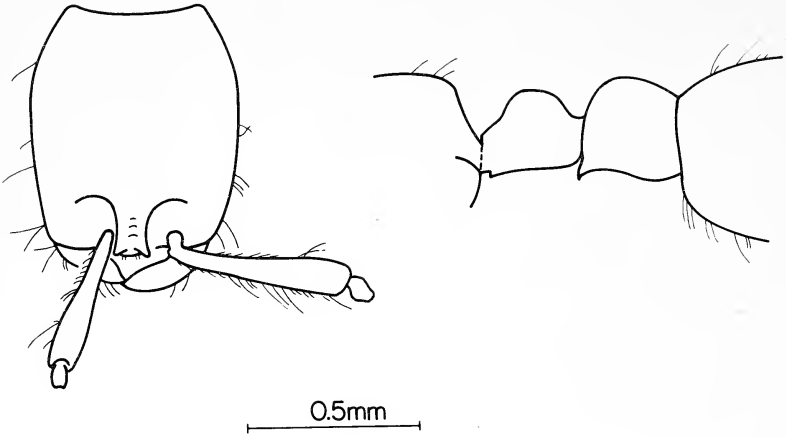

Fig. 1. *Neivamyrmex ectopus* n. sp. holotype worker: frontal view of head (*left*) and side view of propodeum, waist, and first gastric segment (*right*).

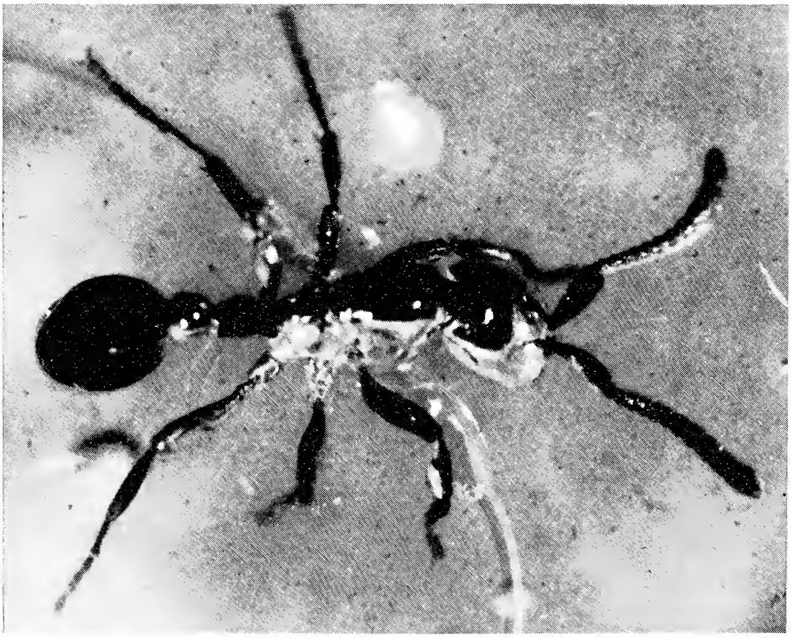

Fig. 2. *N. ectopus* n. sp. paratype worker: view of entire body. (Photograph courtesy of F. M. Carpenter).

Holotype and paratype workers. Well-preserved specimens in two separate amber pieces purchased from separate sources in the Dominican Republic. The material enclosing the ants is typical in quality and inclusions of Dominican amber, and the two pieces were in local collections containing other ant species previously established as typical of the Dominican amber fauna. Although the exact provenance of the specimens is unknown, Mr. J. Brodzinsky of Amberica Inc. states (*in litt.*) that "90–95%" of the material in which the *Neivamyrmex ectopus* holotype originated came from the Palo Alto and La Toca mines, near Santiago. The two types have been deposited in the Museum of Comparative Zoology, Harvard University, among the contemporary *Neivamyrmex* species.

Holotype (Fig. 1): Head Width 0.62 mm, Head Length (from the level of the center of the occiput to the level of the center of the anterior clypeal border) 0.72 mm, Scape Length 0.53 mm. *Paratype* (Fig. 2): Head Width 0.42 mm, Scape Length 0.30 mm, Pronotal Width 0.28 mm. The paratype is smaller and has proportionately shorter and thicker scapes, but otherwise corresponds well to the holotype.

RELATIONSHIPS

In order to interpret the status and possible phylogenetic relationships of the amber species, I considered all of the 61 contemporary *Neivamyrmex* species known from the worker caste. Of these, 51 were examined directly from type and reliably determined series, and the remaining 10 were characterized in the essential characters from the reviews by Borgmeier (1955) and Watkins (1976, 1977, 1982).

The following 8 characters visible in *N. ectopus* were found to vary considerably among the 61 contemporary species: size, shape and length of the scape; shape of the head, especially the occipital border; shape of the alitrunk, especially the profile of the propodeum; shape of the petiole, including the subpetiolar process; shape of the postpetiole; body sculpturing; and overall pilosity. Six species were found to resemble *ectopus* closely or identically in 6 of the characters (no species matched in 7 or all 8). These are listed below, along with an indication of the two traits in which they differ from *ectopus*:

N. agilis. Propodeum more flattened in side view, the basal and posterior faces merging as a single smoothly convex curve; pilosity denser.

N. californicus. Petiolar node more flattened in side view; body pilosity denser.

N. emersoni. Basal and posterior faces of propodeum meeting at only slightly more than right angle; pilosity denser.

N. fallax. Antennal scapes thicker and shorter relative to head capsule; subpetiolar process slightly thicker and pointing straight down (instead of forward as in *ectopus*).

N. manni. Occipital border flat; pilosity denser.

N. melanocephalus. Occipital border distinctly less concave; pilosity denser.

Of these 6 species, no fewer than 5 have ranges predominantly in Mexico and the southern United States, the northern portion of the range of *Neivamyrmex.* Only one (*emersoni*) is limited to the southern part of the total generic range, in this case South America and Trinidad. Yet only 21 of the 61 *Neivamyrmex* species occur in the northern portion; the remaining are so far as known limited to South and Central America. Put another way, *ectopus* closely approaches about 20% of the known northern species but only about 2.5% of the southern species.

DISCUSSION

The exact age of the Dominican amber is unknown, but most writers agree that it is either late Oligocene or early Miocene. The material originates from various mines in two principal areas: in the north of the Dominican Republic between Santiago and Puerto Plata, and in the east between Santo Domingo and the Bahia de Samaná. The age of the many deposits in which insects occur no doubt varies. Foraminiferal fossils associated with amber from mines near Palo Alto are characteristic of the lower Miocene (Baroni-Urbani and Saunders, 1982). I would guess a relative youth for most of the ant fossils I have seen, because the great majority belong to modern genera.

Regardless of its exact age, the discovery of a *Neivamyrmex* in Dominican amber has considerable significance for the interpretation of West Indian biogeography. Army ants are among the least vagile of all social insects. Among the Ecitoninae of the New World, *Neivamyrmex nigrescens* has been recorded from the Islas Marias, 100 km off the Mexican Pacific Coast, while *N. klugi* occurs on St. Vincent in the Lesser Antilles. No ecitonine is known farther away from the mainland, either from the northern arc of the Lesser Antilles or any of the Greater Antilles. Similarly, the Old World Dorylinae, represented by *Aenictus*, extends only as far east as the Philippine Islands, New Guinea, and Queensland (Wilson, 1964). It is wholly unknown from those portions of Micronesia and Polynesia that support a native ant fauna (Wilson and Taylor, 1967). The farthest outlier in the western part of the range is a population of *A. fergusoni* on Great Nicobar Island, 160 km from Sumatra. The existence of *N. ectopus* is therefore consistent with the common view based upon both geological and paleobotanical studies (Graham and Jarzen, 1969) that the ancestral Greater Antilles were larger and extended closer to the Mexican mainland during the middle and late Tertiary than is now the case.

Furthermore, the overall closer similarity of *N. ectopus* to contemporary Mexican and United States species, although far from conclusive, is consistent with a closer approach of the Greater Antilles to Mexico than to the northern coast of South America during the Tertiary Period.

SUMMARY

The first fossil army ant, *Neivamyrmex ectopus*, new species, is described from the Dominican amber, generally considered to be late Oligocene or early Miocene in age. Because of the extremely limited vagility of the Ecitoninae, and their apparent absence today from the West Indies north of St. Vincent, the presence of *N. ectopus* suggests a closer proximity of the Greater Antilles to the mainland during Tertiary times. Also, *N. ectopus* is phenotypically closer to species now living in Mexico and the southern United States than to the much richer Central and South American faunas.

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I am grateful to F. M. Carpenter for making the photograph of the paratype worker and for advising me on techniques of preparing and studying amber inclusions, and to William L. Brown, William H. Gotwald, Jr., and Julian F. Watkins II for critical readings of the manuscript. The research was supported by grant no. BSR 81-19350 from the National Science Foundation.

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ANTS OF THE DOMINICAN AMBER (HYMENOPTERA: FORMICIDAE).

3. THE SUBFAMILY DOLICHODERINAE

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The Dolichoderinae, in particular the species of *Azteca* and *Iridomyrmex,* are by a wide margin the most abundantly represented ants in the Dominican amber. They are also exceptional in the number of genera occurring in the amber but not in the modern fauna of the Greater Antilles. In other words the Dolichoderinae appear to have undergone a considerable amount of retreat entailing local extinction since early Miocene times, and for this reason alone the fossil species deserve close attention. In the present review I have relied principally on the large collections I have assembled for the Museum of Comparative Zoology during the past 10 years, supplemented substantially by material loaned by Dr. Robert E. Woodruff. All of the holotypes (except *Dolichoderus dibolia*) and most of the paratypes have been deposited in the Museum of Comparative Zoology. The holotype of *D. dibolia* and a few paratypes have been placed in the Florida State Collection of Arthropods, Gainesville, Florida. Earlier parts of this series have dealt with extinct myrmicine genera and the ecitonine army ants respectively (Wilson, 1985a, b).

Dolichoderus

This genus of large, slender ants is composed today of 8 species limited to the moist tropical forests of South America. The colonies are mostly or exclusively arboreal. The species to be described below is clearly a member of the distinctive *attelaboides* group, which ranges from the Amazonian region of Bolivia north to Trinidad.

Dolichoderus dibolia, new species
(Fig. 1)

Diagnosis (*worker*). Similar to the living species *D. attelaboides* and *D. imbecillus,* particularly in its attenuated occipital "neck" and overall body shape (including especially the alitrunk and propodeal spines) but differs from both forms in its somewhat larger size; proportionately thicker mesothorax; lower, more rounded petiolar node (quadrate in side view in the case of *attelaboides* and *imbecillus*), and much longer anterior petiolar peduncle.

The name *dibolia,* Greek for lance, refers to the strongly developed propodeal spines.

Holotype worker. Length of alitrunk 3.7 mm. With moderately abundant, coarse, erect hairs, especially on the antennal scape. Sculpturing not determinable due to the obscuring of much of the body surface.

Monacis

The genus *Monacis* may eventually be fused with other blocks of the Dolichoderini (see Brown, 1973, who synonymizes it under *Dolichoderus*), but until a thoroughgoing revision of the tribe is completed I regard it as both prudent and convenient to treat this genus as a separate entity. For the moment all the New World species placed in *Monacis* (Kempf, 1959) are distinguished by their possession of angulate or spiny pronotal humeri and laterally mar-

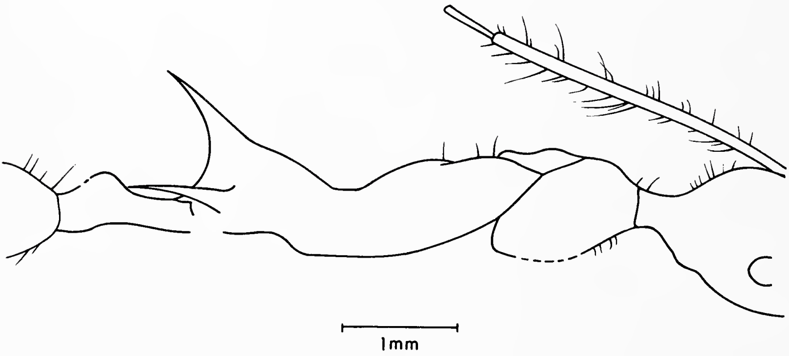

Fig. 1. *Dolichoderus dibolia* worker holotype, side view of body.

ginate mesonotum. Moreover, all recognized *Monacis* are Neotropical. Living members of the genus are almost wholly limited to the mainland from southern South America to southern Mexico, and all evidently nest arboreally. *M. bispinosa,* the most widespread species, also occurs on Trinidad and has been recorded, quite anomalously, from St. Thomas in the Virgin Islands (Mayr, 1862). The latter record was based on a single queen and is almost certainly an error—or at most represents a population introduced by human commerce. No other *Monacis* has been found in the remainder of the West Indies north of Trinidad, despite the fact that the workers of most of the species, including *M. bispinosa,* are large, conspicuous insects.

The two species described below from the Dominican amber are typical *Monacis* not much different from two species (*rufescens* and *laminatus* respectively) in the living fauna. They are of exceptional significance because of the current absence of the genus from the Greater Antilles.

Monacis caribbaea, new species
(Fig. 2)

Diagnosis (*worker*). A relatively small (Pronotal Width including humeral spines 0.49–0.66 mm), slender species resembling the modern *M. rufescens* of the Brazilian Amazon, differing from *rufescens* in its very sparse body pilosity and the more sharply angulate "shelf" separating the dorsal and declivitous (posterior) faces of the propodeum. *M. caribbaea* is also light reddish brown as opposed to light reddish yellow in *rufescens,* although its color might well have been altered during fossilization.

Holotype worker. Head Width 0.80 mm, Pronotal Width 0.51 mm. Alitrunk and petiole densely, finely, and evenly punctate, opaque; head still more finely punctate, grading to shagreened, and feebly shining. Body almost devoid of standing pilosity. Body mostly dark reddish brown, legs and parts of petiole and gaster light reddish brown.

Paratype workers. Eleven specimens in as many amber pieces: 2 from Palo Quemado (Pronotal Width of first 0.47 mm, second not measured), one from Bayaguana (no measurement), and 8 with no further locality within the Dominican Republic (Pronotal Width 0.49–0.66 mm).

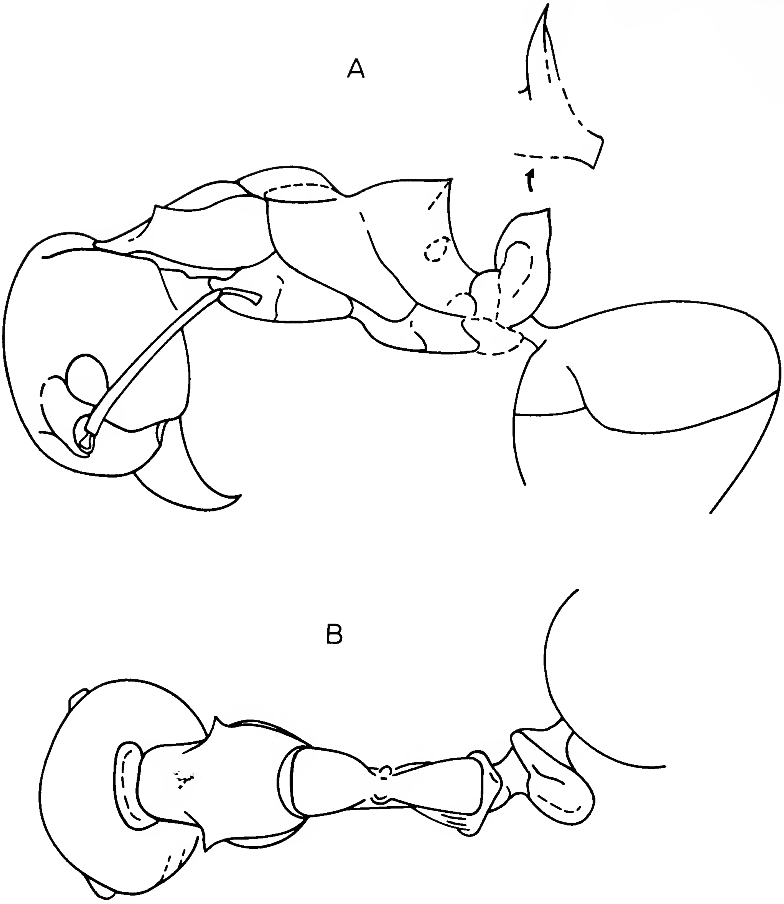

Fig. 2. *Monacis caribbaea* worker holotype: A, side view; B, dorsal view.

The pronotal humeri of the *caribbaea* types vary considerably, from well defined spines as in the holotype to simple acute angles approaching the condition that characterizes the second fossil species, *prolaminata.*

Monacis prolaminata, new species
(Fig. 3)

Diagnosis (*worker*). A relatively large, robust species closely resembling the living *M. laminata* of northern South America and

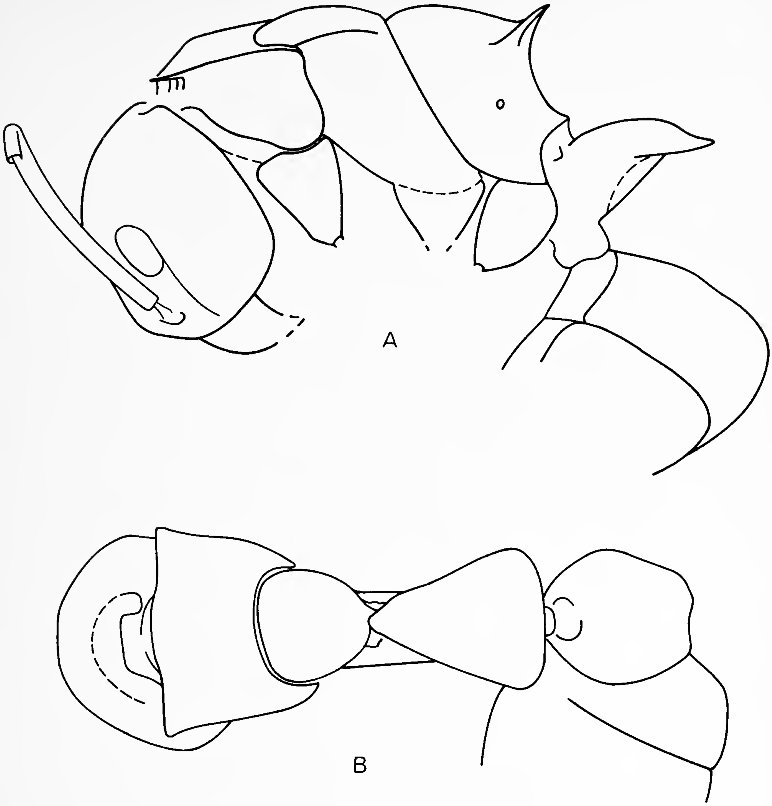

Fig. 3. *Monacis prolaminata* worker holotype: A, side view; B, dorsal view.

Central America, differing in the concave dorsal border of the petiolar scale viewed in full face (as opposed to strongly convex in *laminata*).

Holotype worker. Head Width 1.07 mm, Pronotal Width 0.93 mm. Dorsum of alitrunk shallowly rugoreticulate, the rugae longitudinally oriented on the mesonotum; spaces within the rugoreticular cells densely punctate; the whole surface entirely opaque but with reflections from the numerous evenly packed punctures giving the alitrunk a silvery, "sparkling" appearance. Head, petiole, and abdomen variably punctulate to shagreened and feebly shining. Body almost wholly devoid of standing pilosity. Body uniformly blackish brown, appendages light to medium brown. Dominican Republic amber: no further locality.

Paratype workers. Five specimens in 4 amber pieces: one from Palo Quemado (Pronotal Width 1.11 mm), 4 others from Dominican amber with no further locality, 2 of which are in one piece (Pronotal Width 0.90–1.30 mm).

Hypoclinea

The modern genus *Hypoclinea* as presently defined is nearly cosmopolitan (absent in Africa) and highly diverse in anatomy and behavior. At least 15 species compose the living Neotropical fauna, almost all confined to the mainland of Mexico, Central America, and South America. The most widespread form, *H. lutosa,* occurs from Brazil to Trinidad and southern Mexico. It has also been recorded from St. Vincent in the southern part of the Lesser Antilles, where it is quite rare (Forel, 1893). *Hypoclinea* is apparently absent in the remainder of the West Indies, including all of the Greater Antilles, a circumstance giving the Dominican amber species to be described below more than ordinary biogeographic importance.

Hypoclinea primitiva, new species

(Fig. 4)

Diagnosis (*worker*). A medium-sized (Head Width 0.6–0.7 mm), slender species with several primitive traits for *Hypoclinea* overall, including a relatively unmodified alitrunk, smoothly rounded propodeum, simple petiolar scale, and a "generalized" head shape with reference to the Dolichoderini in general. Closest in appearance to *H. germaini* of South America among living species; *germaini* differs from *primitiva,* however, in having a blunt, transverse ridge that separates the dorsal and declivitous faces of the propodeum, as well as more flattened pro- and mesonota (both of these traits are reasonably interpreted as having been derived in evolution).

The name *primitiva* alludes both to the antiquity of the species and to the set of traits just cited that are provisionally interpreted to be primitive within the genus and perhaps even in the Dolichoderinae as a whole.

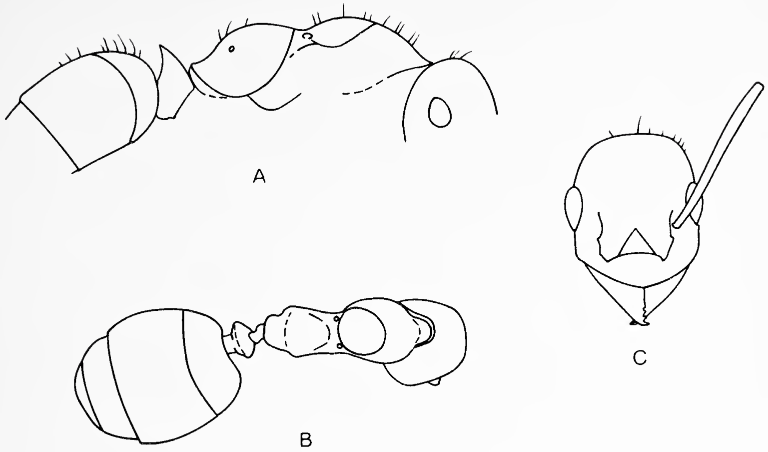

Fig. 4. *Hypoclinea primitiva* worker holotype: A, side view of body; B, dorsal view of body; C, head.

Holotype worker. Head Width 0.68 mm, Head Length 0.93 mm, Pronotal Width 0.56 mm, Scape Length 0.87 mm, Eye Length 0.26 mm. Posterior half of head bearing scattered foveae with the interspaces weakly shagreened and feebly shining. Rest of the body uniformly and lightly shagreened and feebly shining. Body uniformly light reddish brown. Dominican Republic amber: no further locality.

Paratype workers. Four workers: 2 in one amber piece from La Toca, associated with *Azteca alpha* workers (Head Width of one 0.64 mm, other not measured); two others in separate pieces originating from unknown localities (one with Head Width 0.66 mm, other not measured).

Azteca and *Iridomyrmex*

The large and complex genera *Azteca* and *Iridomyrmex* have proved difficult to separate in their entirety by means of external anatomy (a striking difference in the proventriculus makes the cleavage easier when this internal organ can be examined). The classification of fossil material is therefore difficult, since only external structures are usually preserved.

The problem is further complicated by the separation of workers, queens, and males into different amber pieces, so that most linkages across castes and sexes can only be guessed. In the case of the Dominican amber, however, I was able to solve the problem in part by the discovery of three miniature "Rosetta stones": 3 amber pieces with closely intermingled workers and males of the commonest species of *Azteca* (*A. alpha*). One of the pieces also contains a male pupa, further supporting the interpretation that the associated workers and males belonged to the same colony and were trapped during a colony emigration.

With the worker-male connection secured, I made comparisons with material representing 48 contemporary species of *Azteca* and 50 of *Iridomyrmex* (11 Neotropical, 39 Indo-Australian) in the Museum of Comparative Zoology collection, many with workers and males from the same nests. The following characters appear to hold with consistency:

1. In *Azteca* workers the mesonotum is usually moderately convex in side view and hence does not form a smooth line with the pronotum; in New World *Iridomyrmex* workers the mesonotum is only weakly convex in side view and forms a continuous line with the pronotum.
2. In *Azteca* workers the dorsal face of the propodeum is much less convex in side view than in *Iridomyrmex* workers.
3. In *Azteca* workers the petiolar node is longer than high (the reverse is true in *Iridomyrmex*) and inclined more strongly forward than in *Iridomyrmex.*
4. The occiput of *Azteca* workers is usually more deeply concave than in *Iridomyrmex* workers, although extreme species within the two genera overlap.
5. In *Azteca* males, the scape is very short, no longer than the combined second and third antennal segments, while either the second or third segment (depending on the species) is notably elongated, inflated, or both. In *Iridomyrmex* males, the antennae are more typical, with relatively long scapes and unmodified funiculi; an exception is *I. iniquus,* which has the *Azteca* antennal form.
6. In *Azteca* males the mandibles are short and triangular, lacking a well-defined masticatory border; whereas in *Iridomyrmex* males the mandibles have a well-defined masticatory border which also often bears serially arranged teeth.

7. In *Azteca* males the dorsal lobe (digitus) of the volsella is long and finger-like, extending posteriorly as far as the tips of the parameres (see Fig. 6E). They are proportionately broader in *Iridomyrmex* and reach only partway along the length of the parameres.

8. In most cases, the petiole of *Azteca* males is applied more broadly to the gaster than is the case in *Iridomyrmex.*

Using the combination of traits above, it has been possible to establish beyond much doubt that the species of the Dominican amber divide cleanly into either *Azteca* or *Iridomyrmex,* that none falls between the two genera, and that none is especially primitive in overall aspect. The most abundant ant species in the amber is the *Azteca* to be described below.

Azteca alpha, new species
(Figs. 5–8)

Diagnosis. A member of the *alfari* group, in which the worker caste is monomorphic or at most weakly polymorphic; *alpha* is also distinguished from the contemporary species belonging to this and other *Azteca* groups by the unique combination of traits in scape length, propodeal outline, and pilosity illustrated in Fig. 5. In particular, the worker appears especially close to *A. fiebrigi.* This Paraguayan species is distinguished from *alpha* by its slightly shorter scapes (which just reach the occipital corners in repose) and longer, denser body pilosity.

The male of *alpha* (Fig. 6) is close to or identical with that of *fiebrigi,* including the distinctive conformation of the scape and first two funicular segments. Both forms differ from *alfari,* the other member of the species group for which I have seen males associated with workers, in that *alfari* has the scape and first funicular segment short and slender and the second (rather than first) funicular segment conspicuously enlarged.

The queen of *alpha* (Fig. 7), encountered singly in two amber pieces and hence only tentatively associated with the *alpha* worker caste (as opposed to that of *eumeces,* to be described subsequently), is closely similar to the *fiebrigi* queen. It differs in its somewhat thinner petiolar node viewed from the side.

The name *alpha* alludes both to the early occurrence of the species in the geological record and to its numerical dominance in the Dominican amber.

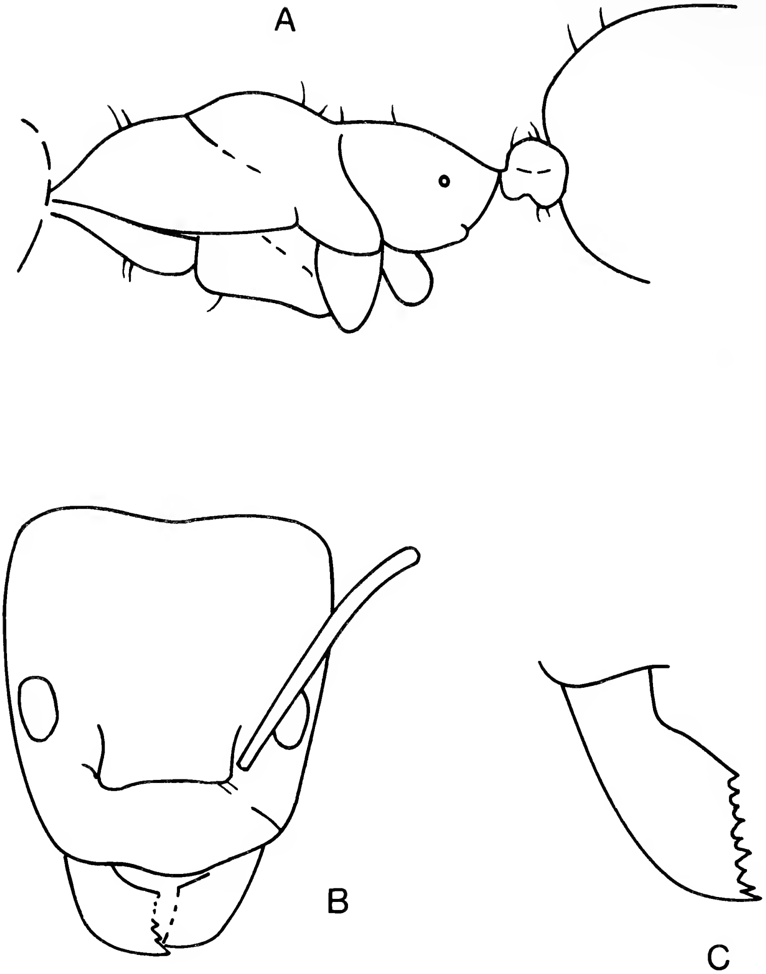

Fig. 5. *Azteca alpha.* A, holotype worker, side view of body; B, head of a paratype worker; C, left mandible of another paratype worker.

Holotype worker. Head Width 0.53 mm, Head Length 0.60 mm, Scape Length 0.48 mm. From a piece of amber with closely intermingled workers and males, known to originate from the Dominican Republic but with no further locality.

Paratype workers. A total of approximately 540 workers in 171 pieces of amber have been placed in *A. alpha.* Most were from

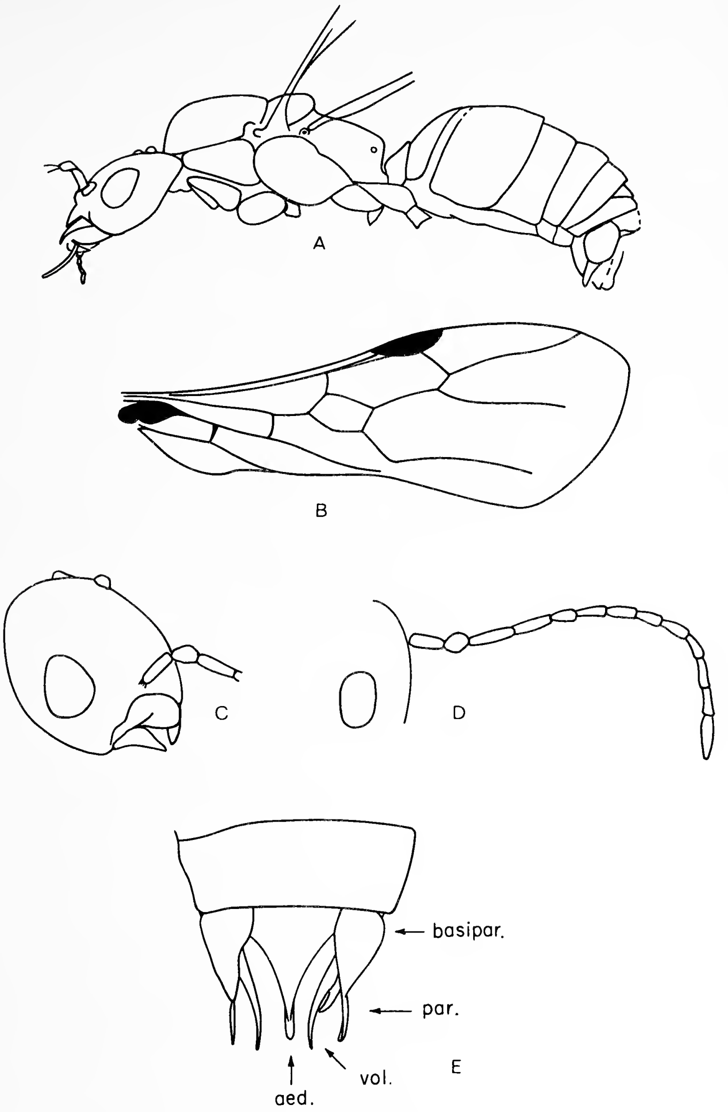

Fig. 6. *Azteca alpha* paratype males associated in same amber piece with holotype worker. A, side view of body; B, left fore wing; C, oblique lateral view of right side of head; D, left antenna; E, dorsal view of genitalia (showing basiparamere, paramere, volsella, aedeagus).

unknown mines in the Dominican Republic, but a large minority originated from the following localities, including almost all from which I have seen ants of any kind: Carlos Diaz, near Tamboril; Cotui; La Bucara; La Cumbre; La Toca; Las Bocas del Licey; Llaroa (Yaroa); Los Cacaos; Marias; Palo Quemado; Bayaguana. The specimens share the key characters of the holotype nest series. They are quite variable in size (Head Width 0.42–1.06 mm overall), but, as documented in Fig. 8, relatively little variation occurs within single amber pieces. Moreover, the size variation in one especially populous piece I have examined appears to be unimodal with little or no skewing. Hence *A. azteca* must be regarded, at least tentatively, as a monomorphic species.

Paratype males. A total of 17 individuals in 8 pieces (3 with associated workers). The essential characteristics, placing the species still more firmly within the *alfari* group and in particular close to *fiebrigi,* are illustrated in Fig. 6. The alitrunk length of the male depicted, from the holotype nest series, is 1.04 mm. The Head Width (including eyes) of another male measured from Palo Quemado is 0.72 mm.

Paratype queens. The elongate head shape of 2 alate queens found in separate amber pieces (Dominican Republic, no further locality) might seem to associate them logically with *A. eumeces,* the second, rarer *Azteca* species occurring in the Dominican amber. Nevertheless, at least some of the contemporary *alfari* group species, in particular *coeruleipennis, fasciata,* and *fiebrigi,* have workers with ordinary head shapes and queens with elongated heads. Moreover, the Dominican amber queens closely resemble those of *fiebrigi.*

General remarks. *Azteca alpha* is by far the most abundant ant species and hence probably the most abundant insect species in the Dominican amber. It occurs in 29% (171 of 592) of the ant-bearing amber pieces I have studied closely to date. Since I passed a large percentage of the pieces back to dealers prior to the revisionary work because they contained *A. alpha* and thus were considered of less interest, the actual representation of the species was much higher, very likely 50% or more.

In addition, *A. alpha* workers have been found in the same pieces as many of the other Dominican amber genera: *Pseudomyrmex, Crematogaster* (*Orthocrema*), *Oligomyrmex, Pheidole, Monacis, Hypoclinea,* and *Camponotus.* This circumstance, plus the occur-

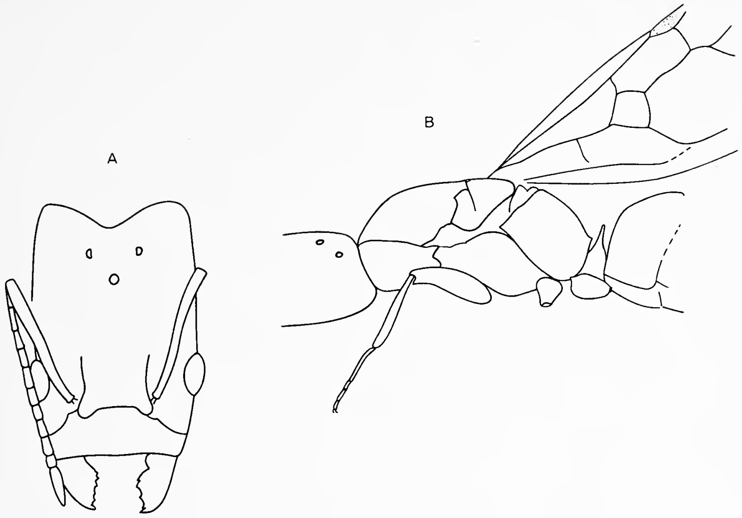

Fig. 7. *Azteca alpha* queen (tentative association). A, head; B, side view of body.

rence of *A. alpha* in pieces from almost all of the identified mines to date (the only exceptions are El Valle and Palo Alto) is evidence that at least the bulk of the Dominican ant fauna is relatively cohesive and did not stretch over a very long period of geological time.

The frequent occurrence of large numbers of *A. azteca* workers in the same amber piece, in a few cases 50 or more, also suggests that the species foraged in groups or at least recruited groups to food sources or enemies. Such behavior characterizes contemporaneous species of *Azteca.* So far as known all of the living *Azteca* species are arboreal, foraging onto the ground only secondarily, and it is reasonable to suppose this was true of *A. alpha* as well. In addition, at least some of the modern members of the *alfari* group are specialized for life on the moraceous tree *Cecropia* (Wheeler, 1942). What this means for *A. alfari,* whose workers were trapped in the gum of the leguminous tree *Hymenaea courbaril* (locust tree or "algarrobo") is unclear.

I have not excluded the possibility that more than one species exists in the large quantity of material placed with *A. alpha.* Many

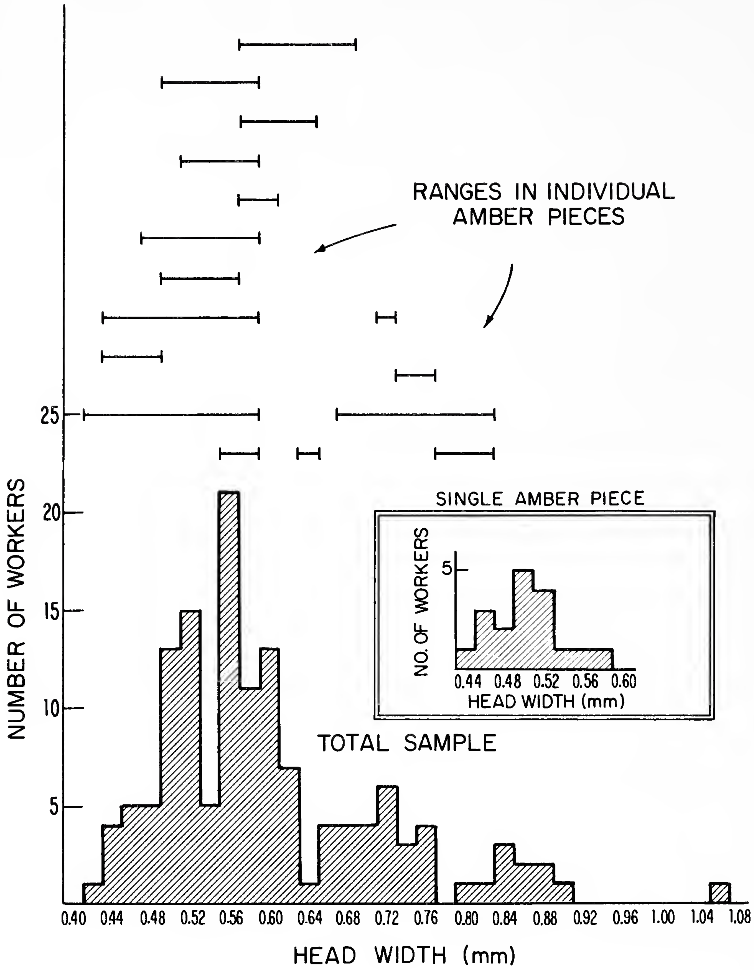

Fig. 8. *Azteca alpha* workers: size range between and within series found within individual amber pieces and hence assumed to belong to the same colony. The larger frequency curve (*bottom in figure*) includes all of the 141 workers measured. The smaller frequency curve (*enclosed in rectangle*) includes the measurable workers from one of the most populous pieces. The series of horizontal bars (*uppermost in figure*) depict the ranges within single amber pieces. The samples originate variously from Carlos Diaz, La Bucara, Las Bocas del Licey, Llaroa, Los Cacaos, Palo Quemado, and still other, unknown mine sites within the Dominican Republic.

of the specimens were so decayed or poorly positioned that the critical characters could not be examined, and in these cases I relied on size and habitus.

Azteca eumeces, new species
(Fig. 9)

Diagnosis (*worker*). A medium-sized member of the *alfari* group distinguished from all known contemporary members of the genus, as well as the Dominican amber *A. alpha,* by the exceptionally elongate head of the worker (Cephalic Index about 70–80 as opposed to 80 or more in other species). In overall appearance *A. eumeces* is similar to *bicolor, fasciata,* and *theresiae,* but in addition to possessing somewhat less elongate heads, these living species also have more convex lateral sides of the head seen in full-face view, with the outer margins of the eyes located well inside the head margins.

The name *eumeces* is derived from Gr. *eumekes,* of good length.

Holotype worker. Head Width 0.43 mm, Head Length (from line of posteriormost reach of occipital corners to line of center of anterior clypeal border) 0.63 mm, Cephalic Index 68, Scape Length 0.47 mm, Pronotal Width 0.27 mm. In an amber piece from Palo Quemado, near Santiago, Dominican Republic.

Paratype workers. Thirty-eight workers in 6 amber pieces, Dominican Republic (no further locality).

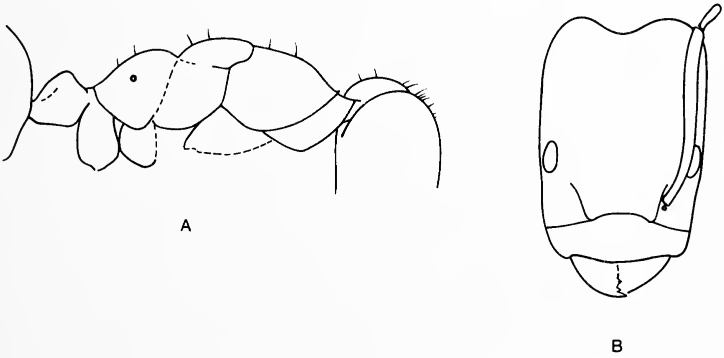

Fig. 9. *Azteca eumeces* holotype worker: A, side view of body; B, head.

Iridomyrmex hispaniolae, new species
(Fig. 10)

Diagnosis (*worker*). A medium-sized (Head Width 0.5–0.8 mm), slender species similar to the living species *I. pilifer* of northern South America, especially close in details of the head and alitrunk, differing from *pilifer* in its distinctly thicker, less symmetric petiolar scale in lateral view.

Holotype worker. Head Width 0.70 mm, Head Length 0.72 mm, Scape Length 1.03 mm, length of alitrunk 1.08 mm. Body overall smooth to lightly shagreened, and feebly shining. Pilosity very sparse, mostly limited to a few hairs on the head, gaster, and appendages. Body light to medium yellowish brown. Las Bocas del Licey, Dominican Republic.

Paratype workers. Forty-six workers in 32 amber pieces variously from Carlos Diaz, El Valle, La Toca, Llaroa, Los Cacaos, Palo Quemado, and Bayaguana; 19 of the pieces have no further localities other than the Dominican Republic. Head Width 0.52–0.83 mm. All closely similar in habitus to the holotype.

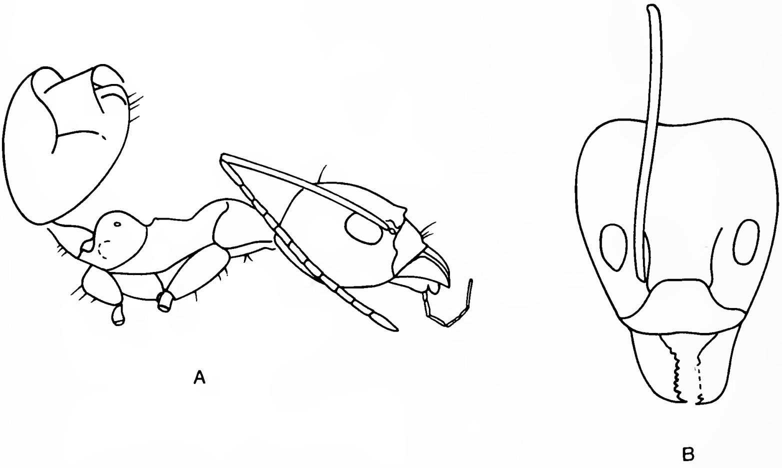

Fig. 10. *Iridomyrmex hispaniolae* holotype worker: A, side view of body; B, head.

I. hispaniolae was also compared with series belonging to 39 Old World *Iridomyrmex* species, including all of the principal species groups. It bears an overall resemblance to certain of them, especially *anceps, emeryi,* and *pallidus,* but differs substantially in various combinations of details in the petiole shape, pilosity, eye size, and sculpturing.

Iridomyrmex humiloides, new species
(Fig. 11)

Diagnosis (*worker*). A relatively small species resembling *I. humilis* of South America. With this living form it differs from other members of the species, including *despertitus* and *pruinosus,* most conspicuously in the concave anterior border of its clypeus. It differs from *humilis* (and other contemporary similar species) by the fact that its eyes exceed the lateral borders of the head in full-face view, whereas in the living species the outer margins of the eyes do not reach the lateral borders of the head.

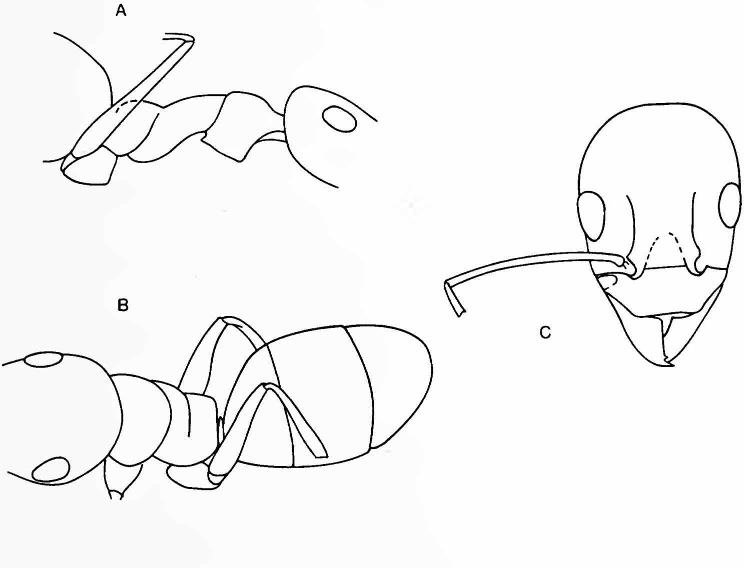

Fig. 11. *Iridomyrmex humiloides* holotype worker: A, oblique dorsal view of head and body; B, lateral view of body; C, head.

Holotype worker. Head Width 0.41 mm, Head Length 0.53 mm, Scape Length 0.60 mm, Eye Length 0.13 mm. Body overall lightly shagreened and feebly shining and subopaque. Body almost completely hairless, light to medium reddish brown in color. Dominican Republic amber: no further locality.

Tapinoma

Although *Tapinoma* is cosmopolitan and composed of numerous, anatomically diverse species, it has not previously been recorded from the fossil record. At least three species (*litorale, opacum, rasenum*) are native to the Greater Antilles while a fourth (*melanocephalum*) occurs there and may either be native or introduced by commerce. The following record establishes the relative antiquity of the genus as well as of the *atriceps* group in the West Indies.

Tapinoma trochis, new species
(Fig. 12)

Diagnosis (*worker*). A member of the *atriceps* group, distinguished by small size and a conspicuous broadening of the fore femora and tibiae. It most closely resembles *canalis* of Panama among living species, which differs from *trochis* by the fact that its scapes reach the occipital corners. Also, the propodeal dorsum of *canalis* is less flattened in side view, and the dorsal and declivitous propodeal faces meet in a rounded but distinct obtuse angle.

The Greek specific name *trochis* means runner and is meant to refer to the powerful-looking fore legs.

Holotype worker. Head Width 0.32 mm, Head Length 0.37 mm, Pronotal Width 0.21 mm, Scape Length 0.26 mm, Eye Length 0.06 mm. Body smooth, feebly shining to subopaque, devoid of standing hairs, medium yellowish brown. Dominican Republic amber: no further locality.

Species Properly Excluded from the Dolichoderinae

Camponotus neotropicus (Baroni Urbani),
new combination

Leptomyrmex neotropicus Baroni Urbani, 1980, *Stuttgarter Beitr. Naturkunde,* Ser. B, 62: 1–10, worker, Type locality: amber, Dominican Republic, no further locality.

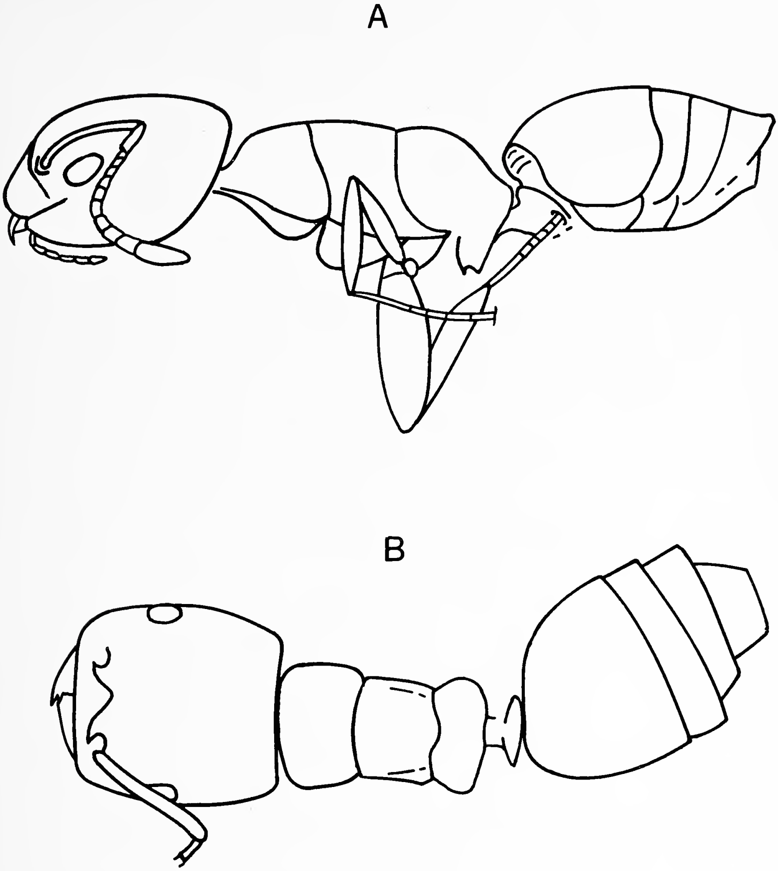

Fig. 12. *Tapinoma trochis* holotype worker: A, lateral view; B, dorsal view.

The living species of *Leptomyrmex* are confined to Australia and Melanesia. All of the other ants thus far discovered in the Dominican amber belong to modern Neotropical genera and, in many cases, living species groups. Hence, as Baroni Urbani (1980) himself noted in his original description, the occurrence of *Leptomyrmex* in the West Indian ant fauna during Dominican amber times would constitute a considerable biogeographic anomaly. The situation is confused by the poor condition and uncertain anatomy of the *Leptomyrmex neotropicus* types, all 8 of which are in the same piece of amber.

During my own study I encountered a single worker in the Museum of Comparative Zoology collection that fits the *L. neotropicus* habitus closely. Although this specimen has the front part of the head missing, there is little distortion in the remainder of the head and body. An apparent acidopore can be seen, placing the species in the Formicinae rather than in the Dolichoderinae. And indeed, the specimen is closely similar to *Camponotus branneri* of Brazil, sharing the same distinctive elongated body form, mesothoracic constriction, petiole, tapered neck, and bulging eyes located toward the rear of the head. *C. branneri* is also similar to *C. santosi* of Cuba and *C. sexguttatus* of Central America and the West Indies.

The status of *neotropicus* will not be settled definitively until additional and better preserved *neotropicus* workers are available. In the meantime, the evidence as well as biogeographic probabilities make it prudent to place the fossil species provisionally in *Camponotus* and to remove the genus *Leptomyrmex* from the Dominican amber faunal list.

Discussion

There has been a remarkable retreat of the Dolichoderinae from the West Indies since Dominican amber times, in other words, since the late Oligocene or early Miocene. Four genera (*Azteca, Dolichoderus, Hypoclinea, Monacis*) have disappeared entirely from the Greater Antilles. Only two (*Iridomyrmex, Tapinoma*) have persisted to the present, while a single genus, *Conomyrma,* has invaded more recently. The dominant arboreal ants are no longer *Azteca*; according to W. L. Brown (personal communication), who has collected intensively over much of the Dominican Republic, the more abundant genera include *Pseudomyrmex, Crematogaster, Paracryptocerus,* and *Camponotus.* In this important respect the West Indian fauna mirrors the general decline of the Dolichoderinae in North and South America, Europe, and Asia, possibly in conjunction with the advance of *Crematogaster* as a competitor of *Iridomyrmex* (Brown, 1973).

Acknowledgments

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HOSTPLANT CHOICE OF CHECKERSPOT LARVAE: *EUPHYDRYAS CHALCEDONA, E. COLON,* AND HYBRIDS (LEPIDOPTERA: NYMPHALIDAE)*

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Introduction

Hostplant preference and hostplant utilization abilities may vary among species, populations (Scriber, 1983; Blau and Feeny, 1983; Singer, 1982, 1983; Holdren and Ehrlich, 1982; Hsiao, 1978; Ehrlich and Murphy, 1981), and individuals (Rausher, 1978; Tabashnik, et al., 1981; Wasserman and Futuyma, 1981; Singer, 1982, 1983). Although such preferences and utilization abilities may be modified by environmental effects such as conditioning (Jermy, et al., 1964; Scriber, 1981; 1982; Grabstein and Scriber, 1982), there is clearly often an obvious genetic component to the patterns of hostplant use observed in nature (e.g., Jaenike and Grimaldi, 1983). The butterfly genus *Euphydryas* (Nymphalidae) is remarkable for the diverse strategies of hostplant exploitation exhibited by the six species that occur in North America. *Euphydryas gilletii,* for example, is reported to be virtually monophagous on *Lonicera involucrata* (Caprifoliaceae), while *E. editha, E. chalcedona,* and *E. anicia* are oligophagous, although individual populations may utilize a distinct subset of available hosts (Ehrlich, et al., 1975; Ehrlich and Murphy, 1981; Singer, 1982, 1983).

In butterflies, as in many other groups of insects, hostplant utilization is a function of oviposition preference of the female coupled with larval adaptation to the host. In the shift to a new hostplant, change in adult oviposition preference may occur more quickly than larval loss of the ability to utilize ancestral hostplants (Wiklund, 1975; Scriber and Feeny, 1979; Shapiro and Matsuda, 1980; Singer, 1982; Scriber, 1983). Thus adult oviposition behavior may not always reflect larval preference or fitness on a particular hostplant. In a series of elegant experiments with *Euphydryas editha,* Singer

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(1982, 1983) has shown that there is genetic variation in hostplant preference among individual females from a single population, as well as differences among females from different populations. Variation in the ability of *Euphydryas* larvae to use different hostplants has been investigated by several workers (Rausher, et al., 1981; Holdren and Ehrlich, 1982; Williams, et al, 1983a,b; Bowers, in prep.); however the genetic basis of larval preference in this genus has not been addressed.

The hostplants of the North American *Euphydryas* include primarily three families: Scrophulariaceae, Plantaginaceae, and Caprifoliaceae; with occasional use of plant species in the Oleaceae (Bowers, 1980); and Valerianaceae (Williams and Bowers, in prep.). These plants are all characterized by the presence of a group of secondary compounds, the iridoid glycosides (Kooiman, 1972; Jensen, et al., 1975; Bowers, 1981) which are used as larval feeding stimulants by *E. chalcedona* and probably by the other species as well (Bowers, 1983).

Neonate larvae potentially provide a powerful tool with which to examine the genetic basis of hostplant selection because their hostplant choice behavior is not complicated by the phenomenon of conditioning (Jermy, et al., 1964). Conditioning causes larvae to exhibit a preference for the plant species on which they have been feeding, and in some cases this may occur over a short period of time (Hanson, 1983). Hostplant choice of first instar larvae is usually considered to be constrained by the oviposition behavior of the female. However, Holdren and Ehrlich (1982) found that neonate larvae of *E. editha* and *E. anicia* may move as much as 15 cm in search of fresh food. *Euphydryas* hostplants include some species that are small annuals, and they may be defoliated or otherwise unsuitable as food, thus forcing even first instar larvae to move in search of other food. Ovipositing females may make mistakes (Chew, 1974), and although this may be rare in *Euphydryas,* in the laboratory, females with their feet on the hostplant, may lay their eggs on an inappropriate substrate (pers. obs.). The ability of newly hatched larvae to move in search of appropriate food is clearly important in the event of such a situation.

With these considerations in mind, I undertook a study of two species of *Euphydryas, E. colon* and *E. chalcedona.* These two species are very closely related (Bauer, 1975) and in the past have been considered a single species (McDunnough, 1927; Gunder, 1929; dos Passos, 1964; Scott, 1980). The hostplants used by the *Euphydryas* populations that I studied are in different families: the *E. colon* population uses primarily *Symphoricarpos albus* in the Caprifoliaceae, while the *E. chalcedona* population feeds primarily on *Penstemon breviflorus* in the Scrophulariaceae. I compared the hostplant choice of neonate larvae of *E. chalcedona, E. colon,* and the hybrids.

MATERIALS AND METHODS

Euphydryas colon larvae were collected from a population at Satus Pass (ST) in Yakima County, Washington. In this population, larvae feed primarily on *Symphoricarpos albus* (Caprifoliaceae), although postdiapause larvae may occasionally be found feeding on *Penstemon* sp. (Scrophulariaceae). Both of these plant genera contain iridoid glycosides (Bowers, unpublished; Kooiman, 1970; Jensen, et al., 1974). *Penstemon* sp. and *S. albus* grow close to each other in this population.

Euphydryas chalcedona larvae were from a population north of Chico, on Crown Point Road (CPR), Butte County, California. The primary hostplant used in this population is *Penstemon breviflorus* (Scrophulariaceae). Oviposition and pre-diapause larval feeding are confined to this plant species; however post-diapause larvae may be found feeding on *Castilleja* sp. and/or *Diplacus bifidus* (Scrophulariaceae). These species all contain iridoid glycosides (Kooiman, 1970; Jensen, et al., 1975; Bowers, unpublished).

The post-diapause larvae collected from these populations, were brought back to Stanford University, and reared to the adult stage on leaves of *S. albus* (*E. colon*) or *P. breviflorus* (*E. chalcedona*). Adults were mated in net bags hung in a sunny window. For oviposition, mated females were put into glass cylinders covered with netting and containing a sprig of the appropriate hostplant. There appeared to be no problems in getting *E. colon* and *E. chalcedona* to hybridize in the laboratory, and a high proportion of the hybrid eggs were viable (Bowers, unpublished).

Egg masses were removed from the leaf on which they had been laid and kept in a growth chamber at 25 C Day:20 C Night, and a photoperiod of 16L:8D. When the larvae hatched, they were immediately given a choice test.

The choice tests were conducted in a small petri dish (6 cm diameter) lined with a piece of damp filter paper. Because *E. colon* and *E. chalcedona* are batch layers and the pre-diapause larvae are gregarious, the tests were conducted with groups of larvae. For each test, a group of 10 larvae was given a 5 mm disc of *P. breviflorus* and one of *S. albus*. These discs were punched out of the leaf with a cork borer, just prior to the beginning of each test. The discs were placed in the center of the petri dish about 1 mm apart, the larvae introduced, and allowed to feed for 48 hours. At 24 and 48 hours, the amounts of the two leaf discs eaten were estimated visually to the nearest ten percent (Jermy, et al., 1964; Bowers, 1979).

RESULTS

For each of the intraspecific crosses, the newly hatched larvae significantly preferred their own hostplant (Table 1, Fig. 1). In contrast, the hybrid larvae showed no preference for either plant (Table 1, Fig. 1). This ostensible lack of preference by the hybrid larvae, however, was not due to each group of larvae eating approximately equal amounts of both plant species, nor was it due to some larvae within a group feeding on the disc from one species and others on the other. On the contrary, each group of hybrid larvae appeared to

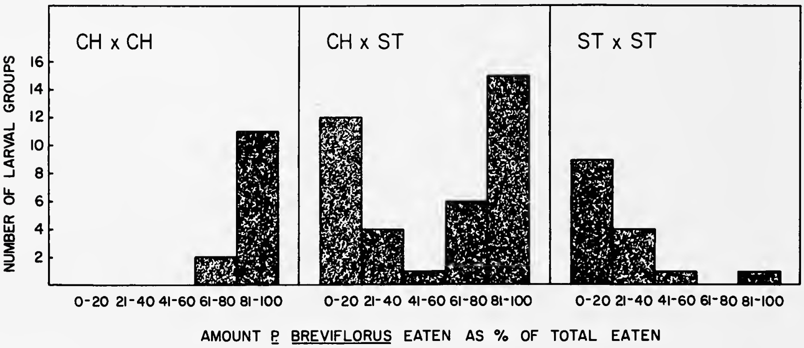

Fig. 1. The amount of *Penstemon breviflorus* eaten by *E. chalcedona* (CH × CH), *E. colon* (ST × ST) and the hybrids (CH × ST). The amount of *P. breviflorus* eaten is shown as the percent of the total amount eaten of both plant species.

Table 1. Comparison of the amounts eaten (percent) of *Penstemon breviflorus* and *Symphoricarpos albus* by *E. chalcedona*, *E. colon*, and the hybrids, after 24 and 48 hours. The data were analyzed by transforming the percentages using the arcsin transformation, and a one-way analysis of variance. Ch = Chico population of *E. chalcedona*, SP = Satus Pass population of *E. colon*.

			Mean amount eaten (%)					
			24 hours			48 hours		
Cross	♀ #	number of groups of 10 larvae	*P. brev.*	*S. albus*	p	*P. brev.*	*S. albus*	p
Ch ×Ch	1(#15)	6	21.7	1.0	<.005	60.8	2.3	<.005
	2(#10)	4	10.0	1.8	<.025	65.0	4.5	<.005
	3(#14)	3	16.7	5.0	n.s.	40.0	10.3	<.05
	total	13	15.4	2.2	<.001	57.31	4.4	<.001
SP ×Ch	4(#5)	18	9.3	6.1	n.s.	28.3	20.3	n.s.
	5(#2)	5	9.0	5.2	n.s.	44.0	19.0	n.s.
	6(#11)	6	6.8	9.3	n.s.	16.0	35.0	n.s.
	7(#12)	10	8.6	9.5	n.s.	32.5	14.5	n.s.
	total	39	8.7	7.1	n.s.	29.51	20.9	n.s.
SP ×SP	8(#9)	15	4.6	7.9	<.01	10.7	44.3	<.005

choose one of the plants, most groups eating more *S. albus* or more *P. breviflorus* (Fig. 1). Of the 39 groups of hybrid larvae, chi-square analysis showed that nine groups of larvae significantly ($p < .05$) preferred *P. breviflorus,* five groups of larvae significantly preferred *S. albus,* and 25 groups of larvae showed no significant preference for either plant. As shown in Fig. 1, however, few of the groups ate equal amounts of both plant species. In virtually all of the choice tests the larvae clearly tasted both plant species, and thus were exercising a definite choice between the two discs.

To compare the amount of variation in hybrid offspring within and between different females, I compared the amount of *P. breviflorus* eaten as a percentage of the total amount eaten of both plant species. One-way Analysis of Variance using arcsin transformed percentages showed that there was more variation within the offspring of a single female, than among the four females (Table 2). Thus there was no genetic variation in hostplant preference among the hybrid offspring of the four females.

Discussion

Larvae from the two populations of *E. chalcedona* and *E. colon* clearly showed a genetic preference for their own hostplant, while

Table 2. A. Amount of *Penstemon breviflorus* eaten by hybrid offspring as a percent of the total amount eaten of both plant species. Mean (S.D.) is given for each female. B. One-way analysis of variance comparing variation within the offspring of each female with that among individual females. Analysis performed with arcsin transformed data.

A.

	Female #			
	11	12	5	2
Percent *P. breviflorus* eaten	33.92 (32.07)	65.59 (28.45)	56.72 (39.05)	64.50 (38.13)
Number of groups of 10 larvae	6	10	18	5

B.

Source of variation	Degrees of Freedom	Sum of Squares	Mean Square	F	p
Among families	3	1955.28	651.76	.87	n.s.
Within families	35	26093.54	745.53		
Total	38	28048.81			

the hybrids were intermediate in their hostplant choice (Table 1). In general, pre-diapause larvae will attempt to feed on any plant that contains iridoid glycosides (Bowers, unpublished), although there may be differences in larval growth, survival, and digestive efficiency on hosts and non-hosts (Rausher, et al., 1982; Bowers, in prep.). Despite this general attraction of iridoid glycosides, purebred larvae in this experiment clearly chose the hostplant normally used in their population of origin. One interesting exception occurred in the offspring of the female from Satus Pass. One group of larvae ate only *P. breviflorus,* while all the others overwhelmingly preferred *S. albus* (Fig. 1). Post-diapause larvae at Satus Pass are found feeding on a *Penstemon* species, and this may be a factor in this result.

The feeding preference of the hybrid larvae overall was intermediate between that of the two parental species. Each group of ten larvae appeared to choose one of the leaf discs, but some groups chose *S. albus* and others chose *P. breviflorus.* Individual larvae were not tested, but hybrid individuals may prefer one or the other plant species, however, there appeared to be no division of the groups of larvae such that some individuals were feeding on one disc and some on the other—the larvae fed together on the same disc. As with many gregarious insect species, survival of individual *Euphydryas* larvae may be lower than that of groups, thus social facilitation or group effect is likely to be important in the feeding patterns actually observed. In these hybrid larvae, the genotype that is in the majority may guide the feeding of the rest of the group. Alternatively, all the larvae may be intermediate between the parental preferences and thus a choice is a function of factors other than genotype, such as position of the larvae.

The offspring of individual females all behaved similarly (Table 1): all purebred *E. chalcedona* larvae preferred *P. breviflorus,* and although the offspring of only one *E. colon* female were tested, these larvae overwhelmingly preferred *S. albus.* Among the hybrid larvae, some groups preferred one plant species and others the other, while some showed no significant preference (Table 1, Fig. 1). There were no significant differences among the four females in the behavior of their offspring. Thus behavior of hybrid larvae did not differ from one female to the next. Although the offspring of only one *E. colon* female were tested, these larvae overwhelmingly preferred *S. albus* (Table 1). There was no significant effect of the female on the hostplant choice of these hybrid larvae, indicating little or no genetic variation among individual females in their hostplant choice behavior. These results are in contrast with those of Tabashnik, et al. (1981), which showed significant genetic variation among individual females of *Colias eurytheme,* and Singer (1982) who found similar genetic variation in oviposition preference among individual females of *E. editha.*

Thus there is clearly a genetic component to the hostplant preferences exhibited by larvae of *Euphydryas.* However, the variation among individual females found by Tabashnik, et al. (1981) and Singer (1982) was not evident here, although the sample sizes were small. The preferences exhibited by the larvae are not absolute as larvae of both species did feed on the alternate food offered. These preferences may be important in the colonization of new population sites as well as in the incorporation of new hostplants into the existing repertoire of a particular population.

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MICRALYMMA MARINUM (STROEM) IN NORTH AMERICA: BIOLOGICAL NOTES AND NEW DISTRIBUTIONAL RECORDS (COLEOPTERA: STAPHYLINIDAE)*

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Micralymma marinum (Stroem) is an amphi-Atlantic intertidal beetle whose wide distribution in the Old World is fairly well known (Lindroth 1931, 1957; Steel 1958), but its range in North America has not been well documented. LeConte (1863) described *M. stimpsonii* from the "coast of Maine." Lindroth (1931:206) regarded this species as merely a variety of *M. marinum* and Steel (loc. cit.) listed it as a synonym of the latter. This synonymy has not been listed in North American catalogues (Leng *et al.* 1933–1948, Moore and Legner 1975) or Arnett's manual (1968). After comparing the unique type of *M. stimpsonii* (a female) with the North American specimens listed below, a specimen from Iceland identified by Lindroth (also a female), and the illustrations (including aedeagus) provided by Steel (1958), I agree that *M. stimpsonii* is synonymous with *M. marinum*. The vague type locality of *M. stimpsonii*, further south than any European records, has been the only record of the species from the United States, and although Lindroth (1957: fig. 32) mapped records from northwest, south, and southeast Newfoundland and Steel (loc. cit.) mentioned seeing specimens from there, neither provided specific locality data. Since it appears that no specific New World locality records have been published for *M. marinum*, it seems worth presenting some recently acquired data, particularly since one recent record extends the known range of the species south to Massachusetts at latitude 42° 25′N. Two specimens collected by Palmén whose records were apparently included on Lindroth's map (1957: fig. 32) are among those listed.

Unless noted otherwise ("no ecol. data"), all of the specimens listed were collected on rocks or in rock crevices in the intertidal

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zone (between high and low tide marks). The records are mapped in Figure 1. Specimens are in the collections of: American Museum of Natural History, New York [AMNH], California Academy of Sciences, San Francisco [CAS], Canadian National Collection, Biosystematics Research Institute, Ottawa [CNC], Field Museum of Natural History, Chicago [FMNH], Paul J. Johnson, Moscow, Idaho [PJJ], Museum of Comparative Zoology, Harvard University, Cambridge [MCZ], Memorial University of Newfoundland, St. John's [MUNF], University of New Hampshire, Durham [UNH], U. S. National Museum of Natural History, Washington [USNM], University Zoological Museum, Helsinki [ZMH], and the author and Alfred F. Newton, Jr., Cambridge [ANMT]. In the following records, A = adults and LI, LII, LIII = larvae of each instar.

CANADA: NEWFOUNDLAND: Change Is., Aug. 1–9, 1981, lot 6, D. Larson [no ecol. data] (12A) [MUNF, ANMT]; Grand Bruit, S. Newfoundland, N:o 55, 18.6.1949, Ernst Palmén [no ecol. data] (1A) [ZMH]; St. John Island, St. John Bay, NW Newfoundland, N:o 195, 3.8.1949, Ernst Palmén [no ecol. data] (1A) [ZMH]; 2mi S St. Pauls, VIII–1–1972, J.M. Campbell (12A) [CNC, ANMT]; same locality, VIII–10–1972, J.M. & B.A. Campbell (15A) [CNC]. QUEBEC: Mont-St.-Pierre, VII–18–1972, J.M. Campbell (1A) [CNC].

UNITED STATES: MAINE: Lincoln Co., Monhegan Island, nr. Seal Ledges, 16.VII.1982, M. Thayer & A. Newton (374A; 312L: 16 LI, 108 LII, 188 LIII) [AMNH, ANMT, CAS, CNC, FMNH, MCZ, MUNF, PJJ, UNH, USNM, ZMH]; Monhegan I., N of Calves Cove, 17.VII.1972, M. Thayer & A. Newton (22A; 12L: 1 LI, 3 LII, 8 LIII) [ANMT]; Monhegan I., Deadman's Cove, 17.VII. 1982, M. Thayer & A. Newton (1 LII) [ANMT]; York Co., Isles of Shoals, Appledore Island, 28–29.V.1983, M. Thayer & A. Newton (25A, 4 LIII) [ANMT, UNH]. MASSACHUSETTS: Essex Co., Nahant, nr. East Point, 10.VIII.1982, M. Thayer & A. Newton (2A) [ANMT, MCZ].

A further collection, undoubtedly of *M. marinum* although I have not seen the specimens, is: NEW HAMPSHIRE: Rockingham Co., Isles of Shoals, ne side of Star Island, 3 July 1981, on intertidal rocks, W. F. Gimpel, Jr., collector (W. F. Gimpel, Jr., personal communication).

There has been speculation about the natural food of *M. marinum*, but no field observations have been made. Laboulbène (1858)

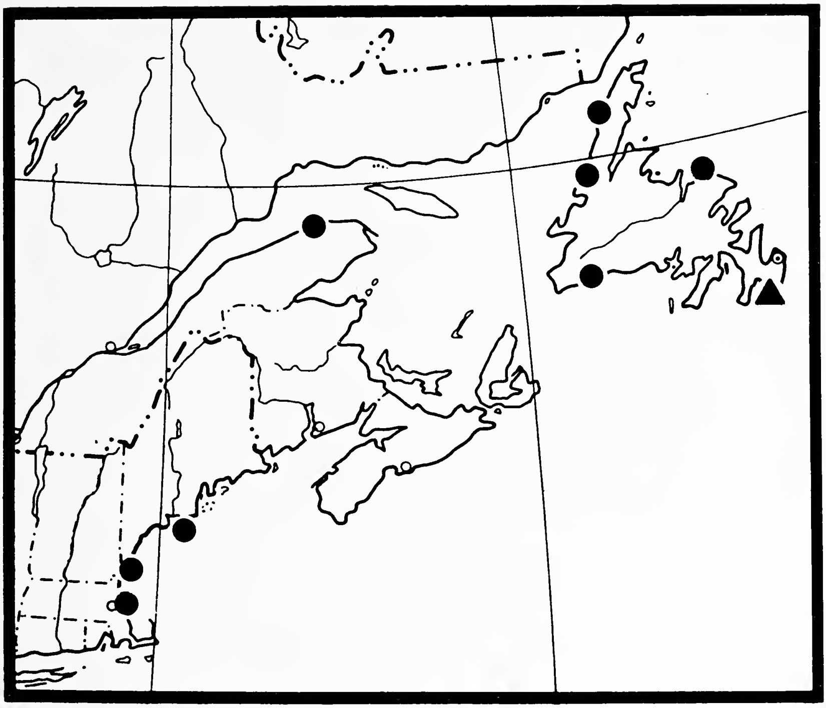

Fig. 1. Distribution of *M. marinum* in North America. Circles represent records given in text; triangle represents a record mapped by Lindroth (1957), exact locality unknown.

mentioned finding with *M. marinum* abundant "Podurelles" (probably *Anurida maritima* (Guérin)), less abundant mites, and annelids and "petits coquillages." It is not clear whether the last refers to mussels, periwinkles, barnacles, amphipods, or something else. West (1930) said that *M. marinum* are "...considered probably to prey on Thysanura," but Lindroth (1931) regarded this claim (without giving any reference for it) as very unlikely because Thysanura are not known to occur at the Iceland *M. marinum* localities. Steel (1958, 1970) stated without giving reasons that "their main food appears to be the Collembolan *Anurida maritima* (Guérin)" (Poduridae or Hypogastruridae). In my collecting I saw very few of these Collembola, some small mites, many barnacles, and many small and large amphipods in the areas where *M. marinum* was common. All except barnacles seem likely as potential food for the beetles. Beetles (both adults and larvae) that I kept in culture fed avidly on freshly-killed adult *Drosophila* spp., and were apparently still healthy after up to three and one-half months of such a diet. One third-instar larva finished its larval development feeding on these flies and pupated successfully. Clearly *Micralymma marinum* are predators, but not obligate feeders on any element of their natural habitat; their usual natural food remains uncertain.

King *et al.* (1979) suggested on the basis of collecting in southern Wales (at ca. 51°30′N) that *M. marinum* overwinter as eggs or as adults, hidden deep in rock crevices. Steel (1970) suggested on the basis of his collecting in southwestern England (at ca. 50°43′N) and in Scotland (at ca. 57°00′N) that adults overwinter and then lay eggs in May and June. One of the third-instar larvae I collected in Maine (at ca. 43°03′N) in late May pupated on 2 July and when preserved on 15 July appeared to be only a few days from adult eclosion. It appears from the last that in Maine some of the beetles may overwinter as larvae, or that the life cycle may be longer than one year. Steel (1970) found that most British Omaliinae overwinter as larvae (Thayer 1985 found the same for the North American species *Brathinus nitidus* LeConte and *Lesteva pallipes* LeConte), but *M. marinum* certainly occurs in a different habitat from most Omaliinae and is undoubtedly subjected to different selective pressures. It is possible that the life cycle varies somewhat in different parts of the species' range.

With two exceptions, the morphological features discussed by King *et al.* (1979) and Elliott *et al.* (1983) in relation to the habitat of *Micralymma marinum* are all normal features of most or all Omaliinae. The aptery of *M. marinum* is unusual, though certainly not unique, within the subfamily. Its connection with the habits of the species is open to question, however, since the other species in the genus (*M. brevilingue* Schiødte, *M. caucasicum* (Melichar)) are also apterous (Steel 1958, 1962) and *M. marinum* is the only one that is stricly marine intertidal (Steel 1962). Of perhaps more interest is the modification of the tarsal setae mentioned by both King *et al.* (loc. cit.) and Elliott *et al.* (loc. cit.). *Micralymma marinum* has, as they pointed out, flattened and widened ventral tarsal setae on the first four segments of all tarsi in both sexes. They are slightly more strongly modified in males than females, and those on the male protarsi are more distinctly flattened than those on the other tarsi. Most species of Omaliinae, if possessing flattened tarsal setae at all, have them only on the protarsi (sometimes also mesotarsi) of males (Thayer and Newton 1979; author's unpublished data), presumably aiding in grasping females during mating. The distribution of the specialized setae in *M. marinum* is very much like that found in omaliine genera whose adults are flower-inhabiting pollen feeders (*Eusphalerum, Pelecomalium, Amphichroum, Austrolophrum,* and *Anthobiomimus*). In both cases it seems to be an adaptation facilitating adhesion to the exposed surfaces on which the beetles occur (see Stork 1980, 1983), with the more pronounced development in males again presumably related to adhesion to females during mating.

King *et al.* (loc. cit.) mentioned the pupa of *M. marinum* as having "a number of long lateral setae . . . which presumably also help in maintaining position" in rock crevices. These long projections (not actually setae) are found in all described omaliine pupae (*Olophrum*, Paulian 1941; *Antarctotachinus*, Jeannel 1940; *Brathinus*, Thayer 1985) and *Microedus* (author's unpublished data). Of these, all but *Brathinus* have pairs of similar projections paramedially on the abdominal tergites as well. (Laboulbène 1858 illustrated the pupa of *M. marinum* but apparently overlooked the dorsal projections.)

Lindroth (1931, 1957) proposed that *Micralymma marinum* originated in North America and that its trans-Atlantic distribution resulted largely through passive transport of beetles by the Gulfstream, attached to pieces of seaweed, driftwood, or other flotsam. This explanation does seem ecologically, physiologically, and meteorologically plausible (Laboulbène 1858 and Elliott *et al.* 1983, immersion tolerance data; Lindroth 1931 and 1957, map of Gulfstream), but another factor that must be considered in analyzing the historical biogeography of the species is its phylogenetic relationship to the other species of the genus: where might the common ancestor of *M. marinum* and its sister-species (or sister-group) have occurred? As this phylogenetic question has not yet been explored, the question of why *Micralymma marinum* is where it is must be regarded as only tentatively answered.

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DISTRIBUTION OF INHIBITORY QUEEN PHEROMONE AMONG VIRGIN QUEENS OF AN ANT, *SOLENOPSIS INVICTA*

By A. Ann Sorensen[1,3], David J. C. Fletcher[2], and
S. Bradleigh Vinson

Introduction

While they remain in the parental nest prior to mating flights, sexually mature virgin queens of the fire ant, *Solenopsis invicta* Buren, are prevented from shedding their wings and becoming reproductively active by means of an inhibitory primer pheromone produced by the mother queen of the colony (Fletcher and Blum 1981a; 1981b; 1983). This pheromone is relatively nonvolatile and is transferred to virgin queens through physical contacts between colony members (Fletcher and Blum 1981b). When removed from the source of pheromone by separation from the mother queen, some virgin queens dealate in as little as 12 h (Fletcher and Blum 1981b). Hence, inhibitory signals must be transferred frequently to each virgin queen.

The production and transfer of inhibitory signals by the queen honeybee, *Apis mellifera,* illustrates the complexity of queen–worker communication. In 1954, Butler hypothesized that the inhibitory pheromone of the queen honeybee is distributed through food exchange among the workers. A second hypothesis, by which workers contacting a queen pick up queen substance on their bodies and then function as "substitute queens", was proposed by Verheijen-Voogd (1959). Although neither hypothesis has been disproved, most of the evidence supports surface transport as the primary mechanism of pheromone transfer (Velthuis 1972; Butler 1974). Recently, Seeley (1979) showed that physical contacts between the workers and a relatively small number of "messenger

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bees" that have been in contact with the queen during the previous 30 min are sufficient to distribute the pheromonal signal effectively.

Using the studies on honeybees as a model, first we investigated the rate at which radiolabel was transferred to virgin queens from a) food; b) the body surfaces of the mated queen, virgin queens, and workers; and c) small glass rods. The frequency of food transfer between workers and virgin queens in this experiment indicated that feeding might be involved in pheromone transfer. In a second experiment we examined whether feeding activity would increase the quantity of radioactive tracer transferred from the surface of the mother queen to the virgin queens.

MATERIALS AND METHODS

Rate of transfer of food and surface materials.

A total of 21 monogynous colonies of *S. invicta* were obtained from the field at College Station, Texas and their composition was standardized so that each consisted of about 20,000 workers, 40 cm3 of worker brood, a moderately physogastric mated queen, and 400 sexually mature virgin queens. These colonies were fed on a diet of insects and 50/50 (wt/wt) honey solution and kept at a temperature of 26° C. Colonies were housed in 2 artificial nests made of plaster of paris inside large plastic boxes. A bridge connected the nest box to a foraging arena (Mirenda and Vinson 1982). Colonies were fed continuously before and during testing.

To determine whether food transfer between workers and virgin queens occurred in substantially less than the 12 h required for the first virgins to dealate after orphaning, egg albumin and egg yolk powder were labeled with 125 Iodine (Sorensen and Vinson 1981) and offered singly to foragers along with the normal food supply. Beginning 15 min after the first forager re-entered the nest after leaving this food source, random samples of 10 virgin queens were taken every 15 min, alternating between the two nests for a total period of 2 h. Radiation was measured individually using a Searle 1195 gamma radiation counter. The threshold criterion for the presence of radiolabel was any level of radiation above that of the background radiation plus two standard deviations. Disturbance to the colony was reduced by wearing face masks during sampling to eliminate exposure of the colony to breath CO_2 (Wilson 1971) and by returning the cover of the nest as soon as possible. Each treatment was repeated three times, using a total of six colonies.

Secondly, the rate at which radiolabeled albumin was distributed to virgin queens from the body surface of the mated queen was determined. The mated queen was dipped in ^{125}I-albumin mixed in phosphate buffer, taking care to avoid contamination of her mouthparts, and allowed to dry for 10 min before returning her to the colony. Samples of virgin queens were taken as before. Roughly 1 picogram (10^{-12}gm) of radiolabeled protein adhered to each queen, a quantity not detectable by workers (Sorensen and Vinson 1981). For comparison, a virgin queen, freshly freeze-killed in dry ice with her wings removed, was similarly dipped to determine the rate of distribution of surface materials among virgin queens. Virgin queens inhibited by the mother queen do not themselves produce the inhibitory pheromone (D. J. C. Fletcher, unpublished data). To correlate grooming with transfer of radioactivity, we also treated and tested freshly killed mother queens, two dead major workers together, and a siliconized glass rod (approximately the same surface area of the queen). Killing prevented these from distributing the radiolabel themselves through contact with other workers. Each treatment was repeated three times using a different source colony each time, a total of 15 colonies. Results were analyzed by comparing slopes of the cumulative number of virgin queens labeled vs. time (Newman-Keuls test) (Zar 1974). Quantities of egg yolk and albumin found in virgin queens were compared using the Kruskal-Wallis ANOVA and Post hoc test.

The role of food in pheromone transfer.

If virgin queens were fed rapidly and frequently enough, the inhibitory pheromone could be passed to them by contaminated workers during feeding. We examined this possibility by dividing small plastic nests in half using a wire screen which prevented passage of ants from one side to the other, thereby limiting contact to trophallaxis and antennal contact (Fletcher and Blum 1981b). After withholding food from the source colony for 24 h, 74 workers, 35 larvae, 15 virgin queens, and the mated queen were removed and the queen together with 37 workers and the larvae placed on one side of the screen, the virgin queens and remaining workers on the other. The mated queen was then removed, dipped in ^{125}I-albumin and returned. After 30 minutes, the radioactivity in each virgin queen was measured (Trial A). The queen was redipped and placed in a clean divided box with new workers, virgin queens, and larvae from the same source colony. Food (*Heliothis* pupae) was added to the queenright side (Trial B) and the experiment repeated. Subsequent trials were conducted with food on the queenless side (Trial C), and, after removing the workers tending the virgin queens, placing food with the virgin queens (Trial D) and placing food on the queenright side (Trial E). These trials were repeated using five other source colonies for a total of 6 replications. Results were analyzed using Scheffe's test to compare mean cpm (counts per minute) per virgin queen.

Each mother queen was weighed as a measure of her degree of ovary development and the quantity of radiolabel removed after each trial determined. Weight loss in fire ant queens is correlated with loss of fecundity and diminished production of inhibitory primer pheromone (Fletcher and Blum 1983). Thus, the weight of our queens could affect the quantity of radiolabel removed and the number of virgin queens labeled.

RESULTS

Rate of transfer of food and surface materials.

Using radiolabeled protein we determined how rapidly radioactivity was distributed from various sources to the virgin queens. When radiolabeled egg yolk or egg albumin was placed in the foraging chamber, 60–100% of the alates sampled contained radiolabel after 15 min. During the first two trials, egg yolk was fed more rapidly to virgin queens than was albumin ($F_{1,4} = 217.3$, $p < 0.001$)(Figs. 1, 2). In addition, the amount of radiolabel retained indicated that virgin queens received 5–30 times more egg yolk by weight than albumin, reinforcing our observations that albumin was not brought into the nest as readily as egg yolk (data not shown). The location of the mated queen in the nest with respect to the virgin queens tested did not significantly affect the distribution of food. During the third trial (C) we noticed that some of the virgin queens in our nests were dealating, indicating that they were no longer receiving adequate levels of pheromone from the mated queen. This was possibly due to weight losses sustained by the queens of 20–30% before beginning the last trial (Fletcher and Blum 1981b). During

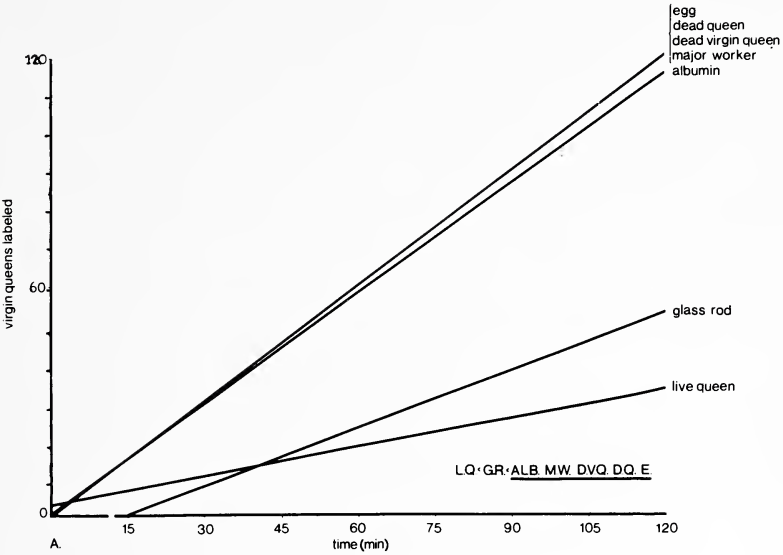

Figure 1. Linear regression analyses on the cumulative number of virgin queens receiving radiolabel during the first trial (A) after the introduction of radiolabeled egg yolk (E) or radiolabeled egg albumin (alb), the reintroduction of the live mated queen (LQ) or freshly killed mated queen (DQ) surface labeled with radiolabel or the introduction of a glass rod (GR), 2 dead major workers (MW), or a dead dewinged virgin queen (DVQ) surface labeled with radiolabel. A total of 10 virgin queens were sampled in each colony at 15 min intervals for a total of 120 virgin queens over the 2 h period. Slopes of the underlined groups do not differ at $p < 0.05$ (Newman-Keuls Test).

these trials the quantity of food fed to the virgin queens dropped significantly ($p < .05$) although the majority were still fed (data not shown).

Virgin queens became radiolabeled more rapidly from the surface of dead queens than from the surface of live queens in two of the three trials (Figs. 1, 2). In the third trial, significantly more virgin queens received radiolabel from the surface of the live queen than from the dead queen (Fig. 3). Virgin queens in the same nest as the queen did not receive significantly more radioactivity than virgin queens in the second nest (data not shown).

There was marked variation in the rate at which radiolabel was transferred to virgin queens from the surface of a small glass rod, 2

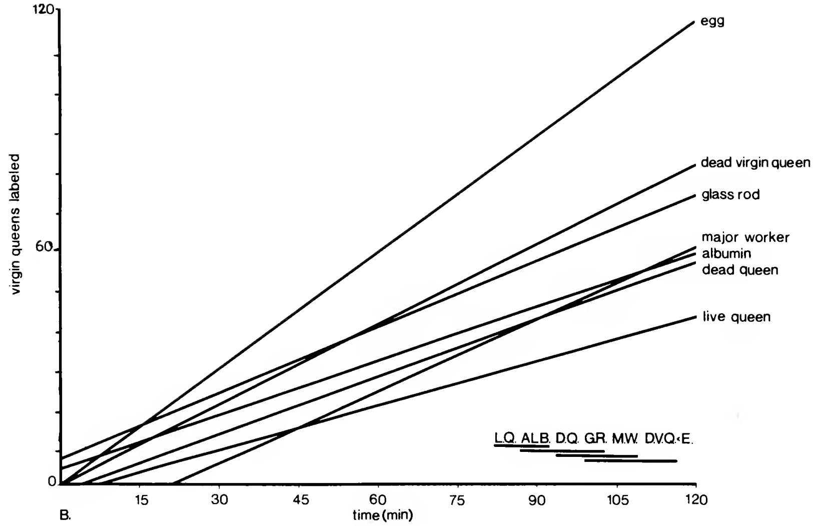

Figure 2. Second trial (B). See Figure 1 for details.

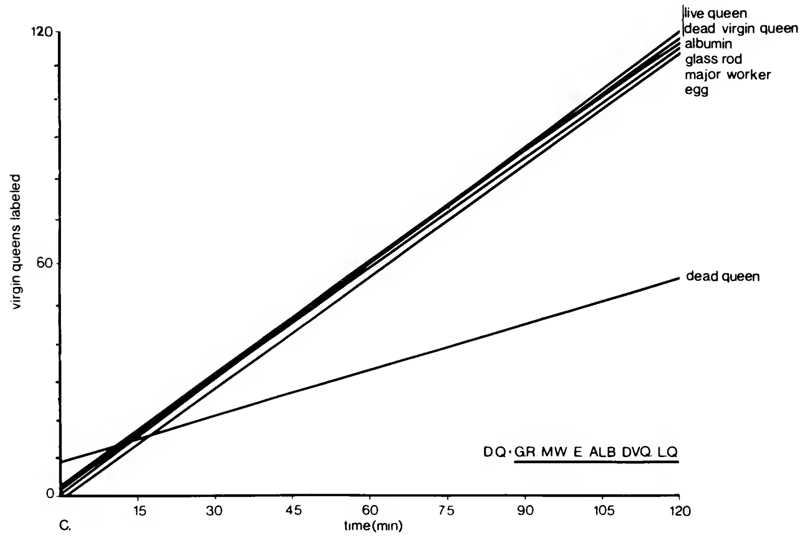

Figure 3. Third trial (C). See Figure 1 for details.

dead major workers, and a dead dewinged virgin queen (Figs. 1,2,3). In all three trials, more virgin queens received radiolabel from the surface of the dead dewinged virgin queen than from the glass rod ($F_{2,18} = 79.3, p < 0.001$). In two of the trials, virgin queens received slightly more radiolabel from the glass rod than from the surface of the dead major workers (Figs. 2,3) but in one (Fig. 1), significantly fewer virgin queens received radiolabel from the glass rod than from the major workers. The location of the virgin queens in the nests with respect to the glass rods or dead dewinged virgin queens did not affect the rate of distribution of radiolabel. Significantly more virgin queens from the nest with the queen and treated major workers contained radioactivity than those taken from the second nest ($F_{1,4} = 15.1, p < 0.05$).

Combining the results of the three trials, within 120 min 98% of the virgin queens sampled received radiolabeled egg yolk; 87% received radioactivity from the surface of dead dewinged virgin queens; 82% received radioactivity from the surface of dead major workers; 79% received radiolabeled albumin; 68% received radioactivity from the surface of the glass rod; 65% received radioactivity from the surface of a dead mated queen; and 53% received radioactivity from the surface of a live queen. All were significantly different ($F_{6,28} = 127.6, p = 0.001$) except for the number of virgin queens receiving radioactivity from either a) radiolabeled albumin or dead major workers and b) glass rods or dead queens.

Role of food in pheromone transfer.

Since 98% of the virgin queens sampled were fed radiolabeled egg yolk within 2 h, we examined the possibility that the presence of food might increase the quantity of radioactivity transferred from the surface of the queen to the virgin queens by encouraging food transfer and subsequent surface contacts among workers and queens. The results are given in Figure 4 as the mean number of cpm per virgin queen. Virgin queens tended by workers were separated from the queen, workers, and brood by a fine screen that permitted trophallaxis but restricted grooming. Only the mated queen was surface labeled and the distribution of radioactive tracer from 1 side to the other was dependent on trophallaxis or antennal contacts through the wire mesh. The virgin queens in Trial C, where food was

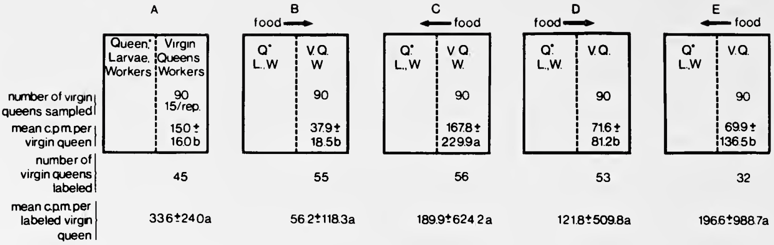

Figure 4. Number of virgin queens containing radioactivity following reintroduction of the mated queen who was surface labeled with radiolabel (*). Five trials (A-E) were conducted on each of 6 colonies with no food, food on the queenright or queenless side, and virgin queens with or without workers. Boxes were divided with screens which allowed trophallaxis and limited antennal contact. Radioactivity (counts per minute or cpm) was measured after 1 h. Results are given as means and standard deviations for all virgin queens measured (within boxes) and for only those virgin queens that received radioactivity (below boxes). Means followed by the same letter in each row are not significantly different at $p < 0.05$ using Scheffe's Test.

placed on the queenless side, received significantly more label than the virgin queens in all other trials (Scheffe's test). Proteinaceous food is normally directed toward the queen and brood (Sorensen and Vinson 1981) so Trial C closely approximated normal food flow conditions. Fewer virgin queens received radioactive tracer (and less of it) when food was absent than when food was present but differences were not statistically significant. Untended virgin queens received radioactivity indicating that workers on the queenright side contacted them through the screen (Trial E) and, when food was placed near them, untended virgin queens contacted workers on the queenright side (Trial D).

The weights of the mated queens used ranged from 16.8 mg to 19.6 mg, considered marginally physogastric by Fletcher and Blum (1983). There was a strong correlation between the weight of the queen and the number of virgin queens receiving radioactivity ($y = 15.71x - 257$, $r_2 = 0.67$). The mean percentage of radiolabel remaining on the queen after each trial ranged from 21–39%. This contrasts with a mean of roughly 6% left in the first experiments. The weight of the queen was also strongly correlated with the quantity of radiolabel removed ($y = -0.05x + 1.26$, $r_2 = 0.65$). As the queens decreased in weight, less radiolabel was groomed from their surface and the number of virgin queens receiving radiolabel decreased.

DISCUSSION

The transfer of food and surface materials to virgin queens in fire ant nests was very rapid. This indicated that rapid transmission of signals or pheromones throughout a colony via trophallaxis, physical contact, and/or mutual grooming was possible. Proteinaceous foods reached the virgin queens within 15 min and up to 98% had received egg yolk after 2 h, well within the 12 h period after which pheromonally disinhibited virgin queens begin to dealate (Fletcher and Blum 1981b). This was expected. In polygynous colonies with 400 workers, queens, brood, and no reproductives, egg yolk is distributed to all of the workers and 80% of the larvae within 10 min (Sorensen et al. 1981) and, in colonies with 4,000 workers, to 95% of the workers and 85% of the larvae within 1 h (Sorensen and Vinson 1981). Results from our third trial indicated that virgin females received significantly less food in colonies when the mated queen was no longer producing enough pheromone to prevent dealation. This suggests that decreased food transfer could have minimized the transfer of pheromone and led to dealation. However, this decrease in feeding could also have been caused by the disruption in normal food distribution as workers began to execute dealates.

The high percentage (68–87%) of virgin queens receiving radioactivity from the surface of dead virgin queens, dead major workers, and glass rods showed that grooming activities and physical contacts between workers and virgin queens were extensive. Mirenda and Vinson (1981) found that active *S. invicta* workers spend 78% of their time grooming themselves, other ants, or being groomed. However, since fire ant workers respond to fresh corpses with vigorous and extended inspection (Blum 1970; Howard and Tschinkel 1976) an initial burst of grooming and inspection by many workers followed by seizure and disposal of the corpses could have been responsible for spreading radioactivity rapidly through the colony. More virgin queens received radioactivity from the virgin queen corpses than from the major worker corpses, although the difference was not statistically significant. Virgin queen corpses may produce competing odors that mask necrophoric signals, delaying their removal and increasing worker–queen corpse contact. The extent of transfer of radioactivity from the virgin queen corpses may indicate that live virgin queens are also groomed and contacted frequently by workers. Workers exhibited aggressive behavior towards the glass rods and large numbers of workers came into contact with them. The high number of radiolabeled virgin queens resulting from all of these encounters showed that contaminated workers either fed, groomed, or contacted them frequently. This rate of distribution of radioactivity suggested that there was a very high level of contact between colony members. This indicates that all pheromones could be rapidly distributed regardless of their origin. This is of considerable general interest and supports hypotheses of pheromonal control of behavior in social insects (Wilson 1971).

Radiolabel was removed from both the dead mated queens and live mated queens and transmitted to over 50% of the virgin queens within 2 h. Radiolabel was transmitted to more virgin queens from mated queen corpses than from live queens in two of the three trials, possibly because a greater number of workers have access to a dead queen. Seeley (1979) has shown that honeybee workers collect queen substance most heavily when the queen is stationary. Since the live queens used in our study were disturbed frequently by sampling, periods in which they remained stationary were limited. This could have reduced the number of worker–queen contacts and thus the quantity of radiolabel removed. Although radiolabel from the surface of live mated queens was transmitted to virgin queens at a slower rate, its transfer was still rapid enough to insure that it would have reached all of the virgin queens in less than 12 h.

Examining the effect of food distribution on the transfer of radioactivity from live queens to virgin queens, we found that the presence of food increased the quantity of radiolabel transferred. Although not conclusive, our results suggested that food exchange may have been involved in signal transfer. We realise that these results could be misleading. A similar experiment with well fed queenless honeybee workers on 1 side of a wire mesh screen and starved queenright workers on the other side also showed that the queenright group passes "information" to the queenless group during transfer of food but that food and information travel in opposite directions (Verheijen-Voogd 1959). Also, recent research supports surface transport over food exchange as the primary mechanism of honeybee queen substance transmission (Seeley 1979). On the other hand, food exchange between workers has been implicated in the transfer of pheromone produced by immature honeybee queens (Free and Ferguson 1982). Because the frequency and extent of food transfer to virgin fire ant queens is high, we cannot rule out food exchange as the primary mechanism for the transfer of inhibitory queen pheromone in fire ant colonies.

Our results from the second experiment also agree with the hypothesis that the quantity of inhibitory pheromone produced is positively correlated with fecundity of the mother queen (Fletcher and Blum, 1983). The mated queens used in this study were only slightly physogastric, thus evidently limiting both the amount of inhibitory pheromone produced and their attractiveness to workers. As predicted, the quantity of radioactivity removed and transferred to virgin queens decreased as the weight of the mated queens decreased.

SUMMARY

Two ways in which an inhibitory queen pheromone of the ant, *Solenopsis invicta* Buren might be distributed by workers to virgin queens in a colony, trophallaxis and surface transport, were investigated.

Using a nonvolatile radiolabeled protein in quantities nondetectable to the ants, evidence suggested that physical contact was an efficient mode of transmission for inhibitory pheromone. On the other hand, when radiolabeled material was incorporated into food, virgin queens quickly received it. A second study indicated that the transfer of food between workers and virgin queens increased the amount of surface contact and grooming and thus could aid in the distribution of inhibitory pheromone. This suggests that trophallaxis may be an additional means of distributing queen pheromones in this species.

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SPONTANEOUS POLYDOMY IN LABORATORY COLONIES OF THE ANT *LEPTOTHORAX CURVISPINOSUS* MAYR (HYMENOPTERA; FORMICIDAE)

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Introduction

Leptothorax curvispinosus Mayr is a small, common ant in eastern North America where it often nests in such preformed cavities as hollow acorns, hickory nuts, galls, stems and twigs. Its range and nesting preferences overlap broadly with those of two closely-related species, *L. ambiguus* and *L. longispinosus* (Creighton 1950; Alloway et al. 1982). Colonies within this group are both intra- and interspecifically aggressive; and although normally considered nonparasitic, they occasionally engage in facultative interspecific slavery, apparently by capturing and rearing brood from one another's colonies. Facultative intraspecific slavery may occur more frequently (Alloway 1980). In addition, these species serve as hosts for the obligatory slave-makers *Harpagoxenus americanus* and *L. duloticus* (Alloway 1979; for terminology see Stuart and Alloway 1983). All five species coexist in some areas, nest in close proximity to one another, and form dense local populations (Alloway et al. 1982; Del Rio Pesado and Alloway 1983).

Approximately one third (36.3%) of individual *L. curvispinosus* nests (e.g. single acorns) are queenless, while about half (46.7%) are monogynous, and the remainder (17.0%) are polygynous (Headley 1943; Talbot 1957; Alloway et al. 1982). Dissections have shown that polygyny in this species is more than just a superficial phenomenon with over 90% of the queens in polygynous nests being inseminated and reproductive. Moreover, young queens often coexist with older queens, indicating that established colonies may

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become secondarily polygynous by accepting young queens into their nests (Alloway et al. 1982; for a review of polygyny in ants see Hölldobler and Wilson 1977). The large proportion of queenless nests led Sturtevant (1927) and Talbot (1957) to suggest that colonies may occupy multiple nests (polydomy); and Sturtevant (1927) provided some experimental evidence for this hypothesis by noting that nests found relatively close together in nature were occasionally non-aggressive toward one another. Similar evidence indicates that colonies of *L. ambiguus, L. longispinosus* and *H. americanus* can be polydomous as well (Alloway et al. 1982; Del Rio Pesado and Alloway 1983).

The discovery of polygyny and polydomy in this group of ants raises numerous questions concerning the structure of colonies and local populations. Colonies possessing these characteristics may be capable of existing indefinitely, and of spreading out and occupying large areas of suitable habitat. Such "super colonies" are highly developed in other groups of ants with these characteristics (e.g. *Formica yessensis* Forel, Higashi and Yamuchi 1979). In addition, there are many questions regarding factors which induce polydomy (both proximately and ultimately) and the social ramifications of this colony structure (see Werner et al. 1979). Leptothoracine ants are especially amenable to laboratory culture and provide an unusual opportunity for the experimental study of polydomy. In the present experiment, *L. curvispinosus* colonies (or colony fragments) were collected from individual nests in nature and provided with multiple artificial nests in the laboratory for an extended period of time. The purpose of the experiment was to discover whether colonies would become polydomous (i.e. "bud", see below) spontaneously under relatively simple laboratory conditions.

Traditionally, the term "budding" has been used to refer to true colony fission in which a group of workers and one or more reproductives depart from the parental nest to form an autonomous daughter colony (see Wilson 1971). However, for polydomous species, the term "budding" has also been used to describe the formation of non-autonomous secondary nests which at least initially may be queenless (e.g. Higashi 1976). In general, the relative autonomy of individual nests as reproductive units within polydomous colonies is debatable, and it is possible that such nests occasionally become isolated and achieve full autonomy (see Alloway et al.

1982). For these reasons, and for convenience, I suggest the continued use of the term "budding" to refer to the formation of daughter nests which contain brood and are spatially distinct from the parental nest, but which may or may not contain reproductives, and which may or may not become truly autonomous.

MATERIALS AND METHODS

The 57 colonies in this experiment were collected in early June from acorns and hickory nuts at several sites in the vicinity of Harpersfield, Ohio. The inhabitants of each nest were treated as separate colonies and established in separate artificial nests and foraging dishes in the laboratory (see Alloway 1979). The artificial nests were composed of two parts. The nest base consisted of the top of a small plastic petri dish (dia = 4.0 cm; ht = 0.5 cm) painted green and drilled with a small hole (dia = 0.3 cm) in one side to serve as a nest entrance. The nest lid was made of transparent orange Plexiglas, milled with a groove so as to fit tightly onto the nest base. With the lid in place, the internal volume of these nests was approximately 4 cm^3 (± 0.2). Each artificial nest was housed in a foraging dish consisting of a large plastic petri dish (dia = 14.5 cm; ht = 1.5 cm). Each foraging dish also contained a water bottle (dia = 1.1 cm; length = 3.5 cm) stoppered with cotton and held in place at one side of the dish by a dab of plasticene. A microscope slide (2.5 × 7.5 cm) served as a food platter in each dish. Water bottles were refilled weekly, and fresh food was added to the food platter 3 times per week. The food was similar to that formulated by Bhatkar and Whitcomb (1970), but was prepared in bulk, frozen, and then thawed prior to use. Food platters were replaced periodically. The colonies were cultured on open laboratory benches illuminated by fluorescent lights mounted approximately 50 cm above the bench surface and providing an illumination of 1830–2150 lux. A daily photoperiod of 14L:10D, and a temperature of 22°C ± 1° were maintained.

The experiment was initiated in early July, by adding a second artificial nest to each foraging dish, such that the two nest entrances were facing each other, approximately 4–5 cm apart. Each colony was briefly observed for budding on days 1, 2, 5, 11, 13, 18, 29 and 76 following initiation. A colony was considered to be polydomous if brood was present in both artificial nests when observed.

Table 1. Census of adults in each nest at the beginning of the experiment: ♀d = dealate queens, ♀a = alate queens, ♂ = males, ☿ = workers (± 2). The figure in brackets after the ♀d count indicates the number of dealate queens that were present in the nest at the time of collection. Asterisks (*) indicate colonies which budded during the experiment (see Figure 1).

#	♀d	♀a	♂	☿	#	♀d	♀a	♂	☿	#	♀d	♀a	♂	☿
1*	2 (1)	2	0	150	20	1 (1)	3	0	55	39	1 (1)	0	3	40
2	1 (1)	0	0	45	21	3 (0)	4	4	35	40	0 (0)	0	18	15
3	0 (0)	0	7	10	22	1 (1)	0	0	45	41	2 (1)	0	0	130
4	11 (1)	6	0	155	23	1 (1)	0	0	20	42	9 (1)	4	28	20
5*	18 (1)	8	7	60	24	1 (1)	1	0	45	43	1 (1)	0	0	35
6	3 (3)	0	0	85	25	2 (1)	0	0	90	44	3 (0)	24	1	20
7	0 (0)	0	0	70	26	1 (1)	0	0	50	45	2 (1)	0	4	90
8*	0 (0)	0	5	30	27	2 (2)	0	0	25	46	3 (1)	7	0	90
9	6 (1)	0	0	75	28	1 (1)	0	0	50	47	1 (1)	0	0	30
10	1 (1)	0	0	45	29	4 (1)	0	0	60	48	15 (1)	4	1	90
11*	2 (1)	5	0	75	30	1 (1)	0	0	50	49	12 (1)	4	0	55
12	0 (0)	8	0	50	31	1 (1)	0	0	70	50*	2 (1)	3	1	75
13	1 (1)	0	0	105	32	1 (1)	0	0	95	51	3 (1)	12	0	30
14*	1 (1)	0	0	105	33	1 (1)	0	0	45	52*	7 (2)	13	2	90
15*	6 (2)	18	0	160	34	1 (1)	0	0	80	53	3 (0)	3	1	10
16	0 (0)	2	11	40	35	1 (1)	0	0	60	54	0 (0)	6	2	35
17*	3 (2)	0	0	110	36	1 (0)	5	22	15	55	1 (0)	8	0	15
18*	1 (2)	1	0	130	37	8 (0)	5	25	15	56	1 (1)	4	5	55
19*	2 (1)	5	0	60	38	13 (0)	7	0	10	57*	14 (1)	6	0	170

Colonies remained undisturbed except for these observations and the normal maintenance indicated above. The data were analysed using Chi-square tests and Student's t-tests. Chi-square tests involving one degree of freedom employed a correction for continuity, and all comparisons of census data with t-tests utilized a square root transformation (Parker 1979).

Census data for each colony are given in Table 1. Between the time the colonies were collected and the initiation of the experiment many of the larger larvae pupated and eclosed to produce workers, alate females and males. Many of the young queens subsequently became dealate, and at least some appeared to function as workers. Nonetheless, males and females were observed flying about in their foraging dishes, and some mating between siblings may have occurred, although none was observed. None of the queens was dissected in this study, and hence the reproductive status of both young and old queens remains unknown. Little colony growth occurred after the initiation of the experiment.

The queen status of colonies at the beginning of the experiment often differed from their queen status at the time of collection due to the occasional death of queens or the dealation of offspring (see Table 1). At the beginning of the experiment, there was no significant difference in the number of workers present in colonies which were queenless, monogynous or polygynous at that time (t-tests, $P > 0.05$). However, worker numbers at the beginning of the experiment did vary depending on what the queen status of colonies had been at the time of collection, with originally queenless colonies having significantly fewer workers than colonies which had been either monogynous ($t = 4.241$, $df = 49$, $P < 0.001$) or polygynous ($t = 3.347$, $df = 18$, $P < 0.01$) when collected. This variation will be considered in the analysis of the results.

RESULTS

During the course of the experiment, 12 of the 57 colonies (21.1%) became polydomous (see Table 1 and Figure 1). Six colonies were observed to be polydomous on Day 1 (10.5%); and 2 more became polydomous by Day 2 (14.0%). Thereafter, the number of polydomous colonies fluctuated between 2 and 7 (3.5–12.3%). Some colonies appeared to remain polydomous only briefly (e.g. #8, #19), but others apparently persisted in this condition for long periods (e.g. #1, #15, #17, #52, #57) (see Figure 1). One colony (#52) appeared to remain polydomous for the entire experiment (76 days). Two colonies became polydomous, reverted to monodomy, and then again became polydomous (#14, #15). Other colonies may also have undergone repeated fissions and fusions between observations.

There was no discernible pattern to how polydomous colonies distributed themselves between the two nests. Often only a few workers and larvae were present in the second nest, but at times large segments of the colonies including dealate queens and alate reproductives could be found in the second nest. The distribution for particular colonies tended to fluctuate between observations, and often the second nest (or the original nest) gradually became depopulated over several days prior to fusion. These kinds of fluctuations indicate that polydomy in these ants is a very dynamic phenomenon and provide considerable scope for future research.

Budding occurred in queenless, monogynous and polygynous colonies containing from 30 to 170 workers (see Table 1), but colony

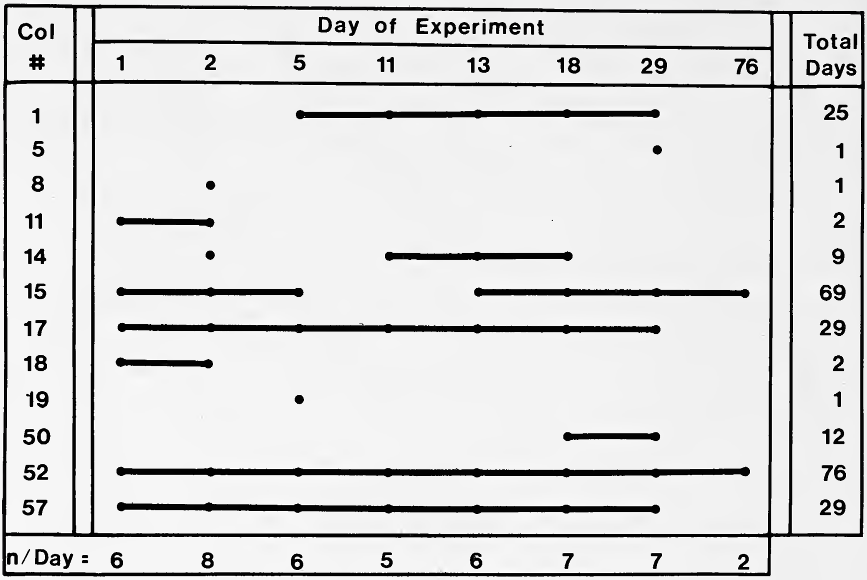

Fig. 1. Occurrence and apparent duration of spontaneous polydomy for all colonies which budded during the course of the experiment. Indicated are colony numbers (Col #), day of experiment on which polydomy was observed (Day of Experiment), number of colonies which were polydomous on each observation day (n/Day), and total number of days over which each colony appeared to remain polydomous (Total Days).

size (as indicated by the number of workers) appeared to have a significant influence on polydomy (see Figure 2). Budding occurred in 11 of 26 colonies (42.3%) which contained 60 or more workers, but in only 1 of 31 colonies (3.2%) with less than 60 workers ($\chi^2 = 9.40$, df = 1, $P < 0.01$). Overall, colonies which budded were significantly larger than those which failed to do so (t = 3.554, df = 55, $P < 0.001$). This relationship held even if colonies which were queenless when collected (n = 14) were omitted from the analysis (t = 3.268, df = 41, $P < 0.01$); or if colonies which were either queenless (n = 14) or polygynous (n = 6) when collected were omitted (t = 2.134, df = 35, $P < 0.05$). Among colonies with 60 or more workers there was no significant difference in size between colonies which budded and those which did not (t = 1.305, df = 24, $P > 0.05$).

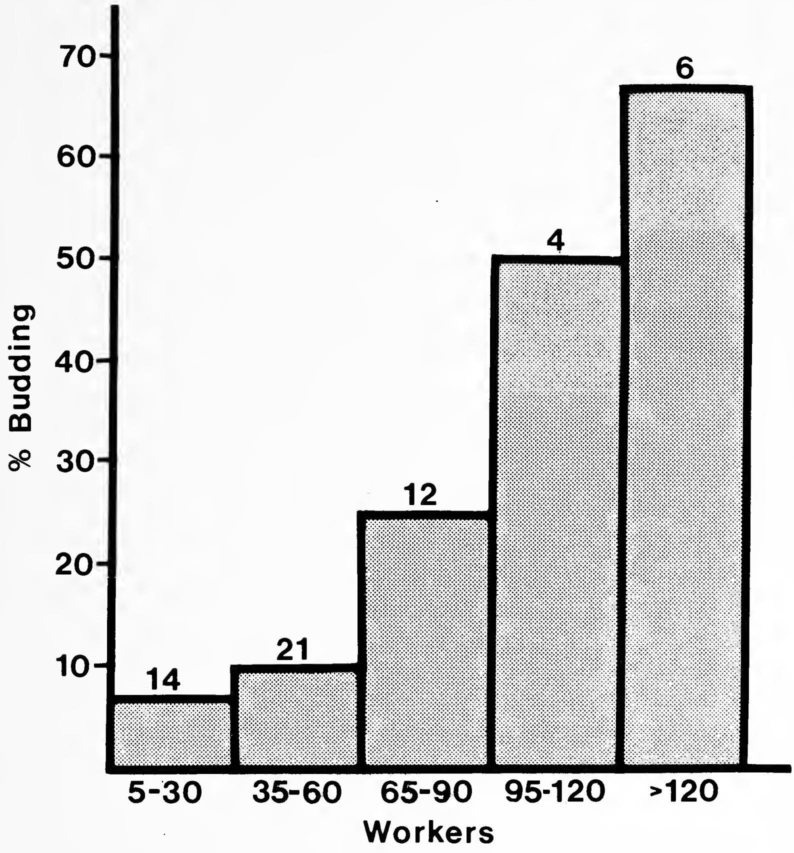

Fig. 2. The relationship between the occurrence of spontaneous polydomy and colony size, as indicated by plotting percent budding relative to the number of workers present. The number of colonies in each size category is indicated above each bar. The significance of this relationship is discussed in the text.

It is possible that polygyny may influence the occurrence of polydomy. In this study only 6 colonies were polygynous when collected; and the 4 of these which budded were fairly large (see Table 1). However, this sample is too small for meaningful statistical comparisons. By the time the experiment was initiated, many colonies had become at least superficially polygynous due to the dealation of offspring. However, colonies which were polygynous at this time (n = 27) did not bud more frequently than other colonies ($\chi^2 = 2.65$, df = 1, $P > 0.05$); and, within this group, colonies which budded were significantly larger than those which failed to do so (t = 2.365, df = 25, $P < 0.05$).

Discussion

The results of this study provide further empirical evidence for the existence of polydomy in *L. curvispinosus* colonies (see Sturtevant 1927). Moreover, these results demonstrate that at least some of the factors which are capable of inducing polydomy in these ants remain active under relatively simple laboratory conditions. The observed relationship between colony size and the occurrence of polydomy suggests that space limitations within nests could be a factor promoting polydomy. Nesting sites such as hollow nuts and twigs might well impose this kind of limitation on colonies in nature. However, other factors associated with colony size, age or maturity could also be involved. Furthermore, it is likely that various factors can effectively induce polydomy in species in which colonies are capable of existing in this condition. In nature, colonies might become polydomous in response to the distribution of food around their nests or to exploit different humidities or temperatures in different nests, perhaps selectively distributing their brood or reproductives in this manner. The present experiment, with its uniform plastic nests and simplistic foraging environment, provided little opportunity for these kinds of factors to operate.

Among leptothoracine ants, a polydomous colony structure could have various important ramifications, depending at least in part on the relative degree of contact between nests within colonies. This colony structure might affect the way in which reproductive rights are apportioned among different queens and workers (see Wilson 1974a, b; Cole 1981; Franks and Scovell 1983), and it might influence the relative susceptibility of colonies to social parasites (see Alloway et al. 1982; Del Rio Pesado and Alloway 1983). Indeed, the combination of polygyny and polydomy is thought to have been an important factor in the evolution of various forms of social parasitism (Buschinger 1970; Alloway 1980).

The existence of polydomy in these ants may explain a peculiar element of their nest emigration behaviour. Möglich (1978) investigated this behaviour in various *Leptothorax* species, including *L. curvispinosus* and *L. longispinosus*, and found that these ants typically use both tandem running and adult transport as recruitment techniques during emigrations. Tandem running is a chemical recruitment technique in which one ant leads a single follower between two points. The response is mediated by a pheromone originating in the leader's poison gland and extruded from its sting (see Möglich et al. 1974; Möglich 1979; Stuart and Alloway 1983). Workers which are led to a new nest in this manner subsequently become recruiters themselves and lead or carry other ants to the new nest. However, most colony members, including workers, are merely carried to the new nest, and do not otherwise become involved in the emigration. The unusual element in this nest emigration system is that in many *Leptothorax* species tandem runs also occur in the reverse direction, from the new nest back to the old nest. Möglich could not rationalize the existence of these "reverse tandem runs" and, using colonies that were emigrating from a single occupied nest to an unoccupied nest, such recruitment appeared to contribute nothing to the efficiency of the emigration. However, if these species are frequently polydomous, emigrations may most commonly occur from one occupied nest to a second occupied nest, and reverse tandem runs could serve to recruit workers from the second nest to assist in the emigration. Thus, the discovery of polydomy may explain the existence of reverse tandem runs; and since this behaviour appears to be so widespread among leptothoracine ants, it is possible that polydomy is also more common than we yet realize.

SUMMARY

Leptothorax curvispinosus colonies derived from single nests in nature will frequently occupy multiple nests under simplified laboratory conditions. Spontaneous polydomy of this type is apparently related to colony size. When budded, the relative distribution of a colony between alternative nests tends to fluctuate, and repeated fissions and fusions occur. These results provide further experimental evidence for polydomy in this species.

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SYNONYMY OF *PSEUDOBERIS* ENDERLEIN WITH *NOTHOMYIA* LOEW, WITH NOTES ON THE GENUS AND A KEY TO THE SOUTH AMERICAN SPECIES (DIPTERA: STRATIOMYIDAE)*

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Pseudoberis Enderlein (1921: 227) was erected for a single specimen of a new species, *P. fallax* Enderlein, from Brazil. The species is still known only from the unique holotype. Enderlein believed that, despite its "habitus gleicht sie auffälig *Beris* Latr.", the genus was related to *Chloromelas* Enderlein, and placed it in the tribe Stratiomyiini of the subfamily Stratiomyiinae. Unfortunately, the genus and the publication within which it was described were overlooked by James (1973), and the taxon has remained unknown to subsequent authors. I have recently examined Enderlein's holotype, which has resulted in proper taxonomic placement of this taxon.

Genus *Nothomyia* Loew

Nothomyia Loew, 1869: 4. Type-species: *N. scutellata* Loew, by designation of Brauer, 1882: 88.

Pseudoberis Enderlein, 1921: 227. Type-species: *P. fallax* Enderlein, by original designation. NEW SYNONYMY.

Berisargus Lindner, 1933: 201. Type-species: *B. borgmeieri* Lindner, by monotypy.

Remarks. Pseudoberis clearly belongs within the tribe Prosopochrysini as defined by James (1942, as Myxosargini), which is placed in the Stratiomyinae by most authors. Important character states, which are exhibited by all members of the tribe, include a generally slender body form, antennal flagellum with six flagellomeres, scutellum usually with two apical spines, crossvein m–cu

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present, vein A_1 slightly though distinctly sinuate, vein CuA_1 distinctly, recurvedly arcuate, and female cercus one-segmented. The character states for veins A_1 and CuA_1 are apparently autapomorphic for the tribe, and I personally feel that the second of these is most convincing. The one-segmented female cercus may also be autapomorphic for the Prosopochrysini, although a similar character state is found in other stratiomyids. Nagatomi (1981) included *Euparyphus* Gerstaecker, *Brachycara* Thomson, *Nemotelus* Geoffroy, and *Oxycera* Meigen in the "Prosopochrysinae" primarily because they have one-segmented female cerci. I believe the placement of these genera requires further documentation before this can be accepted, as all of those genera have vein CuA_1 virtually straight or curved slightly toward the apex of the wing. Based on examination of specimens and figures associated with original descriptions, I believe the following genera can be placed in the Prosopochrysini with some certainty: *Acanthasargus* White, *Hoplistopsis* James, *Melanochroa* Röder, *Myxosargus* Brauer, *Nothomyia* Loew, *Prosopochrysa* De Meijere, and *Rhaphiocerina* Lindner. *Cyphoprosopa* James (1975: 473, 474, Figs. 1, 2) may also belong here, but James' figure of its wing indicates that vein CuA_1 is straight.

Pseudoberis is here synonymized with *Nothomyia* because *P fallax* is so similar to other Brazilian species placed in the genus *Nothomyia* (see below). The genera within the tribe are not well defined, and are badly in need of reevaluation at the world level. *Nothomyia* is primarily found in the New World and is separated from *Myxosargus* on the basis of its slender sixth antennal flagellomere, which ranges from elongate conical (as in Fig. 1) to aristate. This flagellomere is not slender in *Myxosargus. Melanochroa*, the third New World genus in the tribe, has an aristate antennal flagellum, but the eyes are dichoptic in males, while they are holoptic in *Nothomyia. Nothomyia* purportedly occurs in the Old World, but *Prosopochrysa* (another Old World genus in the tribe) is so similar that these species (*N. bicolor* Hollis, Java; *N. brevis* (Bigot), New Caledonia) cannot be considered members of *Nothomyia* with certainty. At present, no apomorphic character state is known which may be used to unambiguously define *Nothomyia.*

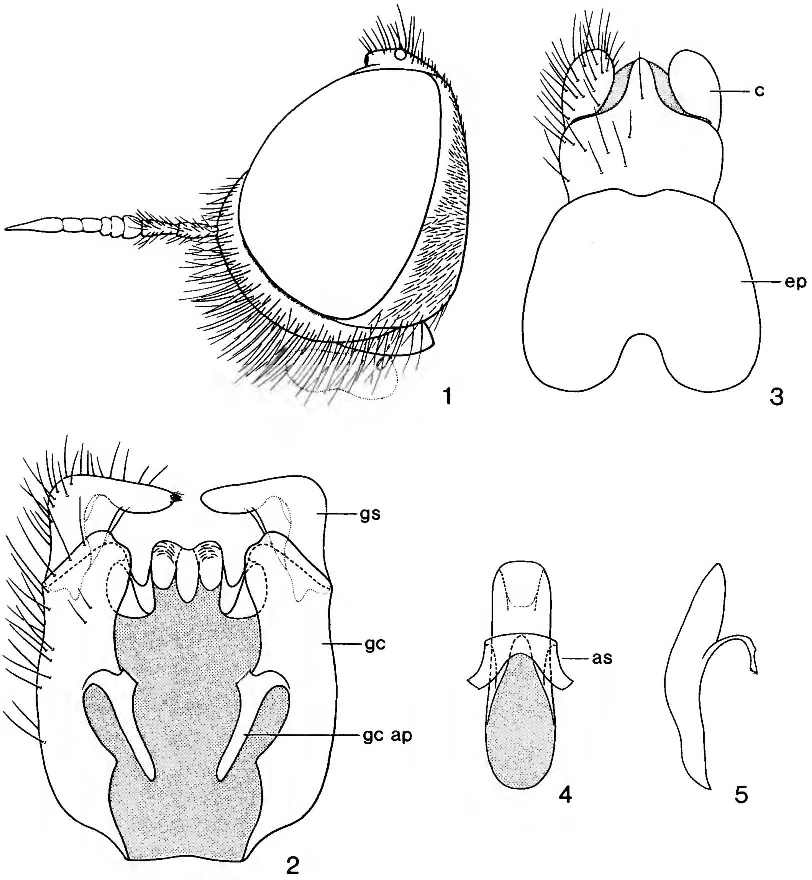
The South American species placed in *Nothomyia* exhibit more variation in the shape of the antennal flagellum than do members of the genus occurring elsewhere. The sixth flagellomere ranges from rather thickened and style like (as in Fig. 1) to aristate in the five known species from Brazil. Caribbean and Central American species all have the sixth antennal flagellomere strongly aristate. In this regard, the South American species are somewhat intermediate between more typical members of *Nothomyia*, as exemplified by the type-species (*N. scutellata* Loew, from Cuba), and species of *Myxosargus*. This further indicates the need for reevaluation of generic concepts within the tribe.

Nothomyia fallax (Enderlein), NEW COMBINATION

Pseudoberis fallax Enderlein, 1921: 277.

Type material. The holotype male is housed in the Zoologisches Museum der Humboldt-Universität, Berlin, East Germany. It is labeled: "Brasilien/9368/[purple square]/Coll. H. Loew/Type/ Pseudoberis fallax Type Ender. ♂ Dr. Enderlein det. 1919/Beris (Nov gen) eupoda m/Nothomyia fallax (Enderlein) Det. N. E. Woodley 1982". The specimen is in excellent condition. The genitalia are preserved in glycerin in a microvial attached to the pin of the specimen.

Description. Male. *Head* (Fig. 1) black, with faint bronzy greenish metallic reflections; eyes essentiallly holoptic, separated on upper frons by less than diameter of a single ommatidium, ommatidia not strongly differentiated in size; lower frons widely triangular, slightly convex, sharply impressed medially in lower half; upper frons very narrowly triangular in front of anterior ocellus; ocellar tubercle moderately prominent; face wide, convex, sides divergent toward oral margin, but not produced downward; lower occiput somewhat convex; lower frons with small, tear-drop shaped, silvery white tomentose spots near upper margins which are contiguous with eye margins, and with very narrow margins inconspicuously tomentose, head otherwise not tomentose; head mostly pilose, hairs longest on face where they are about as long as the basal two antennal segments combined, mostly brownish, but whitish lateral to antennae, most of occipital hairs also pale; antennae subequal to head in length, ratio of segments 13:15: 55[7:4:5:6:7:26], first two segments blackish, very narrowly pale apically, with blackish hairs; flagellum gradually tapering to a sharp apex, first three flagellomeres yellowish brown, last three darker brownish; flagellum with velvety vestiture, but the individual hairs quite long and noticeable; palpi small,



Figs. 1-5. Features of *Nothomyia fallax* (Enderlein), drawn from the male holotype. 1, left lateral view of head. 2, male genital capsule, dorsal view. 3, post-genital segments, dorsal view. 4, aedeagal complex, dorsal view. 5, aedeagal complex, right lateral view.

Abbreviations: *as*, attachment structure; *c*, cercus; *ep*, epandrium; *gc*, gonocoxite, *gc ap*, gonocoxal apodeme; *gs*, gonostylus.

only one segment visible (probably one-segmented as in other species), blackish, with short dense pale hairs over entire surface; proboscis brownish yellow, with pale hairs.

Thorax with mesonotum blackish, with strong dark greenish metallic reflections, post alar calli slightly brownish, scutellum concolorous with mesonotum, but with two pale yellowish spines; pleura similar to dorsum in coloration, although metallic reflections are less strong, with meron + katepimeron brownish; mesonotum finely rugose, thus only somewhat shiny; scutellum rather short and broad, with apical spines short, directed about 45° above plane of scutellum; thorax with thin, inconspicuous, grayish tomentosity on prosternum, meron + katepimeron, anatergite, mediotergite, and subscutellum; thorax mostly pilose, hairs longest on mesonotum where longer hairs are about as long as hairs on face, bare on middle part of anepisternum, posterior fourth of anepimeron, all of meron + katepimeron, subscutellum, and mediotergite; mesonotal and scutellar hairs consist of longer, brownish hairs and short whitish hairs, both types more or less erect, other pilosity uniform and whitish; front legs brownish black, yellowish at extreme apices of femora and bases of tibiae, middle and hind legs similar except that extreme apices of tibiae and entire tarsomeres one to three are pale yellowish; pilosity of legs mostly short, longer on posterior surfaces of femora, mostly pale yellowish but brownish on part of front tibiae, most of front tarsi, and last two tarsomeres of middle and hind legs; wing mostly hyaline, apex of cell sc and all of r_1 brownish, with a brownish spot at apex of R_{2+3} that extends posteriorly through R_{4+5}, and with a vague brownish band extending through most of cell cup to middle of M_1, apex of wing contrastingly hyaline; most of wing with microtrichia, but basal half of cell behind stem vein and posterior three-fourths of alula bare; R_{2+3} short and straight, R_4 absent, M_3 present and distinct but evanescent at base.

Abdomen dark brown, without metallic reflections; typical for genus, long and narrow, gradually widening to apex of third segment, then gradually narrowing to the rounded fifth segment; with little tomentosity, thinly present only at sides of first tergite and sternite; dorsal pilosity brownish, short and only semi-erect over most of surface, long and straight laterally, a little longer than on face, sternites with fairly short, mostly yellowish hairs; genitalia with gonocoxites (Fig. 2) somewhat longer than wide, sides nearly straight; gonocoxal apodemes short, slender; posterior margin of hypandrium with a short, more or less quadrate process that is complex and membranous in part; gonostylus of moderate size, external margin strongly bent near middle, apex sharply rounded in dorsal view, internal surface invaginated medially; aedeagal complex (Figs. 4, 5) small and simple, only slightly arcuate in profile, aedeagus and aedeagal valves apparently strongly fused, thus the posterior part of the complex consists of a single lobe, with a simple attachment structure; epandrium (Fig. 3) slightly broader than long, only narrowly emarginate on anterior margin, thus almost plate like, rounded, with feeble emargination along posterior margin; cerci short, rounded, only slightly longer than wide. Length 5.3 mm.

Female. Unknown.

Remarks. The following key, compiled mostly from Lindner's original descriptions and figures, will serve to identify all known species of *Nothomyia* from South America, and will succinctly compare *N. fallax* with them.

KEY TO SOUTH AMERICAN *NOTHOMYIA*

1. Legs extensively yellow; wings brownish gray with three milky white crossbands . . . . *N. fasciatipennis* (Lindner)
Legs mostly blackish, only yellowish on some tarsomeres; wings may be infuscated, but are without distinct crossbands 2
2. Halter yellowish; last antennal flagellomere very slender, arista like (Lindner, 1935: Fig. 10); R_4 present or absent . . . 3
Halter dark brownish; last antennal flagellomere thickened basally (Fig. 1; Lindner, 1935: Fig. 11); R_4 absent . . . 4
3. R_4 present . . . . *N. longisetosa* (Lindner)
R_4 absent . . . . *N. borgmeieri* (Lindner)
4. Apex of wing hyaline, contrasting with subapical infuscation; sixth antennal flagellomere of male gradually attenuate toward apex . . . . *N. fallax* (Enderlein)
Apex of wing infuscated, not contrasting in coloration with sub-apical region; sixth antennal flagellomere of male more strongly attenuate, the apical portion very narrow, nearly hair like . . . . *N. lopesi* (Lindner)

As can be seen from the above key, *Nothomyia fallax* is most similar to *N. lopesi*. I have examined two pairs of *N. lopesi*, which had been compared to the type by Lopes. Three of the specimens were from the type locality and were probably collected at the same time as the types. The overall coloration and general appearance of the two species are quite similar, as are the male genitalia. In *N. lopesi*, the apex of the aedeagal complex is slightly more truncate, the gonocoxal apodemes are slightly longer, the apical portion of the gonostylus is very slightly more robust, and the shape of the medial invagination of the gonostylus in slightly different. With so few specimens available, the variability of these slight differences cannot be assessed. It is possible that larger series will render the differences less useful in distinguishing the species.

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TEMPERATURE PREFERENCES OF FOUR SPECIES OF FIRE ANTS (HYMENOPTERA: FORMICIDAE: *SOLENOPSIS*)*

By James C. Cokendolpher[1] and Oscar F. Francke[2]

Introduction

Temperature preferences are predicted to occur in insects due to homeostatic considerations. Enzymes should be adapted to function optimally within the narrow range of temperatures encountered by an organism during its peak activity periods (Heinrich, 1981). In ectotherms adapted to function optimally at low temperatures (e.g., living at higher latitudes or higher elevations), their biochemical machinery becomes inactivated or denatured at high temperatures. Conversely, those adapted to function optimally at high temperatures (e.g., living in the tropics or at lower elevations), experience reduced rates of biochemical activity at lower temperatures. Optimality theory predicts that ectotherms which habitually encounter temperature gradients should have the physiological and behavioral adaptations necessary to detect and respond to those gradients.

A temperature gradient which fluctuates with daily and seasonal changes in solar radiation exists in the soil. This gradient is used by ground-nesting organisms to achieve some thermoregulatory homeostasis: they can move up and down their burrows to avoid temperature extremes, especially those occurring near the soil surface. Superimposed on this temperature gradient is a moisture gradient, because the higher temperatures reached at the soil surface during the day promote evaporation. Ants which nest in the soil are known to respond to the temperature/humidity gradients in the soil, and this response is particularly noticeable by the movement of brood among the various nest chambers (Ceusters, 1977; Seeley and Heinrich, 1981). Our research has focused on the responses of four species of fire ants to these soil gradients: elsewhere we (Potts *et al.*,

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1984) examined their responses to humidity gradients in the absence of superimposed thermal gradients, and here we examine their responses to temperature gradients in the absence of superimposed humidity gradients.

Numerous variables have been reported to alter temperature preferences in insects: age, sex, desiccation, hunger, rearing and maintenance temperatures prior to experiments (Deal, 1941; Madge, 1965), relative humidity (Gunn and Cosway, 1938; Deal, 1941), aggregation (Henson, 1960), and experiment duration (Deal, 1941; Ferguson and Land, 1961). In this study treatments consisted of three acclimation temperatures and two experimental relative humidities.

Temperature preferences have been previously investigated in only a few species of ants. Furthermore, the results obtained from most of those studies (Herter, 1923–1925; Hertzer, 1930; Bodenheimer and Klein, 1930: all cited in Deal, 1941) are either inconclusive or the reliability of the measurements are suspect. Although Deal's (1941) study of preference in *Acanthomyops* sp. is not very precise, it demonstrates that the preferred temperature in that species increases with an increase in relative humidity. The temperature preferences of the ant *Formica polyctena* Foerst were reported by Ceusters (1977). In that study a temperature gradient ranging from about 10 to 30° C was established in a battery of 14 consecutive nest cells and numbers of individuals (of workers, queens, eggs, each larval stage, and pupae) were recorded through 12 brood rearing periods (four years). Ceusters (1977) found that each development stage had a different "preferred" temperature, except the differences between eggs/hatchling larvae and small larvae were not statistically significant. Brian (1973), working with the ant *Myrmica rubra* L., determined temperature preferences with both an alternate temperature chamber and a linear gradient chamber. The preferences of the ant *Camponotus mus* Roger, have been investigated by Protomastro (1973). The optimal rearing temperature and thermal preference were considered to be the same by Protomastro (1973).

Few studies have compared temperature preferences among more than two congeneric insect species. The primary objective of this study was to compare the temperature preferences of four fire ant species of the genus *Solenopsis* Westwood. These four species differ in their ecogeographical distributions: one is xerophilous, two are mesophilous, and one is widespread. The northern limits of distribution in North America of the four species studied are between 35° and 37° north latitude. *Solenopsis aurea* Wheeler, the desert fire ant, generally does not occur east of the 100th meridian, whereas *Solenopsis geminata* (Fabricius), the tropical fire ant, and *Solenopsis invicta* Buren, the red imported fire ant, generally do not occur west of the 100th meridian. *Solenopsis xyloni* McCook, the southern fire ant, occurs across the U. S. from coast to coast (Francke *et al.*, 1983). Thus, we sought correlations among the species' temperature preferences in the laboratory and their observed ecogeographic distributions.

MATERIALS AND METHODS

The position to which an insect will move in a thermal gradient indicates its preferred temperature. Orientation and movement in the gradient are stimulated by reactions of avoidance, attraction, or a combination (Deal, 1941). Extensive literature exists on preferred temperatures of terrestrial arthropods (see Bull and Mitchell, 1972; Fraenkel and Gunn, 1961; Mori, 1961; Protomastro, 1973; Singh *et al.*, 1967; and citations contained therein, particularly Deal, 1941). Two types of devices are generally used in these investigations: alternate chambers with temperature ranges of only a few degrees, and a gradual gradient chamber (linear or circular). In either case the movement of individuals or the final distribution of a large number of insects is recorded as a measure of temperature preference.

Temperature is not the only variable in a temperature gradient apparatus. For a review of devices and associated problems, see Fraenkel and Gunn (1961), Madge (1965), and citations contained therein. In the present experiments, like Bull and Mitchell (1972), we attempted to reduce the effects of the non-temperature variables as identified by Madge (1961) by using: (a) a porous false floor, so that the substrate temperature would not differ significantly from the air temperature immediately surrounding it; (b) a large gradient chamber to promote microclimatic stability; and (c) atmospheres as near 0% and 100% R. H. as possible to minimize the effects of moisture gradients on the ants' preferences.

A linear temperature gradient apparatus, slightly modified from that of Bull and Mitchell (1972), was used for the studies (Fig. 1). The lid of the chamber was fitted with three magnets (one on top,

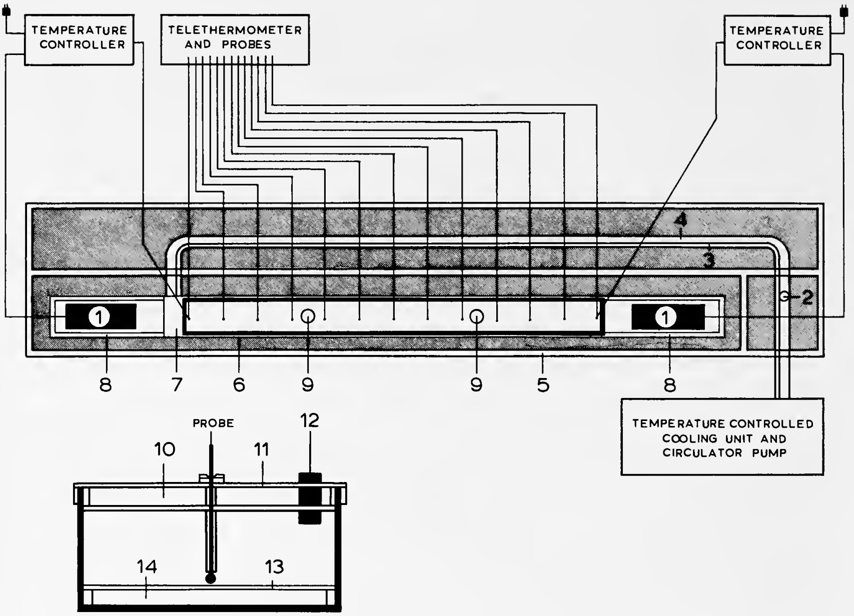

Fig. 1. Linear temperature gradient apparatus, semi-schematic. A. View from above of gradient chamber and associated equipment. B. View of cross section through Plexiglas test chamber. Shaded areas are polystyrene foam insulation. 1, strip heaters; 2, valve for controller flow rate of coolant; 3, cold water input conduit; 4, cold water return conduit; 5, wooden housing for chamber and closely associated parts; 6, Plexiglas test chamber; 7, cold water compartment for cooling aluminum channel; 8, aluminum channel for housing Plexiglas test chamber; 9, introduction ports for test animals; 10, dead air space; 11, lid of test chamber; 12, "condensate wipers", magnets; 13, porous substrate; 14, space for humidity controlling substances; see text for further details.

one in 1.5 cm dead air space, and one below), which were used as "condensate wipers" (Fig. 1B–12). By adjusting the two temperature controllers and the flow rate of the coolant, a linear temperature gradient between 15° and 35°C was obtained. A constant 22 ± 1°C was obtained by turning off both strip heaters and the water bath pump. During the experiments two humidities were employed. A saturated atmosphere was obtained by placing wet paper toweling beneath the substrate in the test chamber (Fig. 1B–14), and 0% R. H. was obtained by the use of Drierite ($CaSO_4$).

Four species of fire ants (*Solenopsis* spp.) from Texas were used: *S. invicta* Buren from Bandera, Kerr, and Harris Counties; *S. geminata* (Fabricius) from Kimble and Val Verde Counties; *S. xyloni* McCook from Bandera, Garza, Kerr, Kimble and Nolan Counties; *S. aurea* Wheeler from Garza, Lubbock, and Reeves Counties. All ants were collected during the summer months except for some *S. invicta*: those from Kerr County (1 April) and Harris County (11 January). The colonies were maintained in the dark at three different temperatures (12 ± 2°, 22 ± 2°, 32 ± 2°C) for a minimum of 14 days prior to experiments. Colonies of ants were collected, separated from the soil, and housed following the methods of Banks *et al.* (1981). All colonies were maintained similarly, being fed cockroaches [*Nauphoeta cinerea* (Saussure)], and mealworms [*Tenebrio* sp.], and supplied free water and a 50% aqueous honey solution daily.

Worker ants without brood failed to make "scorable" choices in the linear temperature gradient. Therefore, workers with brood (larvae and pupae) were utilized. For both experimental and control studies, approximately 25–50 individuals of all worker castes and some brood were introduced to the test chamber via entrance ports located in the lid approximately 35 cm from each end (Fig. 1A–9). Preliminary studies indicated that ants given less than two hours would not settle into a clump; therefore, the ants were allowed at least two hours to move the brood and settle. The temperature where the ants settled was recorded at the termination of each experiment. Like Brian (1973), we found that pheromones left by the ants attracted conspecifics during the following trials. This interference was eliminated by exposing the substrate to light (lid of chamber removed) from a Sylvania Black Light Blue Fluorescent Lamp, F15T8/BLB, at a distance of 30 cm for at least one hour after each trial. After exposure to U.V. light, the chamber was resealed and allowed to equilibrate (humidity and temperature) for at least one hour.

Control trials differed only by having a constant temperature throughout the test chamber (22 ± 1°C). The number of replications and the number of colonies used per species varied, depending on the number of brood tending ants which could be obtained (Table 1).

To determine if the ants showed any preferences during control trials, the Kolmogorov-Smirnov test was used (Siegel, 1956). Differ-

Table 1. Effects of acclimation on temperature preferences of *Solenopsis xyloni* and *S. invicta* collected during the winter.

Species	Relative Humidity (%)	Acclimation (°C)	Temperature Preference ($\bar{x}$ ± s.d., °C)	N
S. invicta	0	12	23.8 ± 1.8	10
	0	22	23.2 ± 1.3	15
	0	32	21.0 ± 2.4	10
	100	12	27.5 ± 1.2	10
	100	22	29.7 ± 2.6	15
	100	32	25.3 ± 2.8	11
S. xyloni	0	12	24.9 ± 1.1	5
	0	22	25.4 ± 2.2	10
	0	32	24.8 ± 3.5	5
	100	12	27.2 ± 1.8	12
	100	22	29.7 ± 2.4	10
	100	32	26.0 ± 2.4	7

ences among species and between *S. invicta* collected during summer and winter months were analyzed with the General Linear Regressions Models and Analysis of Variance of S. A. S. (Helwig and Council, 1979.)

RESULTS

The control responses of each of the four species were analyzed separately with the Kolmogorov-Smirnov test using the null hypotheses that the observed distribution should not differ from the predicted theoretical frequency distribution of the same number of responses on each of the twelve areas in the chamber. The maximum deviation (D) acceptable at the 0.05 confidence level under the specified theoretical cumulative distribution is $D = 0.294$, $N = 20$. The results were *S. aurea* $D = 0.218$; *S. geminata* $D = 0.120$; *S. invicta* $D = 0.117$; and *S. xyloni* $D = 0.168$. Therefore, the null hypothesis was accepted for each of the four species: During the control tests the ants exhibited no preference for any part of the experimental chamber.

Analysis of variance indicated that species identity [$F(3,269) = 7.2$], relative humidity [$F(1,269) = 183.7$], and acclimation [$F(2,269) = 10.2$] were all highly significant ($p < 0.001$) during experimental trials. None of the two way interactions were significant ($p > 0.05$), but the three way interaction (R. H. × acclimation × species) was [$F(6,269) = 2.7$, $0.05 > p > 0.01$].

Intraspecific analyses of temperature preferences indicated that relative humidity was highly significant ($p < 0.001$) for all species: in *S. aurea* F(1,50) = 19.6; *S. geminata* F(1,48) = 65.4; in summer collected *S. invicta* F(1,57) = 38.3, and in winter collected ants F(1,65) = 99.2; and finally in *S. xyloni* F(1,43) = 16.4. The two way interaction (R. H. × acclimation) was significant only for *S. geminata* [F(2,48) = 7.8, $0.01 > p > 0.001$]. The temperature preference responses of the four species of fire ants at both 0% and 100% R. H. appear in Fig. 2.

Acclimation was significant only with *S. xyloni* [F(2,43) = 4.2, $0.05 > p > 0.01$], and individuals of *S. invicta* collected during the winter [F(2,65) = 15.4, $p < 0.001$] (Table 1). *Solenopsis invicta* collected during the summer months showed no acclimation effects [F(2,57) = 1.3, $p > 0.05$].

Discussion

The ability to react rapidly to temperature gradients by the four species of fire ants, and the effect of relative humidity on this response have obviously been shaped by strong selective pressures. In all intraspecific pair-wise (with respect to acclimation) comparisons possible, ants at 0% R. H. had a lower temperature preference by about 3–4°C with respect to those at 100% R. H. Each experimental trial lasted a minimum of two hours, indicating that the ants can perceive and respond to the lower, but constant, relative humidity despite the superimposed temperature gradients in a relatively short period of time. This reaction time is not totally unexpected given that ants can dehydrate quite rapidly. Studies on humidity preferences of the same four species of fire ants, in the absence of superimposed temperature gradients (Potts *et al.*, 1984), revealed that broodless worker ants failed to make scorable choices in a humidity gradient, whereas brood-tending workers always preferred near-saturated relative humidities. When tested at 22°C, this response of negative hydrokinesis required up to 24 hours to become expressed.

These ground-nesting ants build mounds to variable extents depending on soil texture and moisture levels. The soil profile has a thermal gradient which varies with daily and seasonal cycles of insolation. Relative humidity at any given depth in the ant tunnels is influenced by the soil moisture and the temperature at that level. Thus, by detecting temperature and humidity gradients in their nest

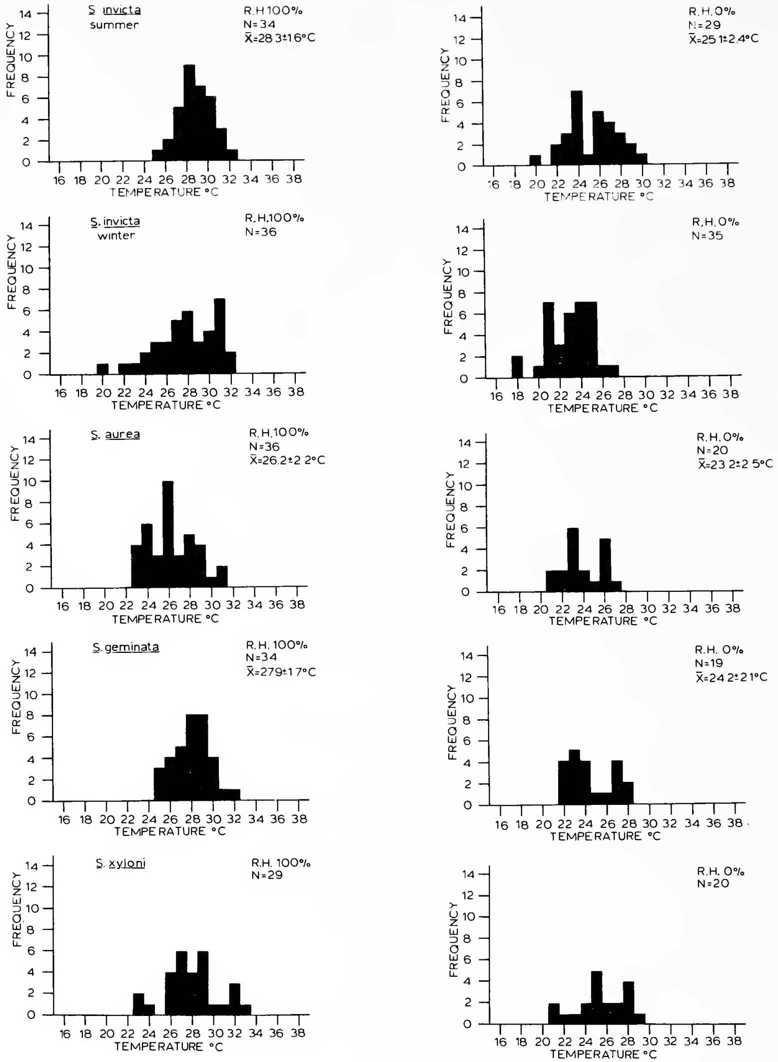

Fig. 2. Temperature preference responses of four species of fire ants (*Solenopsis invicta, S. aurea, S. geminata,* and *S. xyloni*) and preference responses of *S. invicta* collected during different seasons (summer and winter); graphs on right represent responses at 0%, left represent responses at 100% relative humidities. When acclimation was significant, mean temperature preferences are given in Table 1.

the ants can move the brood to optimize the Darwinian fitness of the colony. The "optimum" temperature for fast brood development is often associated with reduced relative humidities which endanger brood survival. Alternatively, saturated air might be present only at soil depths where temperatures are less than optimal for development and survival. Thus, the ants apparently monitor these two environmental factors continuously, and move the brood accordingly to optimize colony growth and productivity. In addition, by shifting the seasonal peak of reproduction, and the daily peak of foraging, the ants can avoid the extremes in temperature and relative humidity which are detrimental to their survival.

The differences in the ecogeographic distribution of the four species of fire ants studied can not be explained simply by differences in their responses in a temperature gradient. Interspecific comparisons among species indicate that the most xeric species, *S. aurea*, has the lowest preferred temperatures at both 0% and 100% R. H. The two mesic species, *S. geminata* and *S. invicta*, follow in that order, respectively. The widespread species, *S. xyloni*, has the highest preferred temperature at both 0% and 100% R. H., and it also showed a significant acclimation effect. Ants acclimated at 32°C had the lowest preferred temperatures, followed by those acclimated at 12°C and 22°C, respectively. These results suggest that ants held at 32°C might have been under some type of water stress, and that the brood-tending workers of *S. xyloni* responded faster to this environmental factor than the brood-tending workers of the other species. Perhaps this faster response time to the needs of the brood is correlated with the broader ecogeographical distribution of *S. xyloni*.

Comparison of the temperature preferences of fire ants with those of other ant species have limited value because of the paucity of data, and the differences in experimental protocols. The only previous study in which both moisture gradients and effects of pheromones (from earlier experimental trials) were adequately controlled was that of Brian (1973). He reported that *Myrmica rubra* L. from England, when tested at 100% R. H., preferred temperatures in the 19 to 21°C range. It is interesting to note that the temperature preferences of *M. rubra* are about 8°C lower than those of the fire ants collected at lower latitudes. Additional species need to be studied before any generalizations can be made about relationships between latitudal/altitudinal distributions of ants and their temperature preferences.

SUMMARY

The temperature preferences of brood-tending fire ants were determined with a linear temperature gradient. The following four species of fire ants were used: *Solenopsis aurea*, the desert fire ant; *S. geminata*, the tropical fire ant; *S. invicta*, the red imported fire ant; and *S. xyloni*, the southern fire ant. The responses of ants acclimated at 12°, 22°, and 32°C were determined at both 0% and 100% relative humidity. The four species differed slightly in their temperature preferences at 100% R. H. (26.2, 27.9, 28.3, and 29.7°C, respectively). Temperature preferences were reduced by 3–4°C at 0% R. H. (23.2, 24.2, 25.1, and 25.4°C, respectively). Prior acclimation was significant only on *S. xyloni*, and on *S. invicta* collected in the winter. The differences in the responses of the four species are not clearly correlated with their ecogeographical distributions.

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A FLY THAT MIMICS JUMPING SPIDERS*

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On August 3, 1984, in the course of field work near Portal, Highlands County, Arizona, I caught sight of a gaudily-colored tephritid fly, which at first completely fooled me into believing it was a jumping spider. Subsequently caught and identified as *Zonosemata vittigera,* it had been resting on a leaf of its larval food plant (Cazier, 1962), the white horse nettle *Solanum elaeagnifolium.* Rather than taking instantly to flight in response to my approach, it moved about erratically over the leaf, or in short darting flights from leaf to neighboring leaf, in patent imitation of the close-range evasive maneuverings of jumping spiders. What made the mimicry uncanny was the fly's seeming predilection during moments of rest of presenting itself in rear-end view (Fig. 1). Thus oriented, with its abdomen masquerading as a prosoma (complete with eye spots), its thorax plus head as an opisthosoma, and the dark bands on its wings as a set of legs, it took on a distinct spider-like appearance. The overall aposematism, so characteristic of jumping spiders, completed the imitation. The fly's abdomen is orange (evenly colored, like many a jumping spider's prosoma), and its thorax yellow and black (mottled, like many an opisthosoma). Its actual legs, irrelevant to the mimicry and potentially distractive from the resemblance, are yellowish-green, in line with the background vegetation. Subsequent sightings that I made of the fly were on both *S. elaeagnifolium* and on sunflower (*Helianthus annuus*).

Imitation of jumping spiders could clearly be of benefit to an insect. Jumping spiders are hard to catch and capable of inflicting poisonous bites, and might thus be shunned by any number of vertebrate and insectan predators.

Other tephritids may show comparable mimicry. Monteith (1972) pointed to the similarity in appearance and movement of *Rhagoletis pomonella* to the sympatric jumping spider *Paraphidippus margina-*

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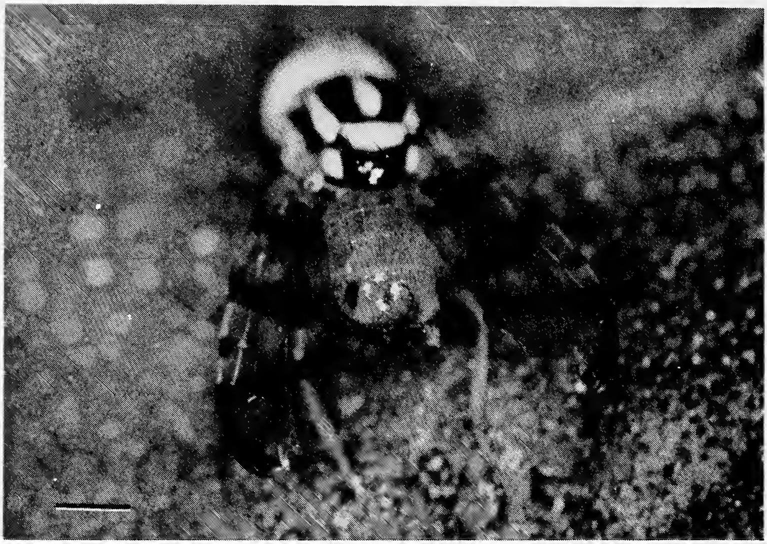

Figure 1. *Zonesemata vittigera*, in rear-end view. Note resemblance to jumping spider in frontal view. For purposes of photography, the animal was briefly cooled by refrigeration. (Reference bar = 1 mm)

tus. Guy L. Bush (personal communication) suggests that other *Rhagoletis* of the *pomonella* species group, including *R. mendax, R. zephyria,* and *R. cornivora,* may be similarly mimetic, and that jumping spider mimicry may have arisen independently in other tephritid lineages as well.

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THE "SAWTOOTHED" ORB WEB OF *EUSTALA* SP. (ARANEAE, ARANEIDAE) WITH A DISCUSSION OF ONTOGENETIC CHANGES IN SPIDERS' WEB-BUILDING BEHAVIOR*

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Convergence has been common in the evolution of orb-weaving spiders' webs, and structures such as stabilimenta, reduced orbs, spring lines, meshes at the side of the orb, and asymmetrically extended "ladder webs" have arisen independently in a number of different groups. This paper describes brief observations of *Eustala* sp. that demonstrate still another apparent convergence that is perhaps more surprising than some of the others since the adaptive advantage of the convergent design is at first glance unclear.

Ontogenetic changes in web design are also documented for *Eustala* sp.; younger individuals make more generalized or less derived webs than those of adults. Data on ontogenetic changes in the web forms of other spider species are summarized, and it is shown that this is a common ontogenetic pattern in spiders. The possible significance of this evolutionary pattern is discussed.

Observations were made in February 1984 in Parque Nacional Corcovado on the Osa Peninsula of Costa Rica in second growth along a small stream near the Sirena station. Webs of six large nymphs and adult females and of two very young nymphs were observed. The construction of three of these webs was observed between 7 and 11 PM.

Spiders were kindly identified by H. W. Levi. They apparently represent an undescribed species; voucher specimens (#2345, SA1-127b, and SAE-106) have been deposited in the Museum of Comparative Zoology in Cambridge, Mass. 02138, U.S.A.

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WEBS OF LARGER NYMPHS AND ADULTS

The webs of larger individuals of *Eustala* sp. (Figures 1 and 2) had several features that were recognizably orb-like. Radial non-sticky lines converged on a single point and were attached to a small, more or less circular hub where the spider rested. Some of the radial lines were fastened directly to a leaf, but other longer ones were attached

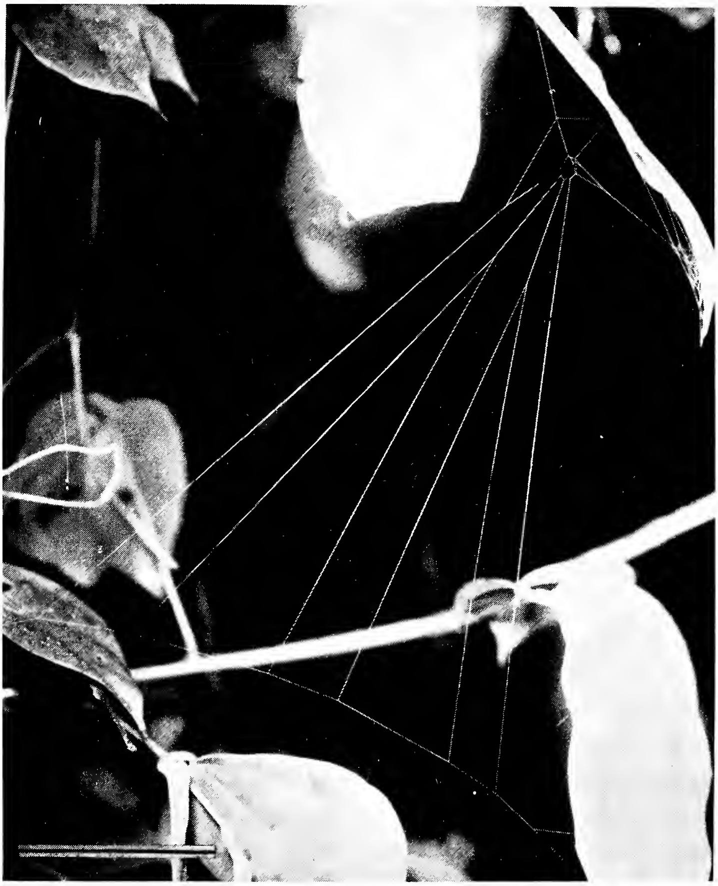

Fig. 1. Web of an adult female *Eustala* sp. The spider rested under the hub-like structure at the upper right. The retreat is visible under the leaf at the far right. Scale marker = 5 cm.

to a supporting frame line or lines attached at either end to a leaf. The numbers of radial lines varied between 5 and 8.

The least orb-like aspect of the webs was the placement of the sticky lines. Instead of forming a more or less spiral pattern centered on the hub, the sticky lines ran both radially and along the frame lines in a sawtooth pattern. As shown in Fig. 2, some of the sticky lines ran directly along non-sticky radial lines, while others spanned spaces between radial and frame lines.

CONSTRUCTION BEHAVIOR

Construction behavior did not vary among the individuals observed, and confirmed the impression that the webs are modified orbs. After an extended period of exploration and repeated replacement of the few lines already laid, the spider finally began by constructing radial and frame lines. One frame construction observed carefully was essentially identical to the frame construction behavior of other araneids that have been observed (e.g. Coddington in press and references therein, pers. obs. of *Leucauge* sp. nr. *venusta*). Subsequent radial lines were attached to the frames with the same behavior as that of other araneine species (Eberhard 1982). No hub loops were laid until the radii were complete, when the spider turned 360–720° at the hub laying a more or less circular non-sticky line, then abruptly switched to laying a non-sticky line apparently equivalent to the temporary spiral of typical orb weavers. This line was laid at some distance from the hub, and the spider did not return all the way to the hub after each attachment; instead it reached laterally to contact each new radius. The temporary spiral was only attached to the longer radii, and consisted of a single incomplete "loop" (Fig. 2).

The spider paused perhaps 15–30 seconds before commencing the sticky line. In one case it clearly moved out to the frame along the radius on which it had ended the tsp before commencing sticky line production; this detail was not checked in the others. It then moved inward along the radius, pulling with quick alternate movements of its legs IV on a sticky line that emerged as it moved. In one case I could see that the spider attached this sticky line at least twice to the radius along which it was moving. When the spider reached the temporary spiral line, it paused and pulled sticky line with several more strokes of its legs IV, and then attached it to the radius.

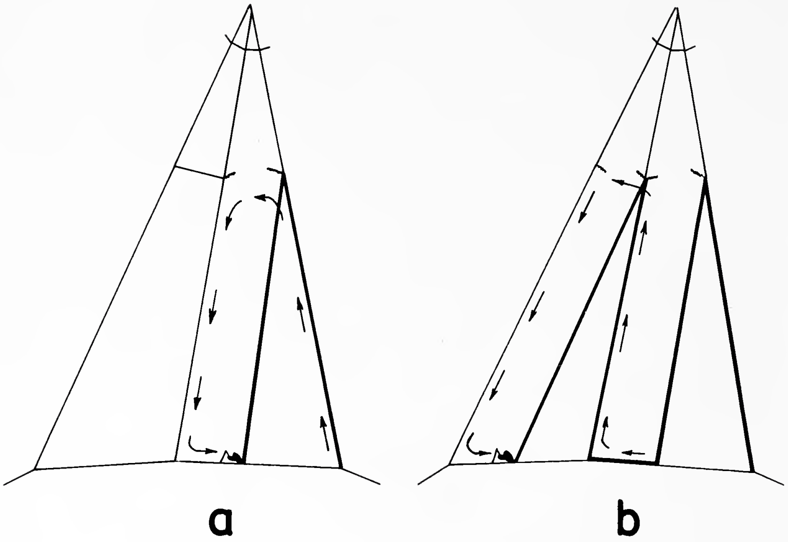

Fig. 2. Building behavior of an adult *Eustala* sp. (thicker lines are sticky thread). a) As the spider laid sticky line, it moved inward (upward in the diagram) along a radial line until it reached the temporary spiral where it attached the sticky line. Then it moved across the temporary spiral to the next radius, and then outward to the frame. Here it moved back partway toward the original radius, and attached the sticky line again. b) the spider then retraced its steps along the frame and went inward along the next radius, repeating the cycle of behavior shown in a.

Without making further attachments, it moved on along the temporary spiral to the next radius and outward along this radius until it reached the frame. I was not able to observe temporary spiral destruction directly, but since temporary spirals were absent in completed webs and this was the only time during web building when spiders passed near this area, I assume that the spiders removed the spiral lines as they moved across them as do other araneids. On reaching the frame the spider performed a behavior never to my knowledge observed in any orb weaving araneid: it moved contrary to the circular direction in which it had been moving (i.e. if it had moved clockwise along the temporary spiral, it moved counterclockwise along the frame - Fig. 2.) before attaching the sticky line; then it reversed direction once again until it encountered the next radius (the one along which it had just moved to the frame), and the cycle just described was then repeated (Fig. 2). When moving outward along radii that were attached directly to the substrate instead of to a frame line, the spider omitted the "backward" segment of the behavior, and simply returned inward along the radius, producing a spiked rather than sawtooth pattern of sticky line.

Sticky line construction terminated when the spider encountered a sticky line it had already laid, and the sticky lines were thus laid in a single 360 degree trip around the web. The spider then moved to the hub of the web and finished web construction by removing the small mesh of lines inside the hub loops, just as do many other araneids (Eberhard 1982).

WEBS OF VERY SMALL NYMPHS

Two nymphs were found on complete, typical orb webs, one in the center of such a web (Fig. 3), and the other crouching in a typical retreat (see below) that was connected to a nearby orb of similar design. Construction behavior of these spiders was not observed. Immature spiders are generally difficult to identify, but these nymphs had the same unusual combination of characteristic white abdomens, white cephalothoracic markings, and dark pink prolateral surfaces on their legs and were of the same size and shape as others that emerged in captivity from egg sacs found with adult females. The nymphs with webs occured on the same *Heliconia* leaves where I found four other individuals (two mature females) of *Eustala* sp., and they had the same unusual retreat design as the older spiders (below). Thus the nymphs' identity is fairly certain despite their lack of diagnostic genitalic characters (voucher specimens are deposited in the Museum of Comparative Zoology in Cambridge, Mass.).

RETREATS

The retreats, which are apparently unique among araneids in their design, were on the undersides of leaves (Fig. 1). The spider sat in the bottom of an inverted truncated cone-like structure, pressing its body flat against the leaf. The flared sides of the cone, which were supported by a small, inconspicuous meshwork of threads had

Fig. 3. Web of a young *Eustala* sp. The spider is resting at the hub. Scale line = 5 cm.

numerous flecks of white silk, and the radial arrangement of the retreat plus the flecks gave the strong impression that the spider was dead and had been attacked by a fungus that was producing fruiting bodies.

DISCUSSION

The webs of adult *Eustala* sp. differ dramatically from the more or less typical orbs of other *Eustala* species (Eberhard 1975, 1976, unpub. obs. of at least 10 other species). Although the usefulness of orb web geometry in grouping species in genera has yet to be demonstrated, the differences documented here are probably unusual.

There is a striking similarity between the webs and building behavior of larger *Eustala* sp. and those of the very distantly related uloborid *Polenecia* (=*Sybota*) *producta* (Weihle 1931) (Fig. 4):

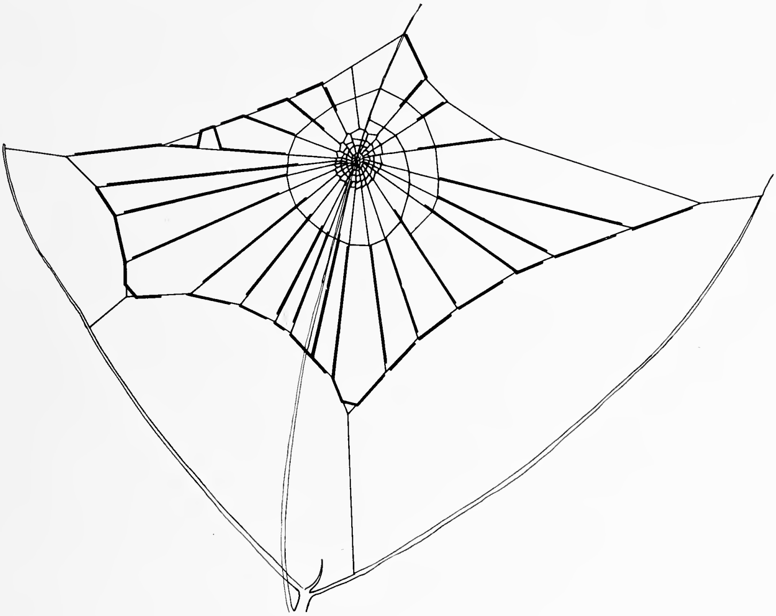

Fig. 4. Web of *Polenecia* (=*Sybota*) *producta* (after Wiehle 1931). Thicker lines are sticky thread.

sticky lines run along both radii and frame threads; the sticky lines on the radii are laid starting from the periphery and working inward; and the sticky lines on the radii extend to about where the temporary spiral crosses the radii. Wiehle's description of building behavior suggests that just as in *Eustala* sp., *Polenecia* lays sticky silk on each radius in succession, and thus probably makes only one 360° circuit of sticky silk construction before finishing. Major differences between *Polenecia* and *Eustala* sp. webs include *Polenecia's* lack of temporary spiral destruction (also occurs at least sometimes in the related uloborid *Hyptiotes* - Opell 1982 - Fig. 1; pers. obs.), periodic interruption of sticky line production (also occurs in *Hyptiotes* Wiehle 1927, Marples and Marples 1937), and a general lack of sticky lines spanning spaces between radii and frames. *Polenecia* is probably derived from an orb-spinning uloborid ancestor (Opell 1979). Other *Eustala* species and species in related genera spin orbs (above), so the sawtoothed web is probably also derived from a typical orb. Thus the two genera have almost incredibly converged on the same strange web architecture, and employ many of the same behavioral sequences to produce it.

A possible explanation for this convergence is related to the fact that sticky lines are usually only able to absorb about one tenth as much momentum as radial lines in completed orbs (Eberhard in press). By laying their sticky lines on radial and frame lines, *Eustala* sp. and *Polenecia* effectively increase the sticky lines' ability to stop moving prey. Such relatively strong sticky lines will most effectively intercept prey when they are placed far enough apart that the probability of "wasting" more than one line intercepting any given prey is reduced (Chacon and Eberhard 1980). Thus the two webs may be adaptations to strengthen sticky lines and array them so as to increase their probabilities of intercepting prey.

The interpretation that the web form of older individuals of *Eustala* sp. is derived from an orb-web is supported by the fact that very young individuals construct typical orbs. A review of the literature on ontogenetic changes in spiders' webs shows that similar tendencies for younger individuals to spin less derived webs occur in a number of other orb weaving araneids, including *Zygiella* (Petrusewiczowa 1938), *Scoloderus* (Eberhard 1975), *Nephila* (Robinson and Robinson 1973, pers. obs.), *Herennia* (Robinson and Lubin 1979a), *Tetragnatha* (=*Eucta*) (Crome 1954), and *Pachygnatha* (Bristowe 1958). Very young *Uloborus conus* (Uloboridae) sometimes also omit the presumably derived cone structure that is consistently present under the orbs of mature females (Y. D. Lubin, pers. comm.). Some species of non-orb weaving spiders also have less derived juvenile webs and/or behavior. These include the psechrid *Fecenia* (Robinson and Lubin 1979b), the mygalomorph *Diplura* (younger spiders more often make webs without lines above the sheet, and the funnel retreat is more often nearer the center of the sheet—A. Deccae, pers. comm.; ancestral spiders presumably lived in holes where silk accumulated on the surface of the ground more or less symmetrically around the edges of the hole), and (perhaps) web-weaving oxyopids of the genus *Tapinillus* (Griswold 1983, Mora in press). Still other possible examples are the salticid genera *Euryattus* and *Simaetha,* in which younger spiders routinely spin sheet webs for prey capture while older individuals only seldom spin webs (R. Jackson, pers. comm.). This case must be considered tentative, since the suspected ancestral nature of web spinning (e.g. Jackson and Blest 1982) in Salticidae is not yet firmly established.

The designs of the webs of other orb weavers (*Araneus, Neoscona, Argiope, Leucauge*) also change as the spiders mature (Mayer 1953, Witt and Baum 1960, Reed et al 1969, Risch 1977, Robinson and Robinson 1978, Maroto unpub.); although in these cases probable ancestral web forms have not been determined, younger individuals of *Araneus, Neoscona* and *Argiope* conform to expectations as they build more similar webs than do adults (Risch 1977) (in *Argiope* the sex of young spiderlings also affects the web design!—Robinson and Robinson 1978).

There are ontogenetic changes in the webs of several other species of spiders, but they differ from the cases just cited. Very young *Zygiella x-notata* can build only incomplete orbs or tangles prior to the age at which they normally emerge from the egg sac (Peters 1969). These changes in behavior differ from the examples above in that they probably stem at least in part from incomplete development of silk glands and from the completion of embryonic cytodifferentiation processes (Peters 1969). Young *Uloborus, Philoponella, Zosis,* and other uloborids spin "orbs" in which sticky cribellar silk is replaced by mats of very fine radial and non-radial lines (Szlep 1961, Eberhard 1977), but again in this case the spiderlings also lack the morphological structures necessary to produce the types of silk used by older individuals.

There are also groups (e.g. *Miagrammopes, Hyptiotes, Ogulnius*) in which young spiders spin the same derived web form as the adults (Lubin et al. 1979, Opell 1982, pers. obs.). There is, however, apparently only one clear case of more derived webs being used by younger spiders: this is *Mastophora dizzydeani,* a species whose ancestors made orbs but in which young spiders generally spin no trapping web whatsoever and adults usually make a remnant web in the form of a sticky globule. There is, however, a probable selective advantage in greater web reduction in smaller individuals, since surface to volume relations may make the use of globules especially difficult for smaller spiders (see Eberhard 1980).

Spiders thus show the same trend in their *behavior* that is well known in the morphology of many animal groups: adult characters tend to be more derived than those of the young. Why this should occur in web building behavior is not clear. Simple adaptive explanations of the changes in spiders' behavior seem unlikely in at least some cases: for example an open sector allowing easier access to the web from a hidden retreat would seem advantageous for young as well as older individuals of *Zygiella;* and the displacement of the hub toward the top of *Nephila* webs would presumably result in more rapid attacks by young as well as older spiders (Masters and Moffat 1983). Some arguments attempt to explain the relative conservatism of younger individuals' morphology as a result of the young being shielded from the action of natural selection from the surrounding environment (e.g. Darwin 1859), and are clearly not applicable to the webs. Others cite the effects of canalization in development and the likelihood that modifications expressed earlier in ontogeny will have especially low adaptive values because their consequences are magnified by subsequent growth (see Futuyma 1979, Gould 1977). This is probably true for some morphological traits, but innate behavioral characters do not obviously build upon each other, and the argument thus loses credibility. Young spiderlings are able to spin complete orbs the first time they try, and in at least some cases (e.g. *Eustala* sp., *Fecenia, Scoloderus*) the spiderlings' webs are made of (presumably) similar types of silk used in approximately the same relative quantities as the silk in adult webs. Learning probably plays little part in the ontogenetic changes in orb-weavers' behavior (Petrusewiczowa 1938, Mayer 1953, Reed et al. 1970, Robinson and Robinson 1976). Thus the reason for greater conservatism in juvenile web design remains a mystery.

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A REDEFINITION OF *STONEMYIA* (DIPTERA: TABANIDAE) AND DESIGNATION OF A NEW GENUS, *PEGASOMYIA*, FROM WESTERN NORTH AMERICA[1]

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The genus *Stonemyia* was erected by Brennan (1935) to receive North American pangoniine species previously assigned primarily to non-Nearctic genera. Brennan placed species with bare eyes in *Stonemyia* s. str. For species with pilose eyes, at least in the male, he proposed the subgenus *Pilimas.* He did not, however, fix a type for *Pilimas* as required by the International Code of Zoological Nomenclature for genus-group names proposed after 1930. *Pilimas,* therefore, was unavailable. *Pilimas* was raised to the generic level by Philip (1941a) and Brennan subsequently (in Philip, 1941b) designated *Diatomineura californica* Bigot as the generotype of *Pilimas* in a note at the end of Philip's paper.

Structurally, both genera are very similar. Authors treating them have used primarily the presence or absence of a spur at the fork of the R_4 and R_5 veins and whether the eyes are bare or pilose. Neither of these characters, however, will absolutely separate these genera. Differences in the male and female genitalia have been used less frequently, perhaps because it is difficult to interpret structural differences observed.

Middlekauff and Lane (1980) summarized the morphological differences between *Stonemyia* and *Pilimas,* but did not mention genitalic differences. In their key, only the presence of the spur vein in *Pilimas* and its absence in *Stonemyia* is used to separate them. However, in their discussion of generic differences, they state that 5% of *Pilimas californica* (sic) lack the spur vein. They also mention that the eyes of *Pilimas* are "slightly" hairy and that those of *Stonemyia* are "practically bare."

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In the most recent key to North American genera, Pechuman and Teskey (1981) used the absence of a spur vein on the fork of the R_4 and R_5 veins, eyes bare in both sexes, the rounded female cerci and projecting process of the male gonostylus to separate *Stonemyia* from *Pilimas.* Except for genitalic differences, these characters will not always reliably separate these genera.

Mackerras (1955) discussed differences in the genitalia of *Stonemyia* and *Pilimas.* In females, *Pilimas* has a prominent apical lobe on the cerci (strongly bilobed in *californicus*) and the caudal ends of spermathecal ducts are membranous and unexpanded, while *Stonemyia* has cerci without an apical lobe and the caudal ends of the spermathecal ducts expanded and sclerotized. The gonostylus of *Stonemyia* has a peculiar outwardly projecting wing that is absent in *Pilimas* males.

The importance of male and female genitalia in generic separation of *Stonemyia* and related genera needs to be re-examined. Because tabanid genitalia are relatively simple and unspecialized, their structural features usually have not been useful for determining relationships below the level of tribe, but such features as are present should be examined critically at the generic level to determine if they can be used reliably to separate closely related genera.

Several years ago, J. R. Vockeroth of the Biosystematics Research Institute, Ottawa, discovered an interesting character in certain species of *Stonemyia* that appears to be unique in Tabanidae: the presence of a row of erect bristles on the ventral surface of the scutellum. I examined the North American species of *Stonemyia* in the collection of the U.S. National Museum and *Stonemyia yezoense* (Shiraki) from Japan and found that both sexes of all species possessed the bristles, although sometimes they were difficult to see because the base of the abdomen was closely appressed to the ventral area of the scutellum.

All other genera of Tabanidae in the USNM collection had the ventral surface of the scutellum bare, except both sexes of *Pilimas californicus,* which had strong bristles on the ventral surface of the scutellum as in *Stonemyia* species. The other two species of *Pilimas* (*P. abaureus* Philip and *P. ruficornis* (Bigot) have the ventral surface of the scutellum bare and also differ from *Stonemyia* species in having the subscutellum conspicuously inflated, whereas in *Stonemyia* it is only slightly enlarged and much less conspicuous. The shape of the body of *californicus* is similar to the bee-like appearance of the *Stonemyia* species, the abdomen being stouter and more rounded, compared to *Pilimas abaureus* and *ruficornis*, whose abdomens are more slender and more nearly parallel-sided.

I therefore believe that *californicus* was mistakenly placed in the genus *Pilimas* and belongs instead in *Stonemyia*. Since Brennan designated *californicus* as the generotype of *Pilimas*, a new name is needed in which to place *abaureus* and *ruficornis*. **Pegasomyia,** new genus, is hereby proposed and contains these two species. The name is taken from Pegasus, the legendary flying horse of Greek mythology. *Pilimas* becomes a synonym of *Stonemyia*, NEW SYNONYMY. I designate *Corizoneura ruficornis* Bigot, 1892 as the generotype of *Pegasomyia*.

Stonemyia can be unequivocally separated from *Pegasomyia* by the presence of a row of bristles on the ventral surface of the scutellum and the relatively unexpanded subscutellum. *Pegasomyia* contains two western species, *P. abaurea* (Philip) and *P. ruficornis* (Bigot). *Stonemyia* in North America contains three eastern taxa: *isabellina* (Wiedemann), *rasa* (Loew) and *tranquilla tranquilla* (Osten Sacken), and three western taxa: *californica* (Bigot), *tranquilla fera* (Williston) and *velutina* (Bigot).

Six Palaearctic species have been placed in *Stonemyia*: *yezoense* (Shiraki), *enokizonoi* (Ouchi), *hispanica* (Krober), *caucasica* (Krober), *tigris* (Bigot) and *bazini* (Surcouf) (=*chekiangensis* (Ouchi)) (Moucha, 1976; Leclercq and Olsufjev, 1975). *Stonemyia yezoense* is a well-known Japanese species and has bristles beneath the scutellum as do the North American species. *St. caucasica* has well-developed ocelli and could be a *Stonemyia* species but this needs to be confirmed. The type male of *St. enokizonoi*, collected from Yaku Island off the southern coast of Japan, is thought to have been destroyed in Shanghai, China during World War II (Hayakawa, personal communication). It is very close to *St. yezoense* and may be conspecific with it. Study of *hispanica* by Schacht and Portillo (1982) revealed that it is a species of *Philoliche* (*Ommatiosteres*), not *Stonemyia*. Chainey (1983) provided a complete description and discussion of *P. hispanica*. It seems unlikely that *tigris* should be placed in *Stonemyia* since Bigot mentions in his original description that ocelli are absent, whereas they are well-developed in all known *Stonemyia* species. It is possible that *tigris* may also prove to be a species of *Philoliche.* Moucha (1976) listed *bazini* as a species of *Philoliche,* but this is unlikely since Surcouf (1922) described it as having well-developed ocelli and posterior cells of the wing wide open. Leclercq and Olsufjev (1975) list it in *Stonemyia,* but this should be confirmed by examination.

Thus, in the Palaearctic Region, only *yezoense* has been definitely confirmed as belonging in *Stonemyia,* but *bazini* and *caucasica* may also belong there.

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SUMMARY

Pegasomyia, new genus, is proposed to replace the name *Pilimas,* the generotype of which belongs in the genus *Stonemyia. Pegasomyia* contains two California species, *abaurea* (Philip) and *ruficornis* (Bigot), the last of which is designated as generotype of *Pegasomyia.* A row of bristles on the ventral surface of the scutellum of *Stonemyia* species will separate them from *Pegasomyia* species which lack such bristles.

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MATING SEASON AND COLONY FOUNDATION OF THE SEED-HARVESTER ANT, *VEROMESSOR PERGANDEI*

By Gregory B. Pollock[1,2] and Steven W. Rissing[1,3]

The seed harvester ant *Veromessor pergandei* is common in most of the Mohave Desert and xeric portions of the Sonoran Desert of the United States and Mexico (Creighton 1950). Throughout extensive portions of its range it is sympatric with ecologically similar *Pogonomyrmex* spp. (Cole 1968, Wheeler and Wheeler 1973, Davidson 1977a, Rissing 1981). Hypotheses to explain coexistence of these species include use of different foraging temperatures (Bernstein 1974), foraging methods (Davidson 1977b), preferred forage item size (Davidson 1977a), and method of predator avoidance (Rissing 1981). While information is available regarding reproductive behavior and colony structure of *Pogonomyrmex* spp. (Hölldobler 1976a, Markl et al. 1977, MacKay 1981, Davidson 1982), comparison with *V. pergandei* is precluded by lack of information for the latter. Accordingly, we have observed mating season and colony foundation of *V. pergandei.*

Materials and Methods

Previous observations of *V. pergandei* in central Arizona indicated mating flights occur in late Winter/early Spring at midmorning, under clear skies as air temperatures reach approximately 22° C. Five *V. pergandei* colonies on an undeveloped section of the desert Botanical Garden, Phoenix, Arizona, were selected for observation of flight activity during this period. The 10 ha study area is native Sonoran Desert with *Larrea tridentata, Carnegia gigantea* and *Prosopis velutina* predominant woody plants. All nests were observed daily from 28 January to 20 March 1984 unless it was overcast, during which time all nests were completely inactive. Each morning an observer visited each nest and counted total number of alates

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flying from the nest during a 2 min. period. Observations continued until above ground activity ceased or reduced to only "nest work", with no further sighting of alates. Fewer than 10 alates flying from a nest per min. was regarded as "low intensity" flight activity while $\geqslant 10$ alates per min. was regarded as "high intensity" flight activity.

We observed colony foundation at several sites in South Mountain Park, Phoenix, Arizona. The habitat at South Mountain is similar to that at the Botanical Garden (the two areas are 17 km apart) but includes several sandy ravines not found at the latter. These ravines attract founding queens which are easily collected or excavated. In 1983 we made as complete a sample as possible of all founding nests along one of the ravines at South Mountain. This survey occurred late in the flight season (in mid-March) when most females were expected to have flown and established nests.

A similar survey of founding nests was conducted in a second ravine in 1984 to chart the course of colony foundation throughout the flight season. Approximately every other day (and every day that flight activity was observed at the Botanical Garden) the ravine was surveyed and all founding nests collected. Care was taken to examine apparently preferred nest establishment sites, e.g. under flat rocks, boards and other such objects. Sixty-one of the queens collected during these 1984 surveys were dissected to determine mating success throughout the flight season.

During the first half of the 1984 mating season we also partially excavated adult *V. pergandei* nests and collected all alates found. Samples were counted according to sex, dried and weighed individually.

RESULTS

Mating season of *V. pergandei* was almost 2 months long (Fig. 1). While there was some coordination of flight activity between nests (e.g. 7 March, Fig. 1), on numerous days only one colony released alates, e.g. nest Vp-1 (lowest histogram in Fig. 1) released alates on 11 days when no other observed nest did so. Most of the days during which no flight activity occurred appeared too cold, overcast or windy for flights. As a proximal cue, even light wind appeared sufficient to preclude flight. We frequently observed alates gather at the nest entrance and then run into the nest in apparent response to breezes or stronger gusts.

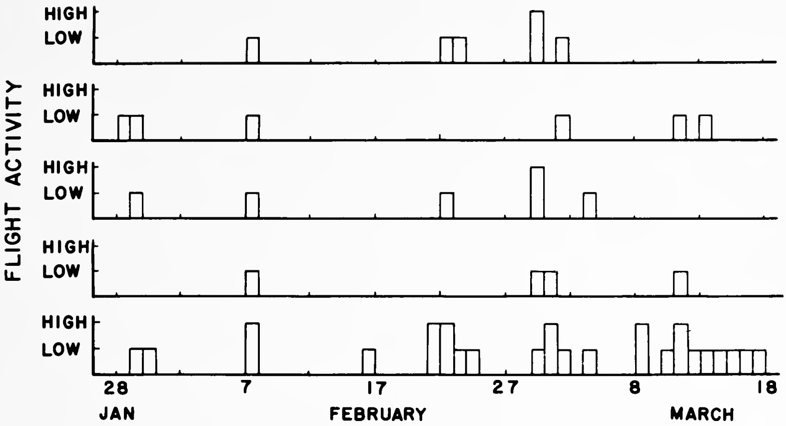

Figure 1. Flight activity of five *V. pergandei* colonies at the Desert Botanical Garden, Phoenix, AZ, January — March 1984. "Low intensity" flights are those where <10 alates flew from the nest per min.; "high intensity" flights had ≥10 alates fly per min.

During observation of flights it was usually not possible to accurately sex individuals leaving the nest. Nonetheless, two cases of unusual sex ratios were noted. One colony discovered at the Botanical Garden in February 1983 was obviously very young, as indicated by the single, small crater and nest entrance as well as the small size of its workers. This colony produced no alates during 1983 and produced only female alates during 1984. Additionally, nest Vp-1 produced only males during the last 7 days of the mating season; an increasing proportion of these males were unable to fly correctly as the season progressed.

Of eight adult colonies partially excavated to determine alate sex ratio, six exhibited a strong bias toward reproductive investment in females; the remaining two colonies produced only males. For those colonies with female alates, the average ratio of reproductive investment (mg females:mg males) was 9.7 (Table 1).

All but five of the 61 *V. pergandei* queens dissected were inseminated suggesting females mate throughout the long flight season. The five uninseminated queens appear randomly distributed with respect to probable flight date, collection locale, and number of cofoundresses.

Veromessor pergandei is strongly pleometrotic; 89.1% of all queens found in 1983 came from multiple queen associations (Fig. 2). Formation of associations is not density-dependent. Percentage of all queens found pleometrotic during regular surveys of ravines in 1984 is uncorrelated with queen density for that survey ($r = -.058$; $N = 9$ days when more than one queen was found).

While searching for foundress associations we regularly found dealate queens in a group under rocks or similar objects in an immobile, "pupoid" state (i.e. legs and head held tightly under the thorax as seen in ant pupae). "Pupoid" queens were usually found when environmental conditions, especially soil temperature, were conducive to *V. pergandei* activity as indicated by simultaneous foraging of nearby adult colonies. Exact function of "pupoid" behavior, following flight and mating but preceeding excavation, is unclear but may promote accumulation of queens into a developing pleometrotic association. There appears a clear cost of predation associated with any such behavior that delays excavation of a burrow. We frequently observed up to 50% of the starting nests in an area destroyed (either by a rodent or lizard); additionally, we observed predation on foundresses at or near the soil surface by centipedes, spiders and fire ants (*Solenopsis* sp.).

DISCUSSION

The mating season of *V. pergandei* is quite long when compared with sympatric seed-harvester species. For example, *Pogonomyrmex* spp. have a brief mating season determined by summer rains; colonies release all alates during one or several days of flight activity (Hölldobler 1976a, Markl et al. 1977, Davidson 1982). By comparison, *V. pergandei* releases alates over a 2 mo. period; frequently a colony releases only a small number of alates for many days (Fig. 1). Method of colony foundation also differs dramatically between *V. pergandei* and *Pogonomyrmex* spp. While *V. pergandei* frequently forms foundress associations (Fig. 2), *Pogonomyrmex rugosus* rarely does so. Of 70 starting *P. rugosus* colonies excavated in Tempe, AZ, 66 contained a single queen (Rissing and Pollock, unpublished data). Similarly, Hölldobler (1976b) reports that "hundreds" of founding *P. rugosus, P. barbatus* and *P. maricopa* colonies contained only a single queen.

Table 1. Reproductive investment of *Veromessor pergandei* colonies according to sex.[1]

COLLECTION DATE 1984	NO. ALATES	% MALE	MEAN MASS OF MALES mg (N; SD)	MEAN MASS OF FEMALES mg (N; SD)	INVESTMENT RATIO mg :mg
29 January	201	17.4	5.666 (33;0.432)	19.686 (129;1.333)	16.5
3 February	104	100.0	6.378 (87;0.407)	0.0	
3 February	122	27.0	6.231 (31;0.417)	20.536 (66;1.090)	8.9
3 February	110	10.0	7.086 (11;0.388)	20.560 (77;1.060)	26.1
6 February	169	33.1	5.812 (49;0.498)	19.953 (93;0.942)	6.9
7 February	486	30.0	5.724 (110;0.466)	19.098 (164;1.190)	7.8
26 February	335	26.0	5.859 (69;0.428)	20.576 (151;0.870)	10.0
26 February	90	100.0	5.671 (85;0.408)	0.0	

[1] Only colonies from which more than 50 alates were collected are reported.

Veromessor pergandei seems similar to the honey ant *Myrmecocystus mimicus* in its founding behavior. Both species form pleometrotic nests (Fig. 2; Wheeler 1917, Bartz and Hölldobler 1982); natal nests of both species are also clumped. Bartz and Hölldobler (1982) suggest that clumping of *M. mimicus* natal nests is due to avoidance of adult conspecific colonies by at least some founding queens, for adult colonies destroy any conspecific colonies they find (Hölldobler 1981, Bartz and Hölldobler 1982). Hence local queen density rises in those areas lacking an adult colony, increasing both the probability of pleometrosis and local density of natal nests. Our observations suggest a different mechanism must exist for *V. pergandei*, for here queen density is uncorrelated with pleometrosis. Further, natal nests do not avoid areas near adult colonies. This is noteworthy, for we have seen foraging columns of adult *V. pergandei* colonies destroy natal nests. Nonetheless, natal nests were regularly found within the foraging radius of an adult colony; often all queens found after a flight were within such a radius.

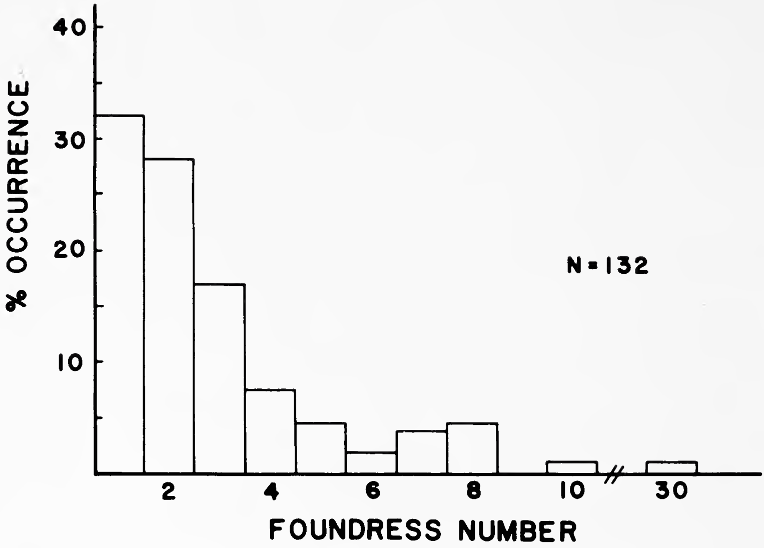

Figure 2. Pleometrosis in *V. pergandei* natal nests collected at South Mountain Park March 1983.

Among other primary pleometrotic ant species, queen density is correlated with average number of cofoundresses/nest (*M. mimicus:* Bartz and Hölldobler 1982; *Solenopsis invicta:* Tschinkel and Howard 1983). Queens seem predisposed to cofound and readily join conspecific queens when encountered. Under high queen density the probability of such encounter is high, insuring pleometrosis. High queen densities are common in *M. mimicus* and *S. invicta*, for adult colonies release alates synchronously during the flight season. Adult *V. pergandei* colonies, however, release alates (often asynchronously; Fig. 1) over a lengthy period. In 1984 queen density after any flight was low; pleometrosis was nonetheless common. Queens seemed attracted to sites relatively protected from predators, e.g., under flat rocks or boards, rather than avoidant of adult conspecific colonies. We believe *V. pergandei's* flight season precludes pleometrosis through random association under high queen density.

Although the exact mechanism generating pleometrosis remains unclear, we have evidence that *V. pergandei's* mating system is involved. We have searched for *V. pergandei* mating sites during the last 3 yr without success. Several observations, however, suggest such sites are small, local and on or near the ground. We have found horned lizard (*Phrynosoma* sp.) fecal pellets consisting soley of *V. pergandei* alate exoskeletons at South Mountain. Absence of workers in these fecal pellets suggests alates were not consumed at the nest site, where workers would have vigorously mobbed any horned lizard (Rissing 1981). We have also noticed starting colonies are clumped along ravines at South Mountain even when queen density is low. Live males occur frequently in these clumps, under debris within 1 m of starting nests or actually associated with one or several females. These observations, along with the high percentage of fertilized females found throughout the protracted mating season, suggest mating occurs on or near the ground in small, localized groups. These observations also suggest males and females do not differentially disperse after mating; this is unusual among insects (Thornhill and Alcock 1983).

Another line of evidence supports this view of *V. pergandei's* mating system. If alates mate in small, localized groups, males do not compete panmitically for females. Such limited alate dispersal should select for female biased ratios of investment among parental colonies (Hamilton 1967, Bulmer and Taylor 1980, Taylor and Bulmer 1980, Charnov 1982, Wilson 1983). All of the colonies we have excavated had such a bias or contained only males (Table 1). This investment pattern cannot be explained through worker control of sex ratio, for observed biases were three times as large as those predicted under worker control (Trivers and Hare 1976, Benford 1978, Oster and Wilson 1978, Charnov 1982). If our sampling method is an adequate measure of a colony's partitioning of sexual investment, this is strong evidence that *V. pergandei* alates exhibit low dispersal with respect to their parental colony-mates. This is what we would expect when colonies release alates asynchronously over a lengthy period.

Veromessor pergandei is sympatric with several *Pogonomyrmex* spp. throughout its range and occurs exclusively in more xeric areas of the Mohave Desert (Creighton 1950, Wheeler and Wheeler 1973, Rissing 1981). If our analysis of *V. pergandei's* mating system is correct, it offers a strong contrast to that of *Pogonomyrmex* spp. *Pogonomyrmex* produce a few massive mating aggregations ("leks"), incorporating alates from many colonies, with females later dispersing to form haplometrotic nests (Chapman 1957; Nagel and Rettenmeyer 1973; Hölldobler 1976a, b; Davidson 1982). *Veromessor pergandei*, however, seems to produce many local, small mating aggregations, both temporally and spatially apart, where females fail to disperse after mating but actively form pleometrotic nests. Such differences may provide insight into the distribution and abundance of *V. pergandei* relative to *Pogonomyrmex* spp.

SUMMARY

Veromessor pergandei, a seed-harvester ant common to the Mohave and portions of the Sonoran Desert, has a mating season lasting almost 2 months. Colonies release small numbers of alates on warm, cloudless and windless days from January to March in Phoenix, AZ. Release of alates from one colony often occurs without similar releases from nearby colonies. Dealate queens captured throughout the mating season are, nonetheless, usually inseminated. *Veromessor pergandei* usually initiates colonies through pleometrosis; 89% of all queens collected in 1983 were pleometrotic. Several lines of evidence suggest males and females do not differentially disperse after mating; this failure to disperse from the mating aggregation may help induce pleometrosis in this species. Colonies of *V. pergandei* produce 9.7 times more mg of female alates than male alates on average. Length and timing of mating season and initial colony structure of *V. pergandei* differ dramatically from that of ecologically similar and sympatric *Pogonomyrmex* spp.; such differences may provide insight into the distribution of this species relative to *Pogonomyrmex* spp.

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FREQUENCIES OF COLOR MORPHS IN FOUR POPULATIONS OF *ENOPLOGNATHA OVATA* (ARANEAE: THERIDIIDAE) IN EASTERN NORTH AMERICA*

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Introduction

Several types of spiders exhibit conspicuous color polymorphisms. Reiskind (1970) has discovered mimetic polymorphisms among clubionids. Examples in which only one sex is polymorphic occur among the jumping spiders, which have keen vision and often show marked sexual dimorphism (e.g. Galiano 1981a, b). In these species the sex-limited polymorphisms may be related to differential predation pressures upon the sexes and/or sexual selection (Stamps and Gon 1983). Many theridiid spiders are polymorphic (Levi 1957; Stamps and Gon 1983), though in this group the eyes are not well developed and recognition of colors or patterns during courtship probably does not occur. Polymorphisms in theridiid species appear not to be sex-limited, though the frequencies of certain morphs may differ between the sexes (Hippa and Oksala 1977, 1981). By far the most extensively studied color polymorphism among spiders is that found in the theridiid *Enoplognatha ovata* (Clerck).

Populations of *E. ovata* frequently contain three distinctive types of adults. The most common morph has a pale yellow abdomen, often with several pairs of dorsolateral dark spots, but with no red stripes (form *lineata*); another form has two dorsolateral red stripes running the length of the abdominal dorsum (form *redimita*); and the least common morph has a solid red band running the length of the abdominal dorsum (form *ovata*) (Bristowe 1958). This striking variation in a common species has long fascinated naturalists. Early arachnologists considered the forms to be three species, but by early last century the three varieties were considered to be conspecific

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(Hippa and Oksala 1979). The three morphs will mate readily in the laboratory, and Seligy (1971) discovered that *lineata, redimita* and *ovata* could be obtained in the progeny of a single female. Although the morphs are usually distinct, recent research of Hippa and Oksala (1979, 1981, 1982) indicates that the genetics of the color polymorphism is more complicated than previously thought; a brief summary of recent findings appears in the Appendix.

Ecologists have uncovered two intriguing aspects to the distribution of these morphs in Europe. Local populations often differ in the frequencies of the three morphs, yet a given population will maintain remarkably constant frequencies over several generations (Oxford 1976). Furthermore, a latitudinal cline in morph frequencies exists, with the red forms tending to be more common in northern populations of continental Europe (Hippa and Oksala 1979).

E. ovata also occurs in parts of North America (Levi 1957), but has not been extensively studied on this continent. Seligy (1971) provided information on the natural history of the species in North America and described details of postembryonic development; however, he did not give data on morph frequencies in different locales. In 1983 we determined morph frequencies in *E. ovata* populations in Maine, Massachusetts, and two regions of New York. We discovered that frequencies varied between local populations within an area, and also found that the overall frequencies for each geographical region were not the same. Most striking was the presence of the *ovata* morph in Maine and a mountainous area of Massachusetts, and its absence from two populations in widely separated regions of New York State.

METHODS

Natural History of *E. ovata*

This brief account is based primarily upon Nielsen (1932), Bristowe (1958), Seligy (1971) and personal observations.

Middle through adult instars are found underneath the leaves of many species of brambles, small saplings and herbs such as golden rod (*Solidago*). *E. ovata* occurs along roadside ditches, open fields and in the forest understory. It is often highly aggregated, with dense clumps sometimes being referred to as “colonies”. The spider builds a small, inconspicuous tangle web underneath a leaf, the edges of which are often pulled down slightly by silk lines. This retreat is readily noticeable when examining vegetation, and the one constructed by the female for her egg sac is particularly obvious. Most females deposit a single sac in July or August, which they guard in a rolled leaf. The 2nd instar spiderlings emerge after several weeks and disperse in September through October. These instars overwinter in the leaf litter and in early spring build small webs in the curls of dead leaves. At this stage they were the most abundant spider in the litter community of one ecosystem studied (Stevenson and Dindal 1982; the population that they studied was the same central New York population that we examined). As the juveniles begin to molt they move into living vegetation where they build small webs similar to those of adults, though the younger instars do not consistently curl down the edges of leaves.

Sampling the North American Populations

During 13–17 July 1983 we surveyed morph frequencies of penultimate and adult *E. ovata* in several local populations in each of four different regions: Mt. Desert Island in Maine, October Mountain State Forest in the Berkshire Mountains of western Massachusetts, Huyck Nature Preserve in eastern New York, and the Lafayette Experimental Station of SUNY Syracuse in central New York (Fig. 1). Local populations were defined primarily as dense aggregations of *E. ovata* in contiguous stands of vegetation. After locating an aggregation, we continued to move systematically through that patch of vegetation until *E. ovata* was no longer common, or until we had scored approximately 50 spiders. This latter criterion was used primarily in Syracuse, where the vegetation suitable for habitation by *E. ovata* was continuous over large areas of the forest. The local populations were 50m to several km apart. We examined each patch carefully, but did not make an exhaustive survey of each geographical area to determine the number of local populations. Instead, we attempted to examine as many different geographic regions as possible, spending from under a day (Syracuse) to two days (Maine) in each area. We scored a total of 1107 spiders in these four areas, but in presenting frequencies in local populations within each region we have only included those with 20 or more individuals.

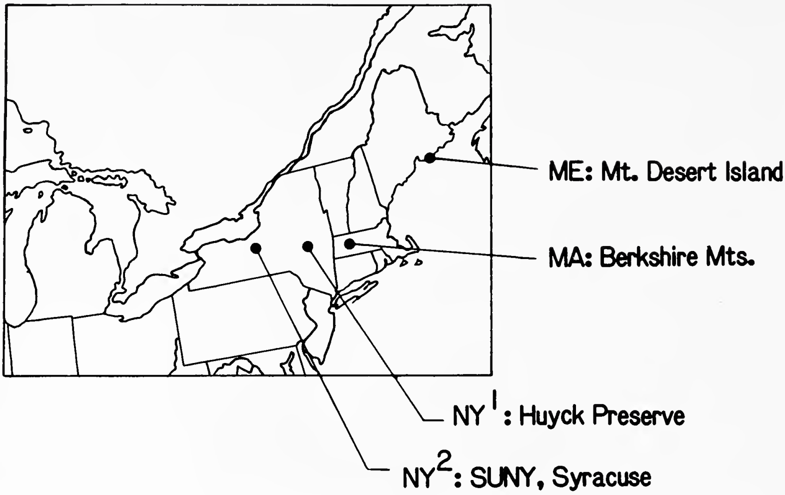

Fig. 1. Sites at which morph frequencies in local populations of *Enoplognatha ovata* were scored.

RESULTS AND DISCUSSION

Pooled local populations from the four geographic regions differed in overall morph frequencies (Fig. 2). Proportions of the yellow morph, *lineata,* differed significantly among the four regions sampled (chi-square = 11.41, $p < .01$, df = 3), due to the lower frequency of *lineata* in Massachusetts compared to the other three areas. The most striking difference involved the solid red morph *ovata.* This form was absent from both New York populations, but occurred in both Massachusetts and Maine. The differences in the frequency of *ovata* among the four regions was significant statistically (chi-square = 34.49, $p < .001$, df = 3).

We uncovered similar differences in morph frequencies between local populations within one of the regions that we sampled (Fig. 3). Variation in representation of the morphs among populations on Mt. Desert Island in Maine was statistically significant (chi-square = 13.2; $p < .05$, df = 5, 2×6 contingency table; comparison of *lineata* frequencies). The frequency of *lineata* varied from .70 to .96, and that of *ovata* from 0 to .15. The difference between population "A" and several of the others was quite striking, in that "A" had no *ovata* and very few *redimita,* whereas the others contained large numbers

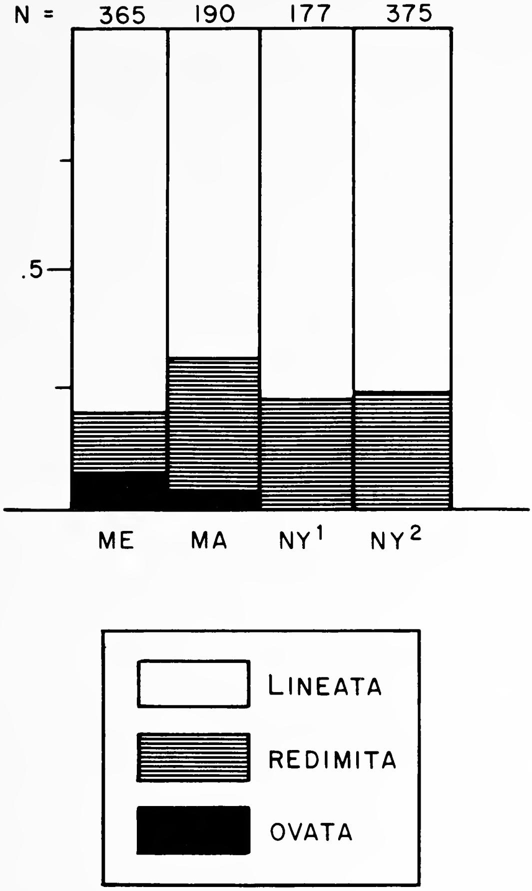

Fig. 2. Morph frequencies in the four different regions that were sampled. Individuals from the local populations (i.e. aggregations ⩾ 20) and also spiders found in aggregations with fewer than 20 individuals have been pooled to calculate the proportion of each morph. Thus, with the exception of SUNY Syracuse, the sample used to derive proportions for each region is larger than the sum total of local populations that appear in Fig. 3.

of both the striped and the solid-red morphs. The number of populations from October Mt. State Forest in Massachusetts and from the Huyck Preserve in New York is too small to make any generalizations about local differences in morph frequencies. Additional sampling might indicate that some local populations in western

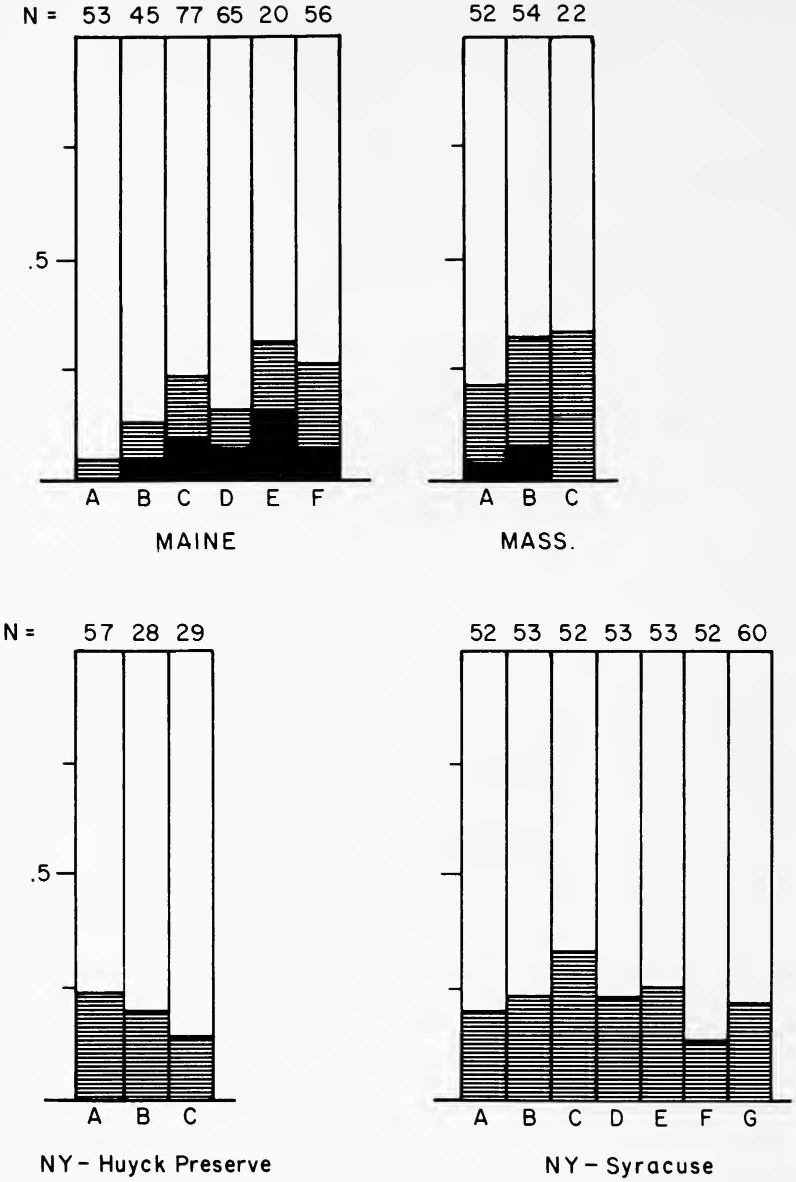

Fig. 3. Variation in morph frequencies among local populations. Key same as for Fig. 2.

Massachusetts differ in the proportion of the *ovata* phenotype. The three populations from the Huyck Preserve were quite similar; they all lacked the *ovata* morph and had similar frequencies of *redimita*. Populations from the forest in Syracuse, New York also lacked *ovata* and did not differ significantly in the proportion of *redimita* (chi-square = 6.0, $p > .4$, df = 6, 2×7 contingency table). This constancy likely reflected both the continuity of the habitat and the proximity of the local "populations" to one another. Each group that was defined as a population was no more than 50 m from another, with continuous vegetation also inhabited by *E. ovata* existing between them. Unlike the local populations in the other three regions, those in the central New York site were not physically separate aggregations.

These preliminary observations of morph frequencies in *E. ovata* populations in eastern North America suggest that patterns similar to those in Europe will be uncovered if more areas are sampled. In the region most extensively researched, Mt. Desert Island, significant differences in morph frequencies occurred among local populations. European workers have reported similar differences (Oxford 1976, Hippa and Oksala 1979). Morph frequencies also differed between widely separated regions. This preliminary evidence is insufficient to judge whether North American *E. ovata* exhibits a morph-ratio cline similar to that found in Europe by Hippa and Oksala (1979), but the absence of the *ovata* morph from both regions in New York is striking. A more detailed examination of *E. ovata* populations along latitudinal and longitudinal gradients in North America might uncover a consistent pattern of variation.

Apparently *E. ovata* is a relatively recent arrival to North America (Levi 1957). Our initial studies indicate that morph-frequency patterns in North America may be equally as intriguing as those already documented in Europe. More detailed examination of the pattern in a recently colonized area could provide comparative data useful to understanding the evolutionary forces responsible for the patterns of variation in morph frequencies occurring on both continents.

SUMMARY

The spider *Enoplognatha ovata* exhibits a conspicuous color polymorphism characterized by three morphs: *lineata* (yellow abdomen with no stripes), *redimita* (two dorso-lateral red stripes on

the abdomen) and *ovata* (medial red band on the dorsum). European researchers have found that local populations often differ in morph frequencies, and that average frequencies differ between geographic regions. We found preliminary evidence of similar variability in North American populations of *E. ovata*. We recorded the phenotypes of 1107 spiders from several local populations, 50m to several km apart, in each of four areas: eastern Maine, western Massachusetts, eastern New York, and central New York. The overall frequency of *lineata* was .70 among the spiders from Massachusetts, but was close to .80 in the other three regions. The most striking geographic differences in frequency involved the *ovata* morph. This form was absent from all New York populations sampled, but occurred in all but two of the local populations from Massachusetts and Maine. Overall frequencies of *ovata* in the Massachusetts and Maine samples were .03 and .06, respectively. In Maine, the most intensively sampled region, morph frequencies differed significantly among local populations. The proportion of *lineata* varied from .70 to .96; *ovata* frequencies ranged from 0 to .15. These observations suggest that further examination of *E. ovata* in North America may uncover morph frequency differences between populations comparable to those in Europe. Since *E. ovata* is likely a recent immigrant to North America, more detailed information from this continent could yield valuable comparative data on a curious phenomena whose evolutionary basis is still unexplained.

APPENDIX

Oxford (1976) found variation in coloration and patterning of the three morphs, particularly among laboratory-reared spiders. Hippa and Oksala (1979, 1981) also found that morphs were not always distinct, and furthermore, that in some groups the red coloration was not expressed until either the third instar or the final molt. Recently, Hippa and Oksala (1982) cited evidence from studies of variability in genitalia structure that some populations of *E. ovata* may consist of more than one species, contrary to previous interpretations of Levi (1957, 1967).

This recent information complicates the situation, but does not detract from the usefulness of our findings, for three reasons:

(1) Only a very few intermediate forms appeared in our sample of over 1000 spiders.

(2) Only the Maine populations appeared to have had significant numbers of penultimate females; however, they were a minority. Most spiders appeared to be mature. Development was more advanced in the southern populations, with many females guarding egg sacs. Thus in Maine we may have slightly underestimated the frequencies of the red morphs (Hippa and Oksala 1979); however, this possible bias makes our conclusion of significant morph frequency differences between regions conservative, since the sample from Maine had the highest frequencies of *ovata,* the phenotype with the most red coloration.

(3) Definition of new species in the *E. ovata* group by Hippa and Oksala (1982) is based upon relatively few museum specimens. This type of information does not indicate whether or not expressions of the red morphs differs between *E. ovata* and the newly recognized *Enoplognatha* species, nor does it indicate the extent of niche differences.

The most extensive sets of data available on morph frequencies in European populations are based on the assumptions of three distinct morphs and one species (eg. Oxford 1976, Hippa and Oksala 1979). Hence our data are directly comparable to that collected by European researchers. Future, more detailed research on both continents will have to take into account the possible existence of more than one species in some *E. ovata* populations. However, this taxonomic problem does not prevent one from making preliminary statements about patterns in morph frequencies.

ACKNOWLEDGMENTS

We wish to thank Diane Debinski for valuable assistance in the field. Debbie Gordon of the Huyck Preserve and Daniel Dindal of the SUNY Lafayette Experimental Station gave permission to examine *E. ovata* populations in the respective research areas and graciously assisted with logistics. This research was supported by National Science Foundation Grant DEB 81-19309.

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MASONCUS SPIDER: A MINIATURE PREDATOR OF COLLEMBOLA IN HARVESTER ANT COLONIES

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Symbionts are common in nests of *Pogonomyrmex* harvester ants (Lavigne 1969, Hunter and Farrier 1976, MacKay 1981 and 1983, Wray 1938). Over ten species of arthropods were found inhabiting *Pogonomyrmex badius* (Latreille) nests near Tallahassee, Florida. Springtails were especially common; literally thousands of white entomobryids and isotomids were found running through nest chambers. The entomobryid was *Pseudosinella rolfsi* Mills, a species often found in ant colonies. The isotomid was an undescribed species in what may be a new genus closely related to *Folsomia, Proisotoma* and *Cryptopygus.*

Perhaps the most interesting symbiont was a small undescribed spider of the genus *Masoncus* Chamberlin (Linyphiidae: Erigoninae). These spiders were about 2 mm long (Fig. 1). Their legs and cephalothorax were pale orange, while the abdomen was slightly darker and grayish. Immature spiders were pale cream colored with a grayish abdomen. Very little is known about the natural history of *Masoncus* spiders. According to Millidge (personal comm.), these spiders are taxonomically similar to the genus *Tapinocyba.*

Masoncus spiders in *P. badius* nests are apparently predators of the symbiotic Collembola. On several occasions, I actually observed these spiders carrying dead collembolans, although I did not see how they were captured. These spiders can spin silk, but probably do not use webs for prey capture because I have never observed more than a few strands of silk in any nest chamber. Symbiotic *Thyreosthenius* spiders in Britain also prey on Collembola (Bristowe 1939).

Mites were very abundant and might be a secondary source of food for young spiders. The ceilings and floors of nest chambers were often covered with droves of small mites (4 species) slowly "grazing" on the substrate. These mites belonged to the families

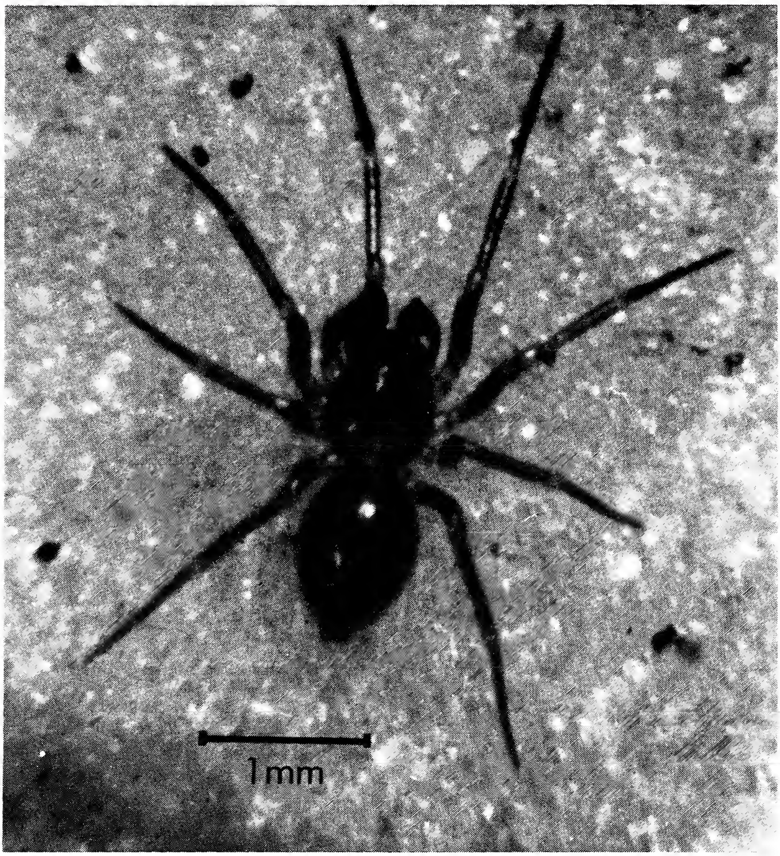

Fig. 1. Male *Masoncus* spider in harvester ant nest chamber.

Belbidae, Uropodidae, Laelaspidae and Rhodacaridae. Belbids are very small mites common in the soil. Uropodids (*Oplitis*) are common in moist litter and are also found in ant colonies (Hunter and Farrier 1976) as are laelaspid mites. The laelaspid found in our nests was probably *Laelaspis moseri* Hunter or *Laelaspis mumai* Hunter. The rhodacarid belonged to the genus *Rhodacarellus,* a potentially predatory genus frequently found in deciduous leaf litter. Harvester ant nests also contained a few silverfish (Nicoletiidae), diplurans (Japigidae) and less frequently millipeds and staphylinid beetles.

I have collected *Masoncus* spiders from harvester ant nests in three widely separated areas south of Tallahassee, but they are probably much more widespread. Spiders were present in almost all of the harvester ant nests I excavated. Each nest contained from a few to several dozen spiders depending on the size of the colony and how carefully I excavated it. Females outnumbered males by four to one in my collections and were consistently the predominant sex.

Spiders were distributed throughout the colony from the uppermost nest chambers to those more than two meters below the surface. Generally, They seem to prefer deeper (>60 cm) chambers with fewer ants, but I have also collected them from brood and seed storage chambers. On several occasions, I have even observed spiders briefly running out of the nest entrance. Spiders seem to prefer the ceilings and periphery of the nest chambers, perhaps because this reduces their contact with the ants.

Spiders were present in the ant colonies throughout the year. Both adults and immatures have been collected in the months of March, May, June, July, August, September and November. These spiders have yet to be collected during mid-winter because cold weather severely inhibits my enthusiasm for excavating half frozen ant mounds. Very young spiderlings appear to be most common in the late months of summer. I have collected eggs in July and September but may have overlooked them in other months as well.

White egg sacks are laid in small depressions on the ceilings of nest chambers about one meter below the surface. The egg sack is 3–5 mm across and contains 2–3 eggs ($x = 2.6$, $n = 10$). The exposed surface of the sack is very smooth and conforms evenly to the contour of the ceiling; if this were not so the ants might destroy the egg sack during chamber maintenance. Spiderlings emerge from the egg sacks after about three weeks (25° C) through a small hole cut in the surface just off center from the egg cluster.

I am not certain whether these spiders are obligate or facultative guests, but the following evidence indicates that they are more than just casual residents of harvester ant nests: 1) I have never found them associated with other ants (e.g. *Solenopsis, Trachymyrmex, Aphenogaster*) nor have I chanced across them living independently. 2) Most harvester ant colonies contain at least a few spiders. 3) Spiders are found in harvester ant nests throughout the year. 4) I have observed spiders feeding in the nests. 5) All life stages are found in the colonies demonstrating that the spiders successfully reproduce under these conditions. 6) Spiders appear to be capable of emigrating with the ant colony because several spiders were present in a colony which was excavated less than a week after it had emigrated. 7) The best evidence that these spiders are specially adapted for life in harvester ant colonies is that the spiders apparently adopt the odor of their host colony. Spiders and ants from the same colony generally ignore one another; workers occasionally displayed mild aggression but the spider was never captured or injured. However, when I introduced spiders into foreign harvester ant colonies, they were almost without exception attacked and killed within minutes or even seconds. Spiders introduced into laboratory colonies of *Trachymyrmex* and *Aphenogaster* ants were similarly attacked and killed.

It would be interesting to know how these spiders disperse among harvester ant colonies, especially how they locate a colony. They are very susceptible to desiccation so it seems unlikely that they would disperse in the daytime. Gaining entrance to a foreign colony would also be a problem since the entrance is sealed at night and guarded by hostile ants in the day.

Many spiders are ant predators (MacKay 1982b, Porter and Eastmond 1982), but relatively few are symbionts (Table 1). Perhaps, this is because spiders have a distinct preference for live prey and are less well adapted to subterranean life than many arthropods. Furthermore, unless a spider actually preys on the ants themselves, colonies must contain rather large and stable communities of symbionts to support a specialized symbiotic predator. The number of symbiotic spider-ant relationships which exist in spite of these seeming impediments (Table 1) is interesting but perhaps not surprising in view of the fact that spiders and ants are among the most abundant of all arthropod groups.

SUMMARY

An undescribed spider of the genus *Masoncus* (Linyphiidae: Erigoninae) was commonly found in colonies of the harvester ant *Pogonomyrmex badius.* This miniature spider is a predator of Collembola and all of its life stages were present in the ant colonies.

Table 1. Symbiotic spiders and their ant hosts.

Spider	Ant Host	Source
Gnaphosidae		
Eilica	*Camponotus*	Noonan 1982
Clubionidae		
Phrurolithus	*Crematogaster*	Emerton 1911
Salticidae		
Cotinusa	*Tapinoma*	Shepard and Gibson 1972
Agelenidae		
Tetrilus	*Formica*	Donisthorpe 1927
Linyphiidae		
Masoncus	*Pogonomyrmex*	Porter
Cochlembolus	*Formica*	Dondale and Redner 1972
Evansia	*Formica*	Donisthorpe 1927
Thyreosthenius	*Formica*	"
Acartauchenius	*Tetramorium*	"

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I thank A. F. Millidge and W. J. Gertsch for identifying the spiders. Voucher specimens have been deposited with H. W. Levi at the Museum of Comparative Zoology at Harvard University. R. J. Snider kindly identified the springtails and P. Hunter identified the mites.

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FURTHER STUDIES ON THE SYSTEMATICS OF AUSTRALIAN DIPLURINAE (CHELICERATA: MYGALOMORPHAE: DIPLURIDAE): DESCRIPTION OF THE MALE OF *TROGLODIPLURA LOWRYI*, WITH NOTES ON ITS AFFINITIES.

By Barbara York Main[1] and M. R. Gray[2]

Introduction

This paper[3] describes a recently discovered male specimen of the troglobitic *Troglodiplura lowryi* Main and attempts to place the genus in the taxonomic perspective of other Australian diplurines.

Troglodiplura lowryi was described by Main (1969) from fragments of a specimen of indeterminate sex collected by J. and D. Lowry from Roach's Rest Cave 43.5 km NE of Madura on the Nullarbor Plain, Western Australia. Because only dead arthropods and no living material of any taxa were known from Roach's Rest Cave, it was unknown whether *Troglodiplura lowryi* was an extant species. It is therefore of considerable interest that in addition to the collection of a dead male specimen, a living specimen has also been observed by A. D. Davey in an unconnected cave north of the Bight in South Australia.

Other records of troglobitic mygalomorphs

Although several other mygalomorphs are known to inhabit caves in Australia, *T. lowryi* is the only fully troglobitic species, i.e. completely cave-adapted species. Prior to Main (1969) recording *T. lowryi* only two other troglobitic mygalomorphs had been recorded from elsewhere: a diplurid, *Accola caeca* Simon from the Philippines (Simon, 1892), which species is now included in *Masteria*

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[3] This paper is the eighth in a series by one of us (BYM) dealing solely with the systematics of Australian Diplurinae. Earlier publications in the series and others in which new diplurine taxa were described are listed in Main (1983b).

Revised manuscript received by the editor January 8, 1985

(Raven, 1979), and a barychelid, *Troglothele caeca* Fage from Cuba (Fage, 1929). Since then Gertsch (1971; 1973; 1982) has recorded 10 additional species of blind or near blind cavernicolous mygalomorphs from the Americas. This brings to about 8 the total of known blind, and an additional five or more near blind cave-adapted mygalomorphs in the world.

AFFINITIES OF TROGLODIPLURA LOWRYI WITH OTHER AUSTRALIAN DIPLURINAE

At the time *Troglodiplura* was described the Australian Diplurinae included six other genera: *Aname* Koch, *Ixamatus* Simon, *Chenistonia* Hogg, *Dekana* Hogg, *Sungenia* Rainbow & Pulleine and *Stanwellia* Rainbow & Pulleine. One species had also been attributed to the extra-limital genus *Brachythele* (Ausserer, 1875). Subsequent descriptions of new genera, and reviews of the Diplurinae (Main and Mascord, 1971; Main, 1972; 1975; 1983b; Raven, 1981; 1984) bring the total of accepted genera to eleven: *Aname, Ixamatus, Chenistonia* [synonymised with *Aname* (Raven, 1981; 1984) but recognized as distinct by Main (1982a,b, 1983b and here)], *Stanwellia, Troglodiplura* Main, *Kiama* Main and Mascord [doubtful placement in the Diplurinae (Main, 1981, p. 869)], *Teyl* Main, *Xamiatus* Raven, *Kwonkan* Main, *Merredinia* Main and *Namea* Raven. However, the affinities of *Troglodiplura* have remained unclear. It is now apparent that one character is shared with several other genera. This is the absence of cuspules from the maxillary heel (see Main, 1969, fig. 1D, and figs 1,3,5,6 here). This arrangement is characteristic of the following genera: *Ixamatus* and *Xamiatus* (Raven, 1981), *Kiama* (Main and Mascord, 1971, see fig. 2) and in part *Stanwellia.* Genera constituting the Anamini as delimited by Main (1983b) and the Teylini which contains the nominal genus *Teyl* (see Main, 1982c) and several undescribed genera (Main, 1983b) and *Namea* (herein included) all have the cuspules spread over the inner side of the maxillae including the modified, projecting heel. [The only exception in these groups is *Aname kirrama* Raven (Raven, 1984) which has the maxillary cuspules confined to the anterior ental region]. On this character then *Troglodiplura* has an affinity with *Ixamatus, Xamiatus, Kiama* and in part *Stanwellia.* Closer affinity with *Ixamatus* and *Xamiatus* is ruled out primarily due to the low tarsal organ in *Troglodiplura* (that is, not rod-like); with *Stanwellia* because of the indented labium and absence of labial cusps in *Troglodiplura*; with *Kiama* due to the different configuration of the sternal sigilla and the U-shaped fovea in *Kiama*.

Collection of a male of *Troglodiplura* initially promised resolution of the relationships of the genus. Criteria used to distinguish male Australian diplurines are predominantly: configuration of the bulb and embolus, spination of the palpal tibia, armature of the first tibia and modifications of the first metatarsus. The Anamini (exclusive of *Merredinia*) comprise the only genera previously described and undescribed (Main in preparation), which bear a pronounced tibial spur on the foreleg, e.g. *Aname, Chenistonia, Kwonkan*. Some of the named Teylini (e.g. *Namea* which is here added to the tribe) may bear heavy spines that are sometimes raised on low spur-like protuberances on the first tibia, but which are never comparable to the single-spined spur of typical Anamini. *Troglodiplura* as described below is shown to have a large tibial spur in the male. However, because it has an unmodified maxillary heel which lacks cuspules the genus would appear not to be closely related to the Anamini and Teylini and the development of the tibial spur is therefore considered as a convergence. Furthermore there is an undescribed genus of the Teylini (Main in press b) in which a tibial spur has clearly arisen independently.

It appears that the tibial spur has convergently evolved at least three times in Australian Diplurinae. It is even possible that it may have evolved independently in several of the Anamini. Finally, *Aname kirrama* which has in combination maxillary cuspules confined to the anterior ental angle of the maxilla and a pronounced tibial spur, would appear to be more closely related to *Troglodiplura* than to *Aname*. However until more specimens are known with *Aname kirrama* affinities, this species is not transferred to *Troglodiplura*. An alternative solution would be to erect another monotypic genus. A disjunct distribution of related taxa, e.g. north Queensland (*Aname kirrama*) and the Nullarbor Plain (*Troglodiplura*) is not really surprising in view of similar distributions of mygalomorph taxa. For example the Homogoninae have representatives in eastern Australian montane areas and southwestern Australia (Main 1983a; description in press a).

It now seems from the morphological features of both male and female specimens that *Troglodiplura* is less anomalous than previously understood. Its main distinguishing features, e.g. lack of eyes, modified tarsi and elongated metatarsi, are associated with its cavernicolous habits. It is known that troglobitic features can evolve fairly rapidly, therefore other less adaptive characters also need to be considered in any postulated phylogeny.

An analogue of the suggested *Troglodiplura* and *Aname kirrama* affinity within the Araneomorphae is the blind *Baiami mullamullangensis* (Gray) from Mullamullang Cave on the Nullarbor Plain. This species was first placed in a new genus *Tartarus* (Gray, 1973) but later shown to have close affinity with species of *Baiami* distributed in southwest Australia, the Lofty Ranges in South Australia and in Victoria (Gray, 1981).

It is of biological interest that while other groups of mygalomorphs, e.g. *Stanwellia* and Homogoninae, which have disjunct east-west distributions (Main 1972, 1976 1983a and in press a) have clearly not been able to persist in the intervening arid central area subsequent to the extinction of humid forested regions prevalent in the early Tertiary, *Troglodiplura* and some araneomorphs, e.g. *Baiami* Lehtinen have survived by adapting to a cavernicolous existence.

Genus *Troglodiplura* Main

Troglodiplura Main, 1969: 9. Type species *Troglodiplura lowryi* Main, by monotypy. Raven, 1981: 340.

DIAGNOSIS

Distinguished by the following combination of characters: absence of eyes, labium with notch-like, anterior identation, unmodified maxillae with cuspules on antero-ental angle only, dorso-ventrally curved tarsi (without spines), male with pronounced tibial spur on first leg, long pear-shaped palpal bulb with tapering embolus in same axis.

Figures 1–10. Figs 1–3. Holotype ♀ *Troglodiplura lowryi*, right maxilla. Figs 1 and 3 ventral aspect. Fig. 2. Antero-ectal angle. Figs 4–10. Metallotype ♂ *T. lowryi*. Fig. 4. Carapace and chelicerae. Fig. 5. Sternal area, maxillae, labium and chelicerae. Fig. 6. Maxillary marginal area. Fig. 7. Ridges on retrolateral side of chelicera. Fig. 8. Left fang, prolateral. Fig. 9. Right tarsus IV, prolateral aspect. Fig. 10. Right tarsus IV, retrolateral view, retroclaw. Scale bars = 1.0 mm; figs 2, 3, 6, 7, 8, 10 not to scale.

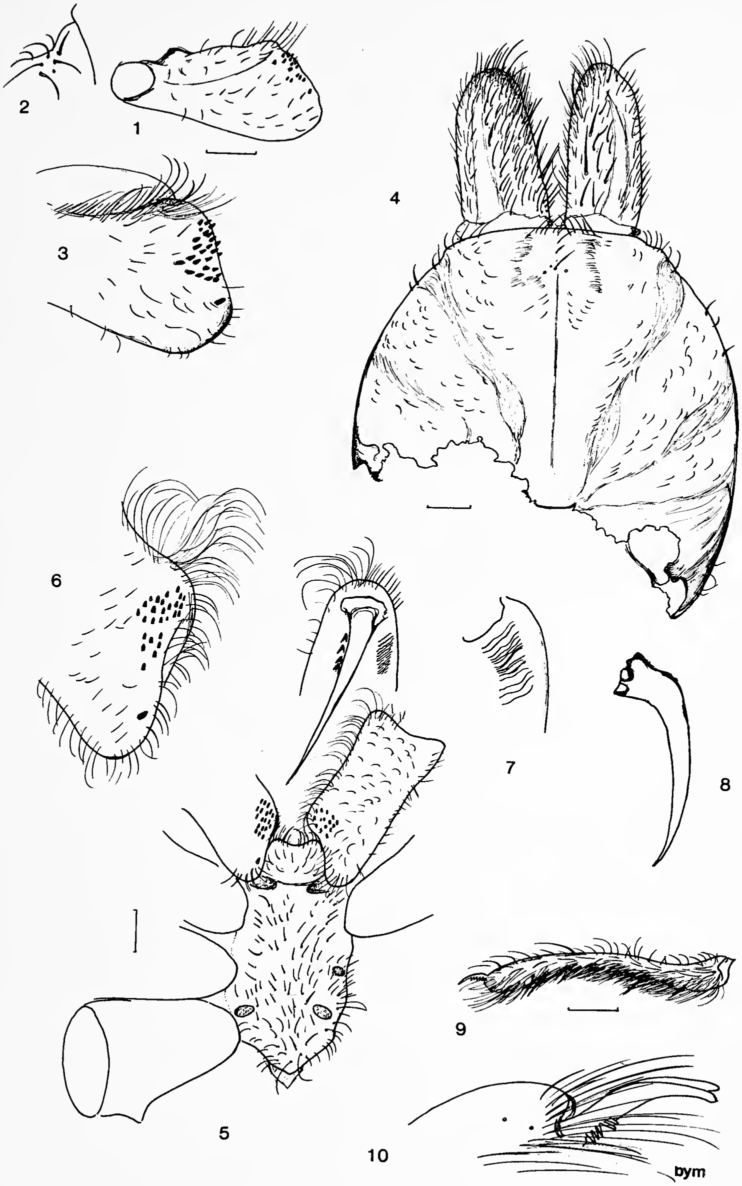
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TABLE 1. Approximate leg measurements of right legs.

	F	P	Ti	Mt	Ta	Total
Palp	8.1	3.9	6.7	—	3.6	22.3
I	12.3	5.8	11.3	14.3	6.7	50.4
II	12.1	5.4	12.1	14.6	6.2	50.4
III	10.7	4.0	10.2	14.0	5.0	43.9
IV	12.7	4.2(?)	12.6	18.3	5.0	52.8+

Width of patella I at knee = 1.6; Tibial index = 9.41.

An absence of eyes distinguishes *Troglodiplura* from all other Australian Diplurinae. It is further distinguished from the Anamini and Teylini by the maxillary cuspule arrangement which it shares with *Ixamatus, Xamiatus, Stanwellia* (in part) and *Kiama*. It differs from these four genera by the presence of a tibial spur in the male.

Troglodiplura lowryi Main

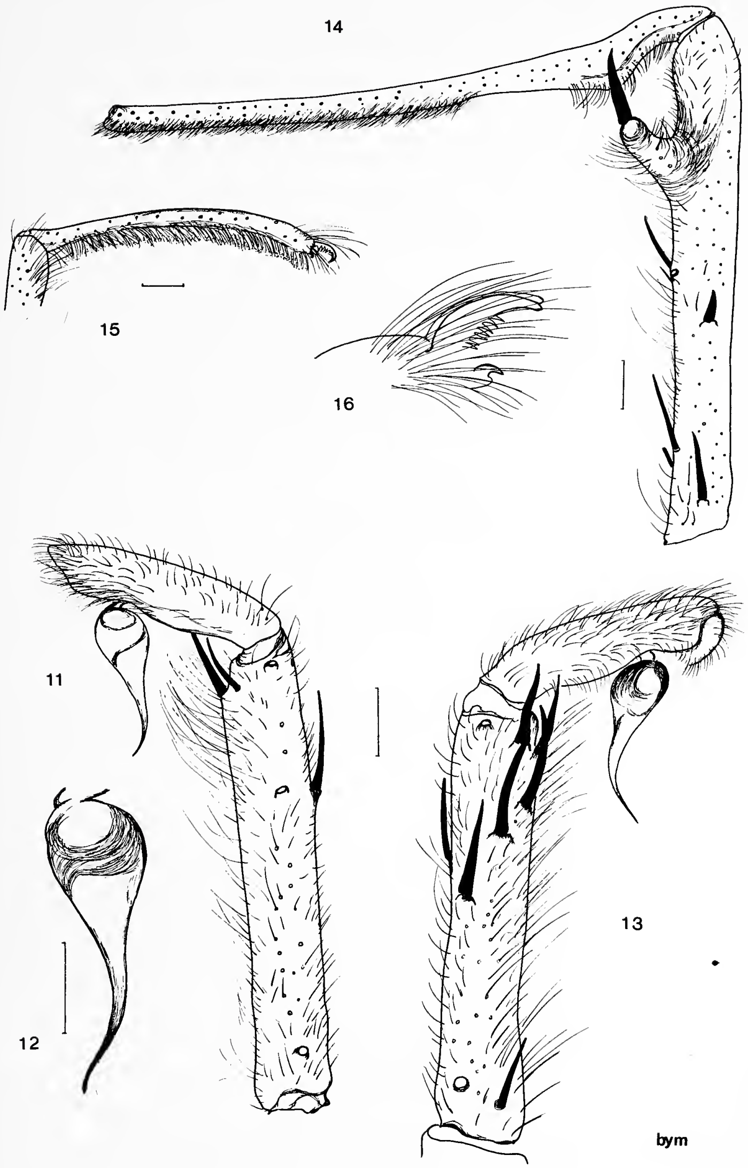
Figs 1–18, Table 1

Troglodiplura lowryi Main, 1969: 9–11. Holotype, indeterminate sex, WESTERN AUSTRALIA: Roaches Rest Cave, NE Madura (Western Australian Museum)

Metallotype, ♂, AUSTRALIA: South Australia, Nullarbor Plain, Cave NR. 6 Bore NNW of head of BIGHT, 27.v.1982 (A.D. Davey) (Australian Museum KS 13389). ["Metallotype"—as defined by Smith, 1983].

Condition of specimen poor, dismembered parts of a dried carcase, some colour still apparent as the dark reddish brown of carapace, chelicerae and tibiae and metatarsi of first legs; many bristles, hairs and spines lost, including trichobothria. Carapace and sternum slightly distorted at margin; left posterior region of carapace missing. Abdomen absent.

Figures 11–16. Metallotype ♂ *Troglodiplura lowryi.* Fig. 11. Left palp, retrolateral aspect. Fig. 12. Bulb and embolus enlarged. Fig. 13. Left palp, prolateral aspect. Fig. 14. Left leg, retrolateral aspect tibia and metatarsus. Fig. 15. Right tarsus I, retrolateral aspect. Fig. 16. Right tarsus I, retrolateral aspect of retroclaw. Scale bars = 1.0 mm; fig. 16 not to scale.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Carapace broad (9.3 mm wide), with cervical depressions, posteriorly damaged with left section missing; caput width 5.4. Probably glabrous in life, caput with thin scattering of golden hairs, finely granulated surface, possibly reticulated. Length from clypeus to fovea 6.5. Fovea very slightly procurved. Eyes absent, a fine bristle and sockets of two others in "ocular area" (Fig. 4); a group of bristle on clypeal margin. *Chelicerae* long and narrow, dark reddish-brown, with coarse, dorsal bristles, no rastellum; transverse ridges on outer (retrolateral face). Promargin of right chelicera with 10 teeth (9 on left), retromargin with at least 6 small basal teeth (11 on left chelicera) extending distally to opposite about teeth 4 and 5. *Maxillae* not indented around labium but with long angular heel obscuring it; cuspules on inner ental angle only (about 31 plus a large one on heel of right maxilla, left with about 26; some loosely attached, some detached). *Labium* broad and deeply indented at margin, length 1.0 mm, width at least 1.5 mm, without cuspules. *Sternum* distorted and curled under at edges, length 4.6. Sigilla separating labium divided. Posterior sigilla broad, roughly oval, well away from margin, median sigilla small, roundish, anterior pair obscured. *Legs*. Scopula complete on tarsi I, II and III, absent from tarsus IV, complete on metatarsus I but thin proximally, almost entire on metatarsi II, distal half only on metatarsus III, absent from metatarsus IV; tarsi with ventral median band of bristles; tarsus IV although lacking a true scopula has a dense brush of fine bristles intermixed with heavy spine-like bristles (Fig. 9).

Metatarsus I very long, ventrally depressed proximally and with pronounced "elbow" in proximal third. Tibia I with a spur, bearing a single megaspine, in apical third. Palp with long slender tibia with several heavy retro- and prolateral spines. Palpal bulb long, ovoid, with embolus arising on long axis; no demarcation between embolus and bulb (Figs 11–13).

Spines (right appendages except leg II). Approximations only. Palp, tarsus 0, tibia d 1, p 3 proximal (lost) 6 distal (lost), r 7 (3 lost), patella p 1 (lost), femur p 2 median adpressed bristle-like spines. Leg I, tarsus 0, metatarsus 0 (left p 1 lost), tibia v 2 + megaspine on spur, pv 2, p 2, d 2 (left pv 2 rv 2, p 2, r 2), patella p 2 (lost) (left p 2 lost), femur d 3, p 6 adpressed bristle-like spines, r 3 rd 1 (left d 4 lost), p 4 (lost), r 4 (lost). Leg II (left), metatarsus v 3 (2 lost), d 1, p 2 (lost), r 2, tibia v 1–2–2–3, p 3 (lost), r 3, patella p 2 (lost), femur d 3 or 4, rd

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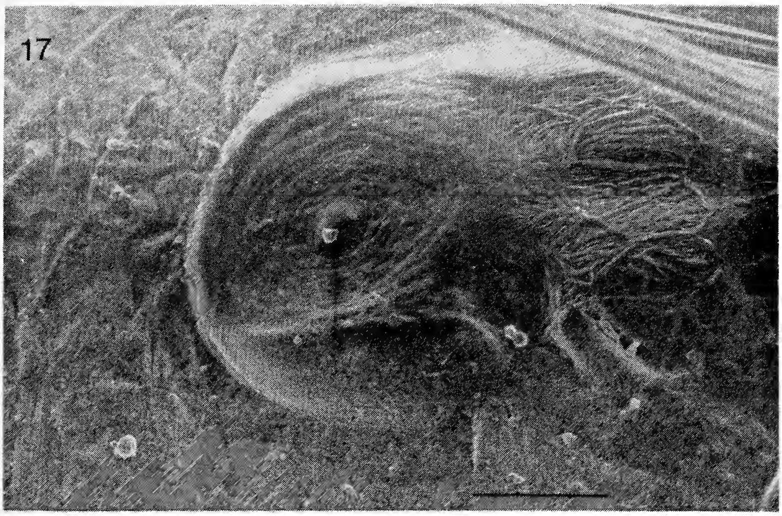

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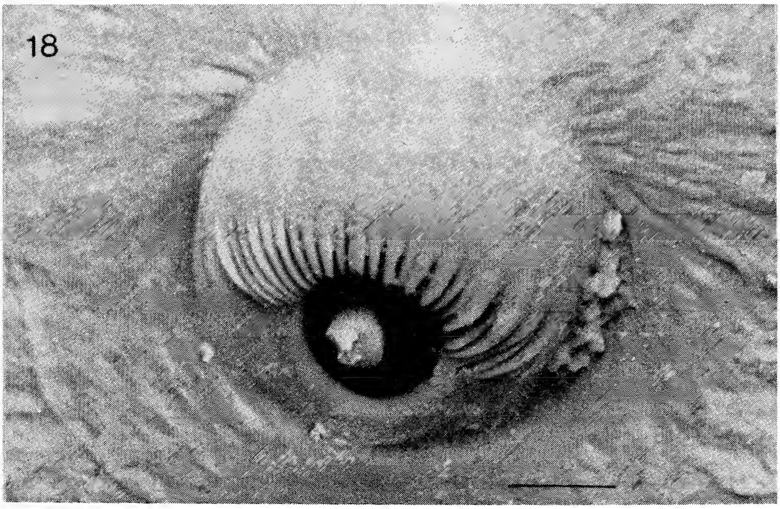

Figures 17, 18. Scanning electron microscope photographs, *T. lowryi*. Fig. 17. Tarsal organ. Fig. 18. Trichobothrial base. Scale bars = 10 μm.

about 4, p about 6 (lost). Leg III, tarsus 0, metatarsus v about 10 (some lost), d about 5, p 6, r 4, tibia v about 10 (some lost), d 3, p 6, r about 4, patella p 2 (lost), r about 3, femur rd 4, p 9, r at least 4. Leg IV, tarsus v with long bristles, metatarsus v about 13, d about 5, p about 8, r 4, tibia v about 7, d about 4, p about 7, r 6, patella p about 3, r ?, femur d 4 or 5, p about 9, r about 5. Trichobothria generally lost, appear to have been less numerous than in most Australian diplurines. *Tarsal claws* all with double row of long and needle-like teeth (up to 9 or more in each row); inner rows of teeth begin distally to base of outer rows.

Remarks

The tarsal "spines" referred to by Main (1969) are not comparable to the usual heavy spines found on diplurine legs and as for the above specimen would be better described as "bristles".

ACKNOWLEDGEMENTS

We are grateful to A. D. Davey who collected the male specimen of *Troglodiplura*. Support from the Australian Biological Resources Study programme to one of us (BYM) is acknowledged.

SUMMARY

A male specimen of the cavernicolous genus *Troglodiplura* is described. It is suggested that a tibial spur, previously considered unique to the Anamini has arisen independently in *Troglodiplura*. Close affinity with other Australian Diplurinae is not recognized.

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EOBRACONUS, A SUBSTITUTE NAME FOR *EOBRACON* RASNITSYN (HYMENOPTERA, BRACONIDAE)

By A. P. Rasnitsyn
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A few years ago I erected *Eobracon* as a generic name for a fossil braconid wasp (Rasnitsyn, 1983). This generic name, however, was previously used by Cockerell (1920) for another fossil braconid wasp. Since *Eobracon* Rasnitsyn is, therefore, a junior homonym of *Eobracon* Cockerell, I herein propose **Eobraconus** Rasnitsyn, new name, to replace *Eobracon* Rasnitsyn, 1983. The only species affected becomes *Eobraconus inopinatus* (Rasnitsyn), new combination.

I am grateful to Professor Frank M. Carpenter for drawing my attention to this homonymy.

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PSYCHE

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BEHAVIORAL NOTES ON THE ASIATIC HARVESTING ANTS *ACANTHOMYRMEX NOTABILIS* AND *A. FEROX**

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The workers of some ants fall into two size classes, each with a distinctive morphology and without intermediates. This condition, known as complete dimorphism, has arisen independently at least seven times among ants (Wilson, 1971). Perhaps the most dramatic examples of the dimorphic worker condition are found in the myrmicine genus *Acanthomyrmex*. One of the most startling species is *A. notabilis* (fig. 1), in which the trunk and gaster of the major are only fractionally larger than those of the minor caste, while the head is relatively enormous. In life, the head is thrown back over the trunk, and in fact much of the trunk fits conveniently into a cavity in the underside of the head capsule. The trunk is therefore virtually concealed even when the animal is viewed from the side. Moreover the waist and gaster are typically drawn up close to the body and are thus inconspicuous. Indeed, an observer's initial impression of a live *A. notabilis* major will likely be one of a "walking head."

Eleven species of *Acanthomyrmex* ants have been collected (Moffett, in prep.), all endemic to the Oriental region. To date no information pertinent to the behavior and ecology of these rarely collected ants has been reported. I present preliminary findings concerning two species here.

**Manuscript received by the editor May 10, 1985*

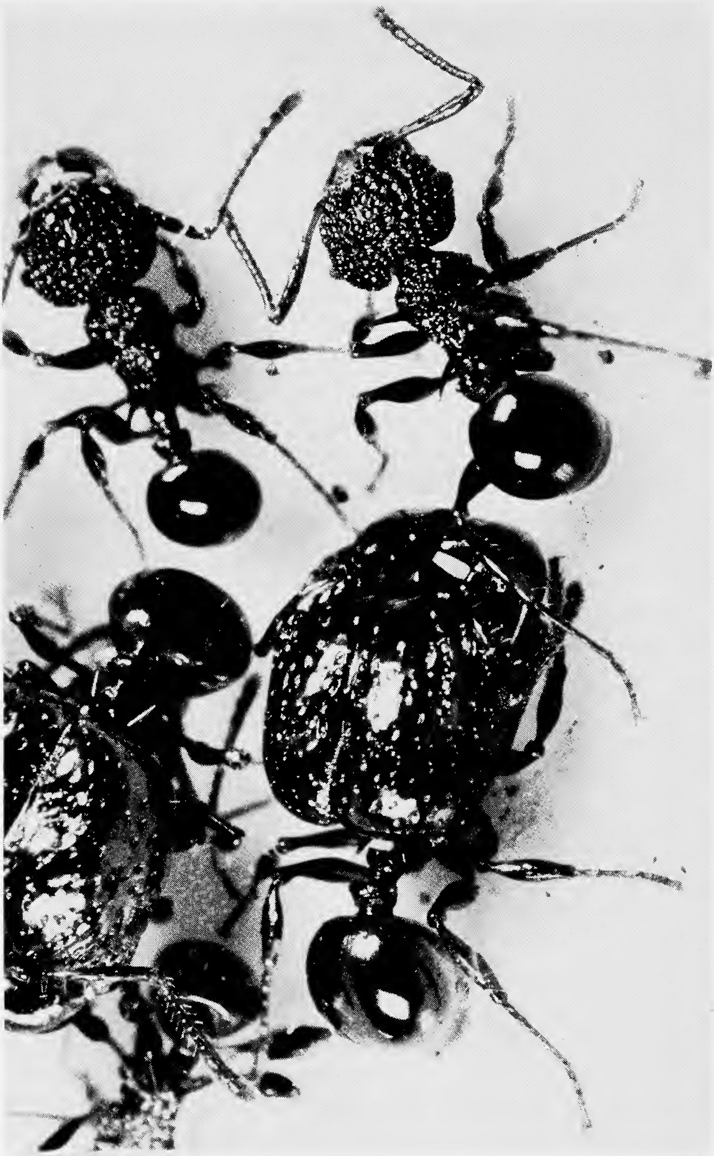

Figure 1. Captive workers of *Acanthomyrmex notabilis.*

FIELD NOTES

Acanthomyrmex notabilis. A colony of *A. notabilis* (F. Smith) was discovered at an elevation of about 200 m in primary rain forest at the Tangkoko-Batuangus Reserve in Northern Sulawesi. The entrance to the nest was a simple, unadorned opening near one end of a 15 cm diameter log. Minors foraged on the mossy surface of the log and in the leaf litter at its side. All foragers located during two hours of behavioral observations were within 40 cm of the nest; no more than three ants were seen foraging at any one time.

The log was dissected with a machete. The wood was hard and in good condition. The nest entrance led into a single passageway, 6 cm long and 4 mm in diameter with smooth, hard walls. This was apparently a natural channel, modified little if at all by the ants. The colony contained three majors, 37 minors, and numbers of eggs, larvae, and pupae. Unfortunately no queen was found. If the nervous behavior of the *A. ferox* queen described in the next section is typical of the genus, it is likely the *A. notabilis* queen escaped while I chopped free the end of the log with the colony. However, few if any workers probably escaped, as no workers were observed even to approach the entrance during this time.

The captive ants were placed in a 8.5 × 13.5 × 3.5 cm high plastic box with a transparent lid and compacted soil substrate. The ants clustered together on the substrate, with the majors at the periphery of the cluster. Later the ants moved into a test tube with stoppered water supply. Before this emigration occurred, one to four minors usually foraged at any given time, but after the emigration no ants were observed to depart from the tube to forage.

Acanthomyrmex ferox. I collected *A. ferox* Emery workers in rain forest at Pleihari-Martipura Reserve Forest in Central Kalimantan, Indonesia. I found foragers in the same area on two subsequent afternoons. These foragers moved largely on top of leaf litter, perhaps in this way avoiding the many relatively aggressive *Lophomyrmex* and *Pheidologeton* ants on the ground below.

A group of workers and males with a dealate queen was eventually located by following ants that carried sugar grains or sesame seeds from baits I had set out. The ants were clustered together between two small leaf fragments suspended above ground level within loose leaf litter. The ants and males were lined up side by side; one minor held a larva in its mandibles. Except for the queen, which quickly rushed off into the surrounding litter, none of the ants made any move during my disturbances, even when I carefully picked up one of the fragments in forceps for close examination.

Additional workers (including a major, a minor carrying a larva, and three instances of adult transport of minors) were taken from a 2.5 m route extending along the ground and over leaf litter to the nest site. The ants had apparently been in the process of emigrating to the site of the leaf fragments. Unfortunately I was unable to trace the emigration route back to its origin because of the scarcity of ants along it. Indeed, during over an hour of observations on this route, the frequency of ants declined until none were seen during the last thirty minutes. Altogether I took 47 minors, two majors, seven males, one dealate queen and a small number of brood. Presuming the emigration had been at or very near completion, this would represent nearly the complete colony.

The captive ants were maintained as described for the *A. notabilis* colony. As in *A. notabilis*, the workers congregated together on the exposed surface with the brood massed together among them and with the majors usually at the periphery of the brood area. The location of the cluster often shifted.

DIET

Acanthomyrmex notabilis. A. notabilis apparently has a broad diet, collecting fruits and seeds, capturing tiny invertebrate prey, scavenging for dead invertebrates and probably accepting a variety of sugary materials as well.

Only one returning *A. notabilis* forager carried food, this a tiny (0.5 mm) fragment of a small isopod. In captivity minors promptly carried small arthropod corpses to the nest. There the corpses were surrounded by minors, which licked them and gradually tore them into pieces. Majors were never observed to feed on animal material (or any other food except by regurgitation).

There is some evidence for predation in this species. In the field four live 2–3 mm immature centipedes were placed before foraging ants; these were picked up and carried directly to the nest. A small entomobryid collemolan, which I held before a forager with fine forceps, was also seized and carried off. In the captive colony a tiny live hemipteran nymph was seized by a minor, carried to the nest, and then torn apart and consumed by several individuals.

A clump of about 35 fig seeds was present within the *A. notabilis* nest (fig. 2). Similar tiny seeds were found in the nests of *A. notabilis* colonies collected from rotten wood by W. L. Brown, Jr. on Mount Klabat, not far from Tangkoko-Batuangus Reserve. A minority of other, unidentified seeds of a size comparable to the fig seeds or slightly larger were also present in these nests. In the field *A. notabilis* minors carried three sesame seeds to their nest from a bait of bird seeds. However, captive *A. notabilis* ants completely ignored all seeds provided, including the fig seeds taken from their own colony.

There are indications that seeds are normally a significant part of the diet. Many of the fig seeds taken from *A. notabilis* nests had their outer layer gnawed away. Moreover, the mandibles of the majors were badly worn, which would be expected if this caste mills seeds. The region of northern Sulawesi that includes Mt. Klabat and the neighboring Tangkoko-Batuangus Reserve is exceptionally rich

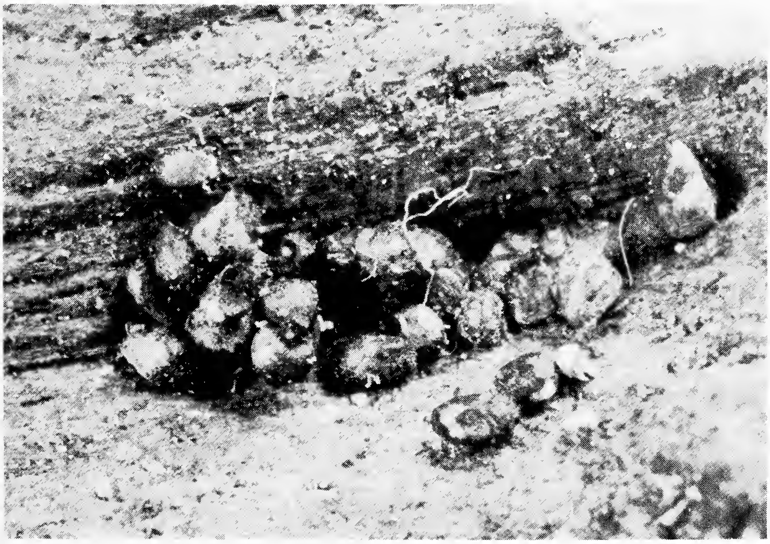

Figure 2. Fig seeds from *Acanthomyrmex notabilis* colony in situ.

in fig trees, which could account for the apparent high density of *A. notabilis* colonies in the area.

The *A. notabilis* minors frequently drank from sugar or honey solutions (while largely ignoring baits of cooking oil). I was unable to find any evidence of recruitment to sugar baits (or any other foods) either in the field or in the laboratory. For example, during a 90 minute period several minors independently found and drank at a sugar bait placed 8 cm from the nest entrance in the field. Although ants that had fed usually returned directly to the nest, their return was not followed by an increased rate of forager exodus. The response of the ants to baits located far from the nest remains to be investigated.

Acanthomyrmex ferox. A. ferox probably has a similar diet breadth to *notabilis*. In the field I provided the foragers with baits of sugar grains, olive oil, and seeds from a canary seed mix with sesame seeds added. Two ants drank from the oil baits and several carried off sugar grains and sesame seeds (but no other seeds). In captivity the minors consumed dead insects and drank sugar water; capture of small prey was not demonstrated. As in *A. notabilis*, no feeding was ever observed on seeds. However, in this case the ants did carry sesame seeds and fig seeds to their current "nest site" on the floor of the plastic box, and when the nest site shifted, the seeds were transferred along with the brood. Most likely this species is also partially granivorous.

A. NOTABILIS BEHAVIORAL REPERTOIRE

A total of 344 behavioral events were recorded during eight hours of observations on the captive *A. notabilis* ants over a 10 day period, during which time 3 majors and 17–18 minors were alive (in addition, about fifteen hours of observations were made before the ethogram data was compiled). The ethogram is presented in table 1.

Workers frequently held immatures in position for long periods, loosely grasping them in their mandibles ("hold eggs, larvae, or pupae" behaviors in table 1). Pupae and large larvae were held while still resting on the ground, and smaller immatures, including clusters of eggs and microlarvae, were often held raised from the ground. A high percentage of workers holding immatures indicated a low level of colony excitement, although one to a few workers

Table 1. *Acanthomyrmex notabilis* ethogram. The actual numbers of acts recorded are followed in parentheses by the relative frequencies of performance of each act. When fitted to a lognormal Poisson probability distribution using a computer program written by R. M. Fagen (see Fagen and Goldman, 1977), the complete repertory of the minor workers is estimated to include 20 behavioral acts, with a 95% confidence interval of [20, 21] acts.

	MINORS	MAJORS
1. Allogroom minor	53 (.1541)	0
2. Allogroom major	17 (.0494)	0
3. Lick eggs	3 (.0087)	0
4. Lick larva	45 (.0131)	0
5. Lick pupa	29 (.0843)	0
6. Hold eggs	11 (.0320)	1 (0.5)
7. Hold larva	30 (.0872)	0
8. Hold pupa	14 (.0407)	0
9. Carry eggs	9 (.0262)	1 (0.5)
10. Carry larva	24 (.0698)	0
11. Carry pupa	14 (.0407)	0
12. Assist ecdysis to pupa	6 (.0174)	0
13. Feed larva	6 (.0174)	0
14. Regurgitate to minor	5 (.0145)	0
15. Regurgitate to major	1 (.0029)	0
16. Lick sugar grain	36 (.1047)	0
17. Eat dead insect	31 (.0901)	0
18. Hold dead minor	2 (.0058)	0
19. Lick dead minor	5 (.0145)	0
20. Carry dead minor	3 (.0087)	0
TOTALS	334 (.9999)	2 (1.0)

commonly held brood even under apparently quiescent conditions. Majors occasionally also held or carried immatures, even when the nest was undisturbed.

Only minors were observed to allogroom and to lick brood. Larvae fed on regurgitated food from minor workers.

Nest Shifts and Emigrations

Acanthomyrmex notabilis. Before the *A. notabilis* colony had moved into the test tube nest, sudden, severe disturbances (such as shaking the box with the ants) caused the ants to rapidly disperse, with many of the workers carrying brood. Following such a disturbance, small groups of two to four ants usually formed within 10 minutes, and often within a half hour virtually all the ants had recongregated at a single site often different from the original site. During four such cases of worker dispersal I recorded one instance in which a major carried a mass of eggs and microlarvae, and three of a major carrying larvae. When majors held immatures in an undisturbed colony they gripped them gently. During disruptions, however, majors squeezed the brood severely, so that the larvae were pinched. Whether this ever resulted in brood death is not known.

If a shaded nest site was made available to the ants after exposing the current site to a moderately strong light, transfer of workers and brood to that site usually began within an hour. The ants which originally held immatures in place were generally not those that carried them to the new site; rather, most or perhaps all of the carrying was accomplished by those often relatively few individuals that had previously been to the new site. If an immature was held by a worker, the approaching ant would antennate the immature, then grasp it in her mandibles and pull gently, her antennae sometimes palpating the other worker. The worker usually released its grip within one to 15 seconds, at which point the first ant promptly carried it away. The ants that had never left the original site gradually appeared to become aroused by the activities of the workers around them, until they, too, sought out and found the new site.

I observed only one instance of adult transport in the course of a shift in colony location, when a normally pigmented minor worker carried a teneral worker. Whether the transfer process also involved some other, more subtle form of recruitment is unclear. However, well defined routes between the old site and the new were lacking. The size of the observation box limited these shifts in nest location to at most a few centimeters; emigrations over greater distances might well be differently organized.

Acanthomyrmex ferox. Shifts in nest location also occurred in captive *A. ferox*. These were initiated by the queen, which often ran out of the brood area following a disturbance; workers and males at the nest site were not so readily disturbed and thus were usually left behind. When one or more workers located her again the colony shifted to her new location. Minor workers carried the brood and males. The males were grasped dorsally at the trunk or waist, with their heads directed either up or down.

During these nest shifts a consistent route often developed between the old site and the new. The emigrating ants observed in the field also followed a distinct route, which in this case could have been at most a few centimeters wide.

DEFENSIVE BEHAVIOR

Acanthomyrmex notabilis. Foraging minor workers of both *Acanthomyrmex* species were very shy, retreating even after slight disturbances. However, when workers of *Pheidologeton, Aphaenogaster,* and *Pristomyrmex* species common in the vicinity of the nest of *A. notabilis* were held in forceps up to the nest entrance, minors soon emerged to bite at the forager and sometimes grapple with it; the *Pristomyrmex* evoked the strongest response. Following such an experiment, no ants emerged to forage for at least five minutes. After withdrawing each "intruder," I could barely make out the head of a major worker just within the entrance, where no major had been previously. The major bit at a forceps tip that I pushed inside the entrance, holding on so tenaciously I could pull it from the nest.

Captive workers could likewise be provoked to seize a forceps tip, particularly when the worker was in or near the brood area. Biting ants commonly held on so tenaciously that they could be pulled free from the ground. When pulled free, they usually released their grip within a few seconds, unless their tarsi still clung to a piece of substrate, such as a bit of soil—in which case majors in particular would maintain a grip for as long as a minute (fig. 3). Minors gripping a loose object usually rotated that object forward beneath them, while majors did not. Possibly this is explained by a tendency for minor workers to pull backwards when grappling with an intruder.

Captive *A. notabilis* workers fled from *Solenopsis* and *Monomorium* ants, and there was a rapid exodus of the ants and brood if an intruder entered the nest area. However, if the intruders first had their gasters excised, the *A. notabilis* ants behaved much as they did towards single *Pheidologeton diversus* minor workers, which lack the severe stings of *Solenopsis* and *Monomorium*. In this case an *A. notabilis* minor often stood its ground for several seconds, either repeatedly biting at the intruder, or swinging its gaster under its body towards the intruder, or both. A major most commonly first

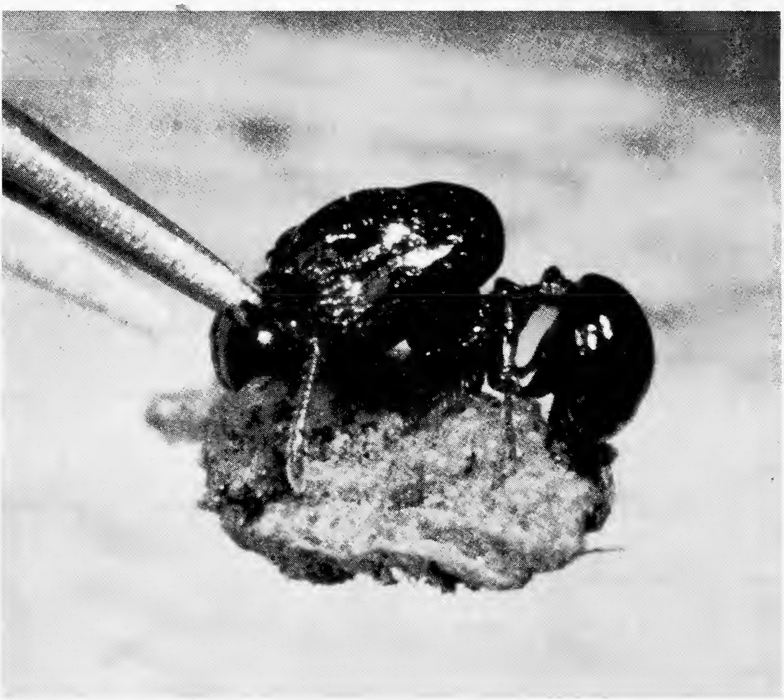

Figure 3. Major worker of *Acanthomyrmex notabilis* biting a forceps tip while clinging to a chunk of soil.

lowered its head so that the intruder was confronted with the broad expanse of the head in full face view, and then brought its gaster under its body, aiming it intermittently at the intruder. Majors sometimes bit and occasionally killed *Pheidologeton* minors, but never *Solenopsis* and *Monomorium* ants, even those with their gasters removed. Workers were most likely to confront an intruder approaching the brood area, and usually fled from workers of other ant species encountered elsewhere.

In two cases I observed an *A. notabilis* major bite and kill insects other than ants; these were a 3 mm embiopteran and a termite worker. Both insects had approached the brood area, at which time the major had responded rapidly and effectively, while minors ignored the intruders or moved away. Thus the majors were apparently responding to nest intrusion. After a period in which the corpse was ignored, the minors found and began feeding on the embiopteran.

Acanthomyrmex ferox. Defensive behaviors of workers of *Acanthomyrmex ferox* confronted with *Lophomyrmex* were similar to those described for *A. notabilis*: both majors and minors antennated the intruder rapidly and then attempted to bite it, or to swing their gasters beneath their bodies in the direction of the intruder, or both. As in *A. notabilis*, the gaster tip was usually brought into contact with the intruder, at least intermittently: examination of photographs indicates that the ants were extruding their stings. *Acanthomyrmex notabilis* workers have the sting apparatus greatly reduced relative to the size of the ant (Kugler 1978), and this is also true of *A. ferox*; however, this appears not to preclude a defensive function.

DISCUSSION

COLONY SIZE. *Acanthomyrmex* colonies appear to be small: the *A. notabilis* and *A. ferox* colonies apparently both consisted of less than fifty individuals. In the *A. notabilis* colony, 7.5% (or three out of 40) of the workers were majors, while this figure is 4.1% (two out of 49) in the *ferox* colony. Colonies of *A. notabilis* from Mt. Klabat collected by William L. Brown, Jr. (pers. comm.) also contained about 40–50 workers, including 1–3 majors.

In both *Acanthomyrmex notabilis* and *A. ferox*, workers frequently held immatures passively in their mandibles for long periods, even during intervals of colony quiescence. Similar behavior has been observed for workers of the trap-jawed formicine ant *Myrmoteras toro* (Moffett, in press). The brood holding behavior in both cases seems to represent a means of insuring that workers can rapidly disperse with brood whenever the colony is disturbed. This is a particularly useful strategy for ants nesting in exposed sites where disturbances are common. As in the *A. ferox* colony described here, the *Myrmoteras* colony, which consisted of 22 workers and one queen, had been nesting between leaves lying loose within leaf litter on the forest floor.

Another common trait of *Acanthomyrmex, Myrmoteras toro*, and many other ants with small colonies (including colonies of many ants at an early stage of growth after the first brood has been raised by the queen, E.O. Wilson: pers. comm.) is the tendency for the queen to be very sensitive to disturbances. While the workers of *Acanthomyrmex* ants are usually timid, the queen of *A. ferox* (and presumably also *A. notabilis*) is exceptionally shy: she often rushed out of the nest at the slightest sign of trouble, leaving her workers, as yet undisturbed, behind her.

HARVESTING ANTS. Nests of the species *A. notabilis* have seed stores, and therefore at least this *Acanthomyrmex* clearly joins the select group of species commonly referred to as "harvesting ants." Harvesting ants are most diverse and abundant in xeric situations. The cosmopolitan genus *Pheidole*, however, includes numerous harvesting ant species found in mesic habitats (W. L. Brown, Jr., pers. comm.). On the other hand, species of the tropical Asian genus *Pheidologeton* have been considered harvesting ants, but while these ants harvest large quantities of seeds, apparently none store seeds (pers. obs.).

The majors of all *Acanthomyrmex* species have traits characteristic of seed millers, including greatly enlarged heads and heavy mandibles with the masticatory borders often severely worn. It is therefore reasonable to infer that the diet of all these species consists at least in part of seeds, but whether all are harvestor ants remains to be ascertained.

BEHAVIOR OF THE MAJORS. In the course of this study various roles have been implicated for majors of *A. notabilis*:

(1) Majors presumably mill seeds.
(2) Majors play an important role in colony defense, guarding the entrance when there is a disturbance there, and often biting intruders that attempt to enter the nest.
(3) Majors sometimes carried immatures following severe nest disturbances that led to worker dispersal with brood.
(4) Majors occasionally held or carried immatures in an quiescent colony.
(5) I have one observation of a major holding and carrying a piece of prey.

As in other *Acanthomyrmex* species, the gaster of *A. notabilis* is small, contracted and beadlike; there is apparently no tendancy for majors to take on a replete condition.

Majors of *A. ferox* are involved in attacks on intruding ants, and, as in *A. notabilis*, a role as seed millers is probable. During my limited observations on this species majors were not observed holding or carrying brood.

Majors probably never forage. In the captive colonies, majors of both species were invariably at the nest unless there was a disturbance serious enough to cause the ants to disperse. The only major seen away from the nest site in the field was an emigrating *A. ferox* individual.

Although seed milling has yet to be confirmed by direct observation, this activity very likely represents a primary function of the major caste. Oster and Wilson (1978) point out that seed specialists tend to be monomorphic or at most weakly polymorphic, while ants that have a broad diet consisting only partially of seeds are most likely to be polymorphic, with an extreme miller caste. Strongly dimorphic *Acanthomyrmex* ants have diets composed of small prey and scavenged material as well as seeds, and thus adhere to this rule.

In *Acanthomyrmex* only a very few individuals of the major caste are present in any one colony. Indeed, majors form only a small fraction (less than 10%) of the total worker population, even though the colonies as a whole are very small. This is as would be predicted on the basis of ergonomic theory (Wilson 1968, Oster and Wilson 1978). Because the morphology of *Acanthomyrmex* majors is so specialized, they would be expected to be very efficient at those specialized behavioral acts which they do perform. Therefore, relative to a species in which majors are anatomically less deviant from the minors, fewer individuals are necessary to perform the specialized tasks.

Ergonomic theory also predicts that the more specialized the anatomy of the major, the more specialized its behavior, and the more limited should be its behavioral repertoire (Wilson 1968, Oster and Wilson 1978). It is therefore somewhat surprising to find that *A. notabilis* majors, perhaps anatomically the most extreme majors of any dimorphic ant, perform at least five social behaviors, among them holding and carrying brood.

Wilson (1984) has shown that in *Pheidole*, majors normally perform a more or less restricted set of behavioral acts. However, they can expand their repertoire to nearly equal that of the minor workers if the ratio of majors to minors is increased experimentally to beyond a set threshold value. This occurred within an hour of the reduction of minor worker numbers to below the threshold. Wilson suggests that *Pheidole* majors serve as an "emergency stand-by caste" following periods of high minor worker mortality.

One possibility is that the apparent behavioral flexibility of *A. notabilis* majors could be a result of the small size of *Acanthomyrmex* colonies. In small colonies it is likely that the number of minor workers available at any given time will often drop below some minimum necessary to carry out the normal affairs of a colony; as a result frequent temporary crises can be expected to occur. For example, a single rich food find could divert much of the limited population of minors to food harvesting activities, so that for a time an insufficient number of minors are available to care for brood; a larger colony will probably be able to draw upon a reserve force of minor workers to handle such situations. If such labor crises are indeed common, it may be most effective to lower the thresholds beyond which majors perform the behavioral acts typical of minors, so that the threshold is closer to the normal ratio of majors to minors than Wilson (1984) found for *Pheidole*. Perhaps the death of about half of the original minor worker population prior to the start of my observations on the captive *A. notabilis* colony had been sufficient to elicit an expansion of the major behavioral repertoire. If so, further studies may show that under most conditions the repertoire of majors is restricted to defense and seed milling.

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FECUNDITY, DEVELOPMENT AND NATURAL HISTORY OF *MERONERA VENUSTULA* (ERICHSON) (COLEOPTERA: STAPHYLINIDAE: ALEOCHARINAE)*

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Introduction

Knowledge of habits of the large, diverse and taxonomically difficult staphylinid subfamily Aleocharinae is very incomplete (Ashe 1981, 1984, Ashe and Watrous 1984). It has been generally assumed that, except for aberrant groups such as the fungus-feeding Gyrophaenina (Ashe 1984), aleocharines as a whole are mostly generalist predators (Fenyes 1918–21). Yet the diversity of aleocharines and their abundance in many habitats suggests that other means of resource use may have been evolutionarily explored. A greater understanding of the diversity of ways that aleocharines use the habitat, the distribution of use patterns and relationships of these patterns to phylogenetic relationships among taxa is essential for clarifying major evolutionary features within this subfamily.

This paper represents a contribution toward that knowledge. It developed from attempts to keep a variety of aleocharine adults in the laboratory, and to encourage them to lay eggs with the hope of obtaining identified larvae which could be compared with aleocharine larvae frequently encountered in he field. The procedures were particularly effective for specimens of *Meronera venustula* (Erichson) (Tribe Tachyusini).

The genus *Meronera,* described by Sharp (1887) from Central America, includes 9 species (Fenyes 1918–21). Most described species occur in Central or South America, and the group appears to be primarily Neotropical in distribution. In America north of Mexico, 1 species, *Meronera venustula* (Erichson) [including 2 species described by Casey (1906) and synonomized by Fenyes (1918–21)] is

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known. Little information on biology, habitat or life history of any member of *Meronera* is available.

Meronera venustula (Erichson 1840) is distributed throughout the eastern half of the United States. Only Blatchley (1910) provides sketchy notes on its biology. He noted that specimens of *M. venustula* were collected by sifting vegetable debris, and stated that specimens overwinter as hibernating adults, though he gives no data to support this statement.

Adults of *Meronera venustula,* collected in the early spring, were easily maintained in the laboratory. Though cultures were maintained primarily to provide correct larval associations, observations of such colonies has provided considerable information about feeding habits, fecundity, longevity and developmental times of adults and immatures. It is recognized that such observations under artificial conditions may not accurately reflect life history characteristics in natural situations. However, they are suggestive and provide a first approximation to understanding the natural history and ecology of these aleocharines.

In this paper, I provide information about the feeding habits, egg-laying rate, immature developmental times and longevity of adults of *Meronera venustula* based on colonies maintained in the laboratory. Late instar larvae are described and illustrations of distinctive features are provided.

MATERIALS AND METHODS

Adults of *Meronera venustula* were collected by sifting dead grasses and sedges at the edge of a partially dried slough on April 26, 1984 in Palos Hills, Cook Co., Illinois. Sifted material was transferred to a white enameled pan, and adults were aspirated and transferred to snap-top glass vials filled with crushed fresh leaves. Survival of adults during return to the laboratory is very good under these circumstances. Sifted material was returned to the laboratory in plastic bags, and berlesed to determine relative proportions of different aleocharine species and the presence and type of larvae in the sample. No aleocharine larvae were found, suggesting that aleocharines had not begun oviposition at this time of year. A similar sample from the same locality and microhabitat collected on May 3, 1984 also contained adult *M. venustula* but no larvae.

Litter in the forest surrounding the slough where specimens of *M. venustula* were collected did not yield any specimens of this species after similar collecting techniques.

Adults were returned to the laboratory and placed in petri dishes with a uniform layer of about 0.5 cm of plaster of paris in the bottom. Plaster of paris was moistened whenever it became dry by adding drops of water directly to the surface. Small pieces of Purina Puppy Chow® were moistened and provided as food for the beetles and were readily accepted. A few short strips of paper toweling were placed in the dish to provide concealment for adults and as substrate for oviposition. Fungus began to grow on the food within 24 hours. Fungus covered food was replaced daily with fresh food except when fungus feeding occurred. In this latter instance food was changed every 3 days.

Cultures of adults were examined daily for the presence of eggs and to monitor general health of the colony. Eggs were transferred to similar petri dishes, and larvae were fed and maintained in a similar way to adults. Selected eggs and resulting larvae were periodically monitored to determine developmental rates.

All cultures were maintained at room temperature. This temperature generally varied between 22° and 25° C, but fluctuated widely, occasionally reaching 29° C in the latter stages of the study. These occasional high temperatures may be responsible for the relatively slight success in rearing larvae to maturity, especially in latter stages of the project. However, the possibility that a buildup of pathogens in the cultures could cause similar mortality cannot be eliminated.

Mature larvae were transferred to vials of finely ground peat moss for pupation.

Selected adults and larvae of each instar were preserved, cleared in Nesbitt's solution and mounted on microscope slides in Hoyer's medium for study. Detailed studies of slide mounted specimens were carried out with a Wild M-20 compound microscope. Drawings were facilitated by use of a drawing tube attachment.

BEHAVIOR

Feeding was regularly observed, and both adults and larvae readily accepted Purina Puppy Chow® as food and appeared to survive well on it. An unexpected observation was that at least adults and probably larvae actively fed on the fungus mycelium infesting the food particles. Normally, within 24 hours fungus would invade the food substrate. This was a serious problem in most cultures of aleocharines since fungus mycelium would quickly spread throughout the petri dish, commonly entangling the adults or otherwise restricting their activities. This problem did not become serious in colonies of *M. venustula.* In these cultures the food became covered by uniform velvety pile of fine short fungus fibers, but these did not develop into the large fibers of fungus mycelium common in other cultures. Adult *M. venustula* were often observed grazing in numbers on fibers of the pilose fungus growth on food particles. These observations suggest that growth of the fungus was restricted by continual grazing of the beetles. This hypothesis is further supported by the fact that as adults of the colony began to age, toward the middle of June, and become less vigorous and many had died (Figure 1), fungus on the food began to form a more normal mass of long mycelial fibers. This was first noticed on June 11, after egg laying had ceased.

Comparable observations for larvae are not available. Larvae were kept in individual dishes and could not have the same effect on fungus growth as could the more numerous adults. However, fungus mycelium and spores, along with bits of food substrate, were found in the guts of many slide mounted larvae. It is not possible to eliminate the possibility that the fungus was ingested accidently while feeding on the more normal food. However, this seems unlikely in view of the large amount of fungus in the guts of many larvae.

Mating was commonly observed in the petri dishes and was typical of that described for other aleocharine staphylinids (Peschke 1976, Ashe 1981). The relatively low proportion of males collected and included in the cultures (Figure 1) appears to reflect a natural unequal sex ratio present in early spring when collections were made.

A behavior which may be associated with mating activity but which appeared to be of much more general occurrence was regularly observed in cultures of *M. venustula.* If one individual crawled across or touched another, it often initiated a short, very rapid chase, with the mouthparts of the following beetle at the apex of the abdomen of the leader. This chase would continue for distances of

1.0–2.5 cm. Often each beetle would try to bend its' mouthparts to the apex of the other's abdomen. In this instance, the two beetles would run rapidly in a very tight circle. The reason for this activity is not known, but it seemed to occur without discrimination as to sex. The virtually invariant application of mouthparts to the apex of the abdomen rather than to other parts of the beetle suggests that important glandular secretions may be produced there, though this possibility obviously requires additional verification.

EGG LAYING, FECUNDITY AND ADULT LONGEVITY

Egg laying was not observed. Therefore, it was not possible to gain any information bearing on Topp's (1975) suggestion that aleocharine females take their eggs in their mandibles and distribute them within the litter or other substrate. He based this on observations of members of the Bolitocharini (1973) and Athetini (1971, 1975b). Eggs of *M. venustula* were most commonly found on strips of paper or occasionally on bits of vegetation placed in the petri dish. However, they were also found unconcealed on the plaster or on particles of fungus covered food. Fungus surrounding the eggs did not cause any noticable ill effects. There did not appear to be any difference in hatching success or survival of eggs, whether they were on plaster, paper or fungus covered food. No instance of egg cannibalism was observed even if eggs were occasionally left in association with adults for extended periods and adults were observed to come in contact with or crawl over eggs.

Daily production of eggs over the life of the colony is shown in Figure 1. No eggs were laid during the first 20 days from the time adults were taken in the field. During this period adults were active, feeding and apparently healthy (no mortality which could be associated with trama of collection occurred after the first 2 days of the colony). This may represent a normal preoviposition period for *M. venustula*. This supposition is strengthened by the fact that no larvae of *M. venustula* were found in berlesed litter samples on April 26 or on May 3, suggesting that egg laying had not yet occurred under natural conditions, though adults were common and active. It is not possible to surmize how long adults had been active before they were collected. Therefore, preoviposition period of *M. venustula* appears to be at least 20 days at room temperature, though it may be longer under natural conditions.

FIGURE 1

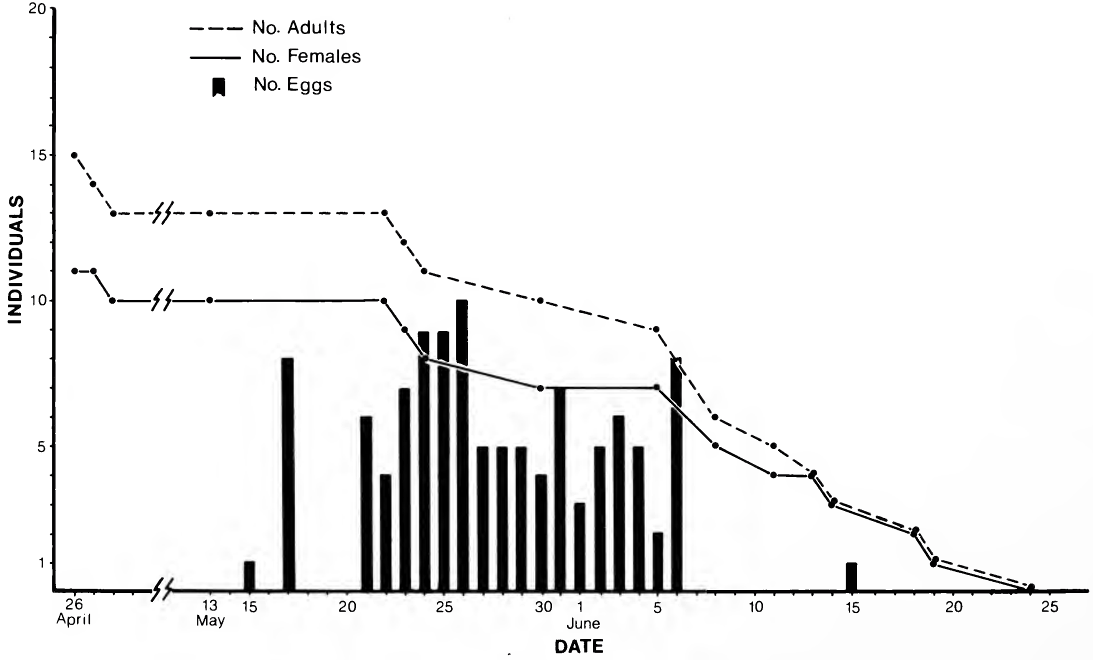


Fig. 1 Relationship among number of adults, number of females and oviposition rate per day in a laboratory maintained colony of *Meronera venustula* (Erichson).

Total egg production over life of the colony was 104. From the time of first egg laying until cessation of oviposition was 25 days with 1 egg laid 9 days later. Most eggs (91%) were produced during a period of 17 days between May 21 and June 6. From time of first oviposition until egg production decreased to zero (June 6), an average of 4.3 eggs were laid per day. Based on an average of 8.5 females alive during this period, average egg production per female per day is 0.51. There were, however, 4 days in which more eggs were deposited over a 24 hour period than there were females alive during that period. This occurred on May 24 (8 females: 9 eggs), May 25 (8 females: 9 eggs), May 27 (8 females: 10 eggs) and June 6 (7 females: 8 eggs). On these dates it is necessary that at least one female had laid 2 eggs during a 24 hour period. The average total number of eggs per female over the entire oviposition period is 12.1 (based on an average of 8.5 females alive during this period).

Fertility of eggs laid by *M. venustula* was very high. Only 2 eggs failed to hatch out of 52 observed closely, a fertility and/or hatching success of 96%. Less detailed observations of other eggs suggests similar hatching success. It is interesting that the last egg laid was also fertile and hatched.

Adults survived an average of 43.5 days from the time of collection (May 26), with a maximum survival of 61 days. This then represents minimum life expectancy of adults under laboratory conditions. It is not known whether adult longevity under these conditions reflects survival in the field. Nor is it possible to determine how long adults had been active before they were collected. Possible factors that could cause survival of laboratory maintained colonies not to reflect natural longevity include increased survival due to more stable laboratory conditions or decreased survival due to build up of pathogens or inadequate and/or stressful conditions in artificial colonies.

DEVELOPMENT AND PUPATION

Available developmental rates for eggs, all instars of larvae, and pupae are summarized in Table 1.

Eggs are white, ovoid and translucent and average 0.45 × 0.35 mm (N = 10). They were laid singly on the substrate with no apparent tendency to form clusters. Under conditions in the laboratory aver-

Table 1. Developmental Rates of Eggs, Larval Instars, and Pupae of *Meronera venustula* (Erichson)

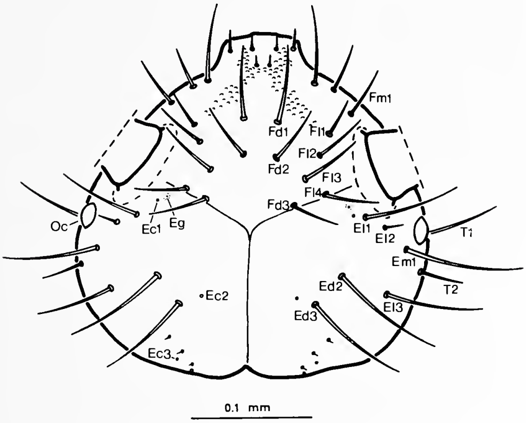
Stage	Duration	x̄ ± S.D.	N
Egg	1–4 days	2.8 ± 1.2	17
Instar I	1–4 days	1.8 ± 1.1	9
Instar II	1–2 days	1.4 ± 0.5	7
Instar III	4–5 days	4.5 ± 0.71	2
Pupae	4–5 days	4.5 ± 0.71	2

age duration of the egg stage was 2.8 days. The first instar lasted an average of 1.8 days, the second 1.4 days and the third 4.5 days. Survival of larvae beyond instar I was not good, especially during the latter stages of the study, during which laboratory temperatures fluctuated widely. It is not clear whether reduced survival of larvae was a result of temperature regime, temperature fluctuation or other inadequate environmental conditions. Only 2 larvae completed development to the adult stage though several other third instar larvae were killed for study.

Both larvae which reached the prepupal stage completed pupation without production of a cocoon. Production of a silken cocoon for pupation has been noted among a variety of aleocharine larvae (see Ashe 1982, Frank and Thomas 1984) and is presumed to be characteristic of members of this subfamily. Pupation of *M. venustula* larvae without production of a cocoon is therefore quite unexpected. One of the 2 larvae produced a thin, shiny deposit on which the pupa lay. In the other, no such deposit was observed. It is possible that this deposit represents a vestigial or poorly formed pupal cocoon, but this cannot be confirmed without additional observations.

Though these larvae did not form a pupal cocoon, it does not represent positive proof that larvae do not form a cocoon for pupation under natural conditions. A number of conditions in the laboratory cultures, including nutrition, humidity, temperature, substrate and others, may not have sufficiently approached natural conditions. Still, lack of a pupal cocoon is suggestive and deserves further investigation.

The form of pupal cuticular modifications may have a bearing on this problem. Examination of the pupal exuvia showed that the pupa of *M. venustula* is covered with a distinctive arrangement of very long, stiff cuticular spines. These spines are much more reminiscent of the cuticular modifications found on pupae of many staphylinids (for examples see Paulian 1941, McCabe and Teale 1981) than they are the more scattered fine hairs found on most described aleocharine pupae (see, for example, Chamberlin and Ferris 1929, Ashe 1981). Crowson (1967) suggested that these large spines served to hold the body of the pupa in position in the pupal cell. Such spines would presumably not be required in aleocharine larvae which pupate within a silken cell. However, very little is known



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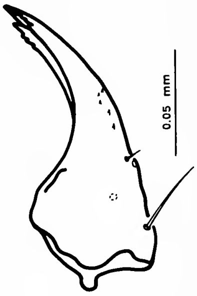

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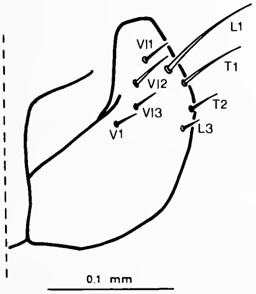

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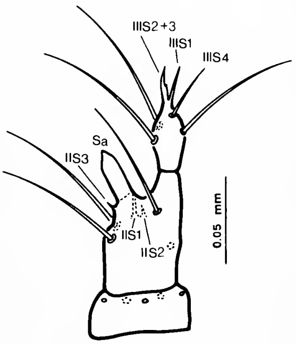

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Figs. 2–5. *Meronera venustula,* larval instar III. 2, head, dorsal aspect; 3, mandible, ventral aspect; 4, head, ventral aspect; 5, antenna, dorsal aspect.

about aleocharine pupae, and few have been described. Therefore, discussions of possible differences in pupal structure or habits of pupation are presently based on very incomplete comparative information.

The total rate of development from hatching to fully mature larvae averaged 7.7 days with a maximum of 10 days at room temperature (described above). The pupal stage lasted an average of 4.5 days. Time required for development from oviposition to emergence of adult averaged 15 days. Adults which emerged were active and fed well, suggesting that more than one generation per year is possible.

Oviposition rates, fecundity and developmental rates observed for *M. venustula* in the laboratory cultures provide a base line of information about the group. However, average daily temperature under natural conditions, especially in the wet detritus where adults were collected early in the spring, are almost certainly much lower. It is likely that this would lead to much slower developmental rates, and perhaps retardation of other physiological functions associated with fecundity, than those reported in this study.

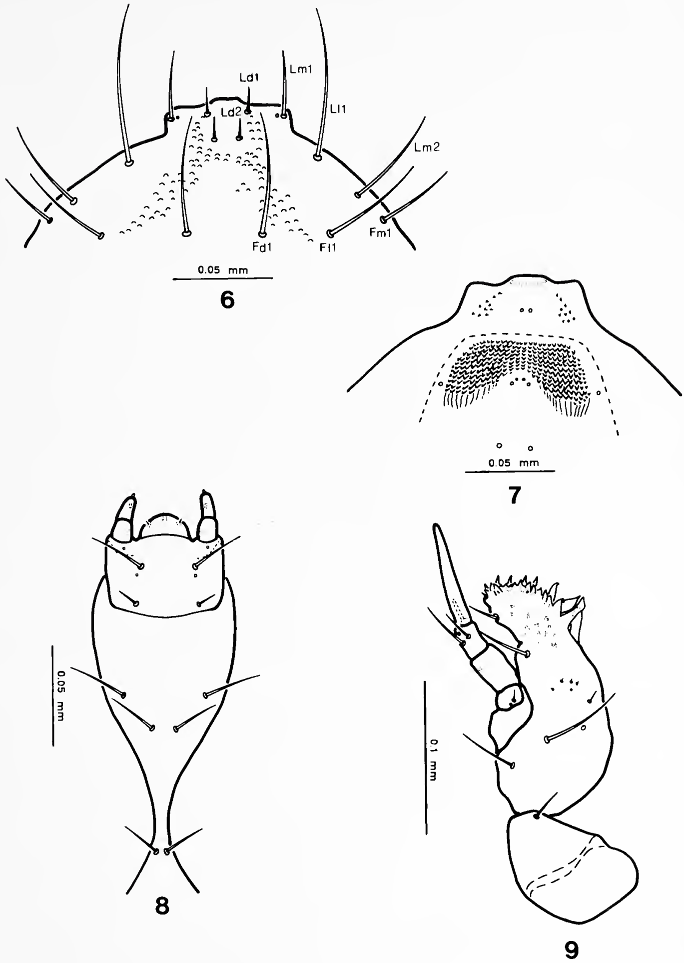
DESCRIPTION: LATE INSTAR LARVA OF *MERONERA VENUSTULA*

(Figures 2–16)

(Chaetotaxic nomenclature according to Ashe and Watrous 1984)

General: Length of mature larva 2.2–2.7 mm. Head width about .29–.23 mm. Antennal length about .14 mm. General body form elongate, more or less flattened, parallel sided and very slightly tapered to apex in apical half of abdomen. Color of mature larva white with slight greyish cast, especially on head and apical abdominal segments. Microsculpture absent except for distinctive patches of small dome-like microsculpture on frontal and clypial regions of head and short rows of microspinules medially on abdominal segment VIII. Vestiture of scattered long simple setae.

Head: (Figures 2, 4) Length to width ratio 0.9–1.0. Ocellus single on each side, small. Ecdysial sutures distinct, lateral arms attaining antennal fossae. Chaetotaxy as in Figures 2, 4; frontal region with all normal setae present, campaniform sensillae absent; epicranial region with Edl absent, epicranial lateral row complete with setae El1-3, El2 much smaller than El1 or El3, epicranial marginal row with Em2-3 absent, epicranial campaniform sensillae Ecl-3



Figs. 6–9. *Meronera venustula,* larval instar III. 6, labrum and antero-frontal region of head, dorsal aspect; 7, labrum, adoral aspect (epipharynx); 8, labium; 9, maxilla, dorsal aspect.

present, posterior epicranial setae P1-4 present, microspinose; temporal region with setae T1-2 present, T1 ventral to ocellus, T1 larger than T2; lateral region with lateral seta L2 absent, L1 much larger than L3; ventro-lateral setae V11-3 present; ventral seta V1 present; campaniform sensillae of lateral and ventral regions absent.

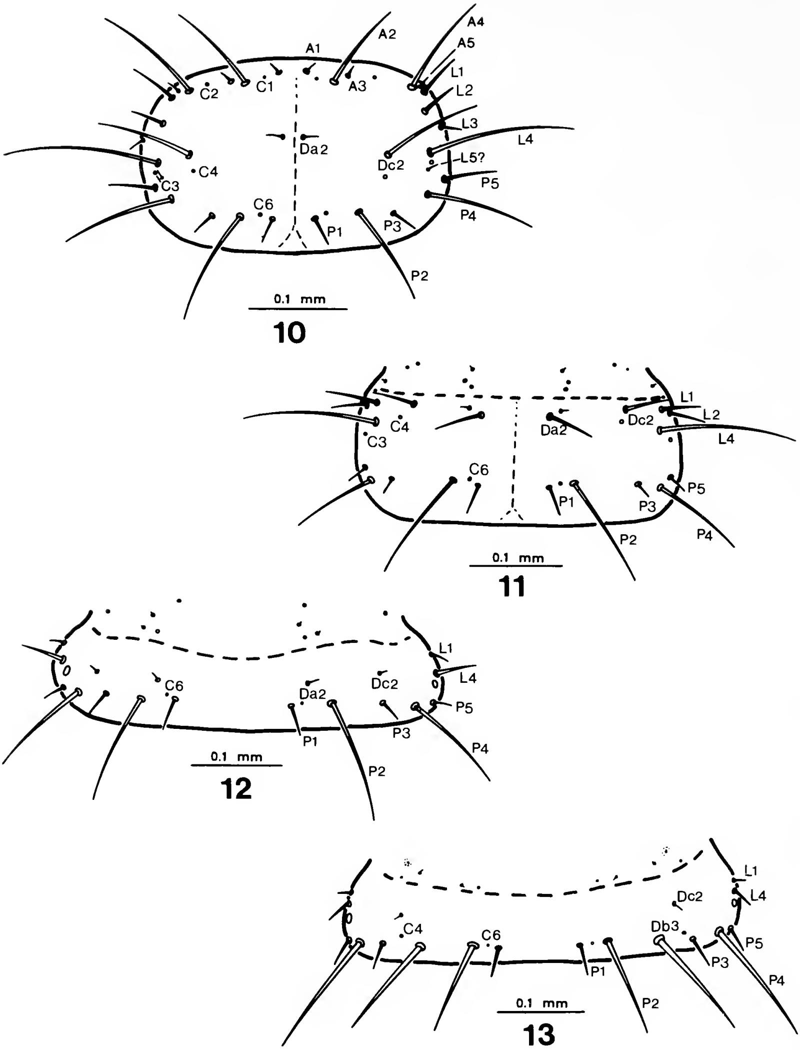
Antenna as in Figure 5; three articled, antennomere 1 transverse, about 2.5 times as wide as long, with 5 campaniform sensillae equidistant around apex; article 2 about 2.9 times as long as 1, constricted apical portion about 0.24–0.25 times length of 2; article 3 about 0.5 times length of 2; sensory appendage of antennomere 2 inflated, more or less parallel sided and obtusely and bluntly pointed, about 1.8–1.9 times length of constricted portion of antennomere 2; antennomere 2 with solenidia IIS1-3 present, IIS1 more or less digitiform, slightly tapering to obtusely rounded apex, about 0.5–0.6 times length of sensory appendage, IIS2 spinose, about 0.3–0.4 times length of IIS1, IIS3 very small, spinose; solenidia of antennomere 3 with IIIS1 setose, as long as IIIS2+3, IIIS2 and IIIS3 fused, IIIS2 present as slight projection on side of IIIS3; IIIS4 setose. Labrum as in Figure 6; not separated from head capsule by a suture; anterior margin protruded as broad, truncate, parallel sided lobe; with dome-like microsculpture medially and latero-medially; not divided by sutures into distinct sclerotized areas; all normal setae present, setiform, Ld1 and Ld2 small, Ld1 larger than Ld2, other labral setae larger. Epipharynx as in Figure 7; with patch of densely arranged, well developed rows of spines medially. Mandibles (Figure 3) curved apically, flattened and broad internally, without molar lobe basally; internal tooth in dorso-ventral plane, forming a distinctly bilobed apex to mandible with ventral tooth larger than dorsal tooth, edges of apical teeth serrate; 2 setae present externally in basal half, more proximal seta much larger than very small distal seta. Maxilla (Figure 9) with cardo broadly oval, incompletely divided medially by internal sclerotized ridge, with moderate seta on antero-lateral margin; stipes rounded at base, not distinctly separated from mala by suture; mala (Figure 9) with apex oblique, adoral surface with several setae and numerous blade-like cuticular spines, proximal seta blade-like, proximal spine thickened, longer than wide, blunt at apex; mala with 2 large setae near lateral margin, dorsal surface with scattered, minute cuticular spines; maxillary palpus (Figure 9) of three articles and palpifer consisting of cresentric sclerite at base of palpus, surface of palpifer with 1 seta and 1 campaniform sensilla, article 1 1.3 times as long as 2, article 3 1.4 times as long as 2 and 3 together, article 3 with small digitiform sensory appendage on external surface. Labium (Figure 8) consisting of premental and fused mental-submental sclerites; ligula transverse, about 2.5 times as long as wide, broadly rounded apically;

labial palpus 2 articled, article 2 about 1.2 times length of 1; seta on mentum near base of labial palpus large.

Thorax: Pronotum as in Figure 10; anterior row of setae with A1-5 present, A1, A3 and A5 very small; lateral setae wih L1-5 present, L3 very small, L5 displaced medially to near C3, L5 very small; posterior setae P1-5 present; discal setae reduced, represented only by Da2 and Dc2, Da2 very small, Dc2 very large; campaniform sensilla C1 present or absent, very small if present, C2 and C3 present, C4 present postero-lateral to Dc2, C5 absent, C6 present. Mesonotum (Figure 11) with lateral setae represented by L1, L2 and L4, L1 slightly medial to L2; posterior setae P1-5 present; discal setae Da2 and Dc2 present, of similar size; campaniform sensillae C3, C4 and C6 present. Metanotum similar to mesonotum. Legs as in Figure 14; chaetotaxy characteristic of subfamily (see Ashe and Watrous 1984), rather long and slender, femur 3.0–3.1 times as long as greatest width, tarsungulus long and slender.

Abdomen: Abdominal tergum I (Figure 12) with lateral setae L1 and L4 present, posterior setae P1-5 present; discal setae Da2 and Dc2 present, minute; campaniform sensilla C6 present. Abdominal terga II-VII (Figure 13) similar to abdominal tergum I except Da2 absent and additional very large seta (here interpreted to represent Db2) present in posterior row between P2 and P3, campaniform sensillae C4 and C6 present, C4 displaced posteriorly to near posterior row between Db3 and P3. Abdominal tergum VIII (Figure 15) not prolonged posteromedially in association with tergal gland structures; lateral setae L1 and L4 present; posterior setae P1-5 present, P1 reduced to pore, P2 and P4 very large; Pa1 present, very small, microsetose; discal setae Dc2 present, Da2 absent; campaniform sensillae C5 and C6 present. Tergal gland reservoir indistinct, completely membranous, about 0.7 times length of tergum VIII; gland ducts terminating in small, round papillate sclerotized structures attached to reservoir sac (Figure 15). Abdominal terga IX-X as in Figure 16; urogomphus single articled, short, about 0.3–0.4 times length of tergum IX. Hooks of pseudopodium 4, reduced, very small to minute (Figure 16).

Diagnostic Features and Discussion. Larvae of *M. venustula* are particularily distinctive and can be distinguished from those of other aleocharines by the combination of: fusion of labrum with head and distinctive patches of dome-like microsculpture on labrum



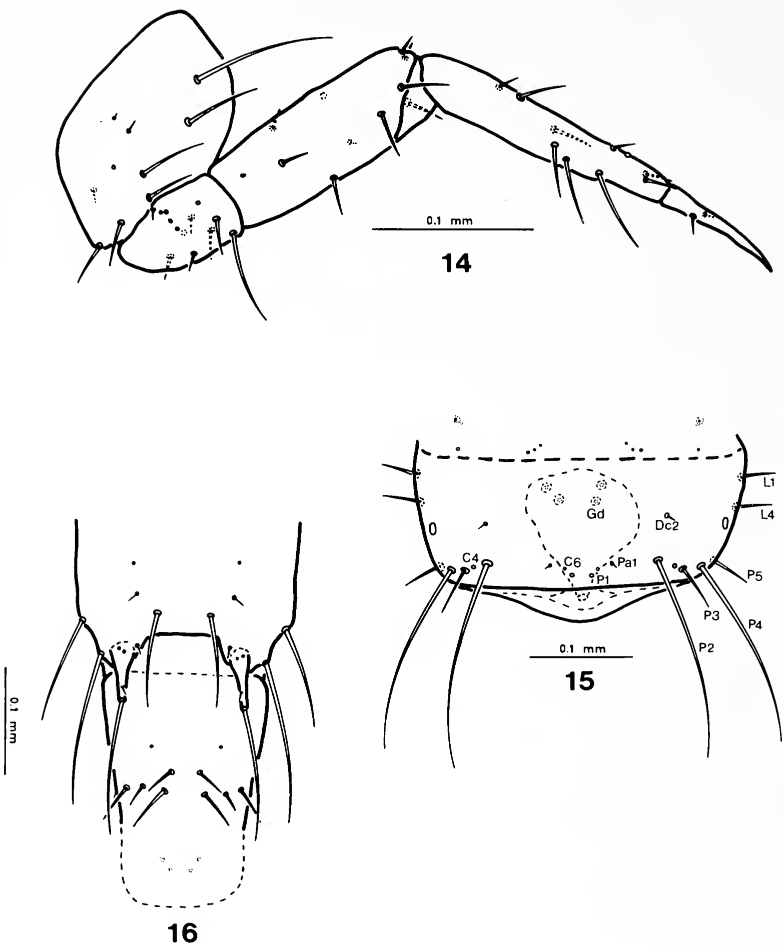
Figs. 10–13. *Meronera venustula,* larval instar III. 10, pronotum; 11, mesonotum; 12, abdominal tergum I; 13 abdominal tergum II.

and anterofrontal margins of head (Figure 6); distinctive structure of the maxilla (Figure 9); short, broad ligula (Figure 8); apically bifid mandibles (Figures 3); sensory appendage of antennomere 2 inflated, parallel sided and obtusely pointed apically (Figure 5);

fusion of solenidia IIIS2 and IIIS3 of antennomere 3 (Figure 5); pronotal chaetotaxy with discal setae represented only by Da2 and Dc2, and Dc2 very large in comparison to Da2 (Figure 10); abdominal terga II-VII with 3 long setae (P2, Db3, P4) in posterior row (Figure 13); completely membranous and indistinct tergal gland reservoir, without associated external modification of posteromedial margin of tergum VIII (Figure 15), and small, papillate sclerotized termination of gland ducts; and, 4 very small to minute anal hooks of the pseudopodium (Figure 16).

The description provided here highlights and illustrates the distinctive characteristics of larvae of Meronera venustula in comparison to other known aleocharine larvae. Nomenclature and abbreviations for chaetotaxic structures are those developed by Ashe and Watrous (1984). Presumed homologies of setae are based on relative positions in relation to other more stable chaetotaxic features which provide reference points as proposed by these authors. The possibility of incorrect designation of homologous setae remains (for example, note problems associated with designation of Db3 of abdominal terga II-VII). However, usefulness of a general reference system for naming and discussing setae is apparent in spite of this limitation. Such errors in designation and weaknesses inherant in the system can only become clarified after chaetotaxy of larvae of a significant number of aleocharine taxa have been studied comparatively and in detail. Inaccuracies which can result from this approach are discussed in Ashe (In press) and are recognized here.

Though the relatively reduced chaetotaxy of larvae of *M. venustula* causes problems in determining homologies of some setae, most are readily homologizable with comparable chaetotaxic features of *Atheta coriaria* Kroatz (see Ashe and Watrous 1984). However, some are problematic and require additional discussion of rationale and alternative possibilities. Head setation (Figures 2, 4) is similar to that described for *Atheta coriaria* (Ashe and Watrous 1984). It differs primarily in that one seta is absent from the epicranial dorsal row and one is absent from the lateral row. These missing setae are respectively determined to be Edl, based on position of Ed2 and Ed3 in relation to Ec2, and L2, based on position of remaining lateral setae in comparison to other rows of setae. Labral setae are initially difficult to identify because of absence of sutures which delimit the labrum from the head capsule; however, once frontal setae are identified, homologies of labral setae become apparent.

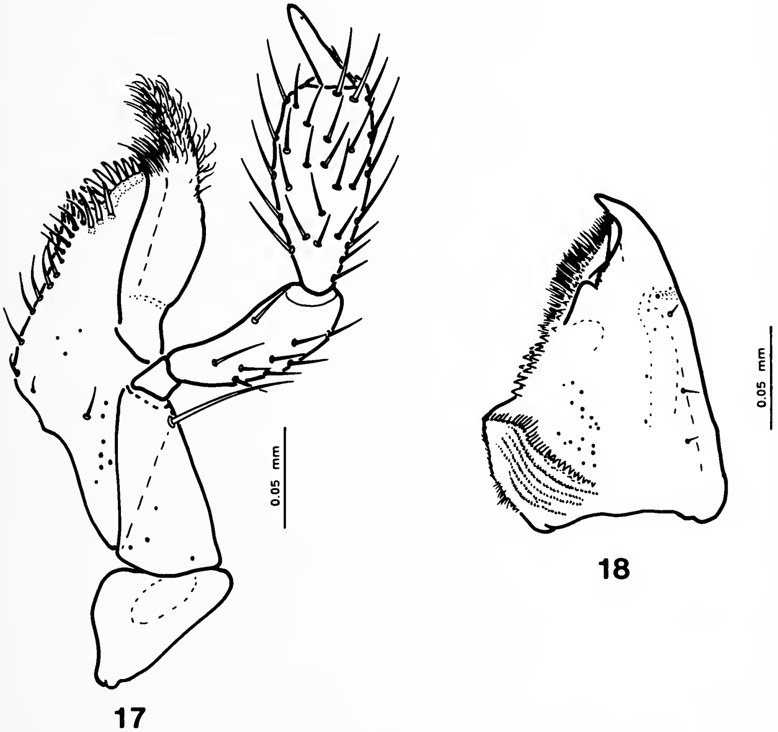


Figs. 14–16. *Meronera venustula,* larval instar III. 14, left proleg, anterior aspect; 15, abdominal tergum VIII with outline of gland reservoir and sclerotized portions of gland ducts; 16, abdominal terga IX-X.

Antennomere solenidia IIIS2 and IIIS3 appear to be fused for almost their entire length (Figure 5). A small projection on the lateral side of the more internal solenidium of antennomere 3 is interpreted to represent a vestigial IIIS2 based primarily on its' position in relation to other solenidia.

Discal setae of the pronotum are reduced to a medial and a lateral seta on each side. These are interpreted to represent Da2 and Dc2 respectively. Identity of the very small pronotal seta postero-medial to campaniform C3 is problematic (Figure 10). It is here interpreted to represent lateral seta L5 which is displaced medially; however, it could be homologous to a discal seta and L5 may be absent. The first medio-lateral seta of the mesonotum is interpreted to represent L1 even though it is more mesal than the usual position of L1 (Figure 11). Because of the relatively discal position of this seta, an alternative possibility is that it is actually Dd2.

Interpretation of the posterior row of setae of abdominal terga II-VII is complicated by presence of a large seta between P2 and P3



Figs. 17–18. *Meronera venustula,* adult mouthparts. 17, maxilla, dorsal aspect; 18, right mandible, dorsal aspect.

(Figure 13). This is very tentatively interpreted to represent Db3 (consistent with Ashe and Watrous (1984)), but the homologies of this seta are uncertain. Similarly, the campaniform sensilla between Db3 and P3 on abdominal terga II-VII is interpreted to represent C4 which has been displaced posteriorly, rather than C5. This is based on the facts that C5 is not found on other terga, and C5 is located between P3 and P4 in all other aleocharine larvae which have been examined for this characteristic. However, this sensilla could actually represent C5 which has been displaced into an aberrant position.

Resolution of these and other problematic chaetotaxic homologies will hopefully be facilitated by future comparative studies of larvae of both closely related and more distantly related aleocharines.

The tergal chaetotaxy of larvae of *M. venustula* is reduced to a pattern very suggestive of that described by Ashe (In press) for larvae of the fungus feeding Gyrophaenina. However, there are significant differences between members of these groups in mouthpart structure of both larvae and adults as well as other gross body differences. In addition, structure of the tergal gland and associated structures differ in significant ways. Based on these very striking differences between *Meronera* larvae and those of the Gyrophaenina, similarities in tergal chaetotaxy of larvae of these two groups are almost certainly derived in parallel and do not indicate a close relationship.

CONCLUSIONS

Several general features of the life history and ecology of *Meronera venustula* are suggested by this study. Presence of adults (and absence of larvae) in early spring implies that adults are the overwintering generation. This is consistent with a similar report of Blatchley (1910); however, he did not give data to support his statement. Available data do not preclude the possibility that pupae or prepupal larvae overwinter and emerge to adults in spring. However, absence of tenerals from among adults collected is not consistent with this interpretation.

The sex ratio in the early season adult population appears to be strongly biased toward females (11 females:4 males in this sample). It is possible that this represents a collecting artifact. If, however, this reflects a true population sex bias then such an unusual sex ratio could result from several factors, including, but not limited to, differential production of sexes at zygote level, differential survivial of sexes of larvae, or differential survival of sexes in overwintering adult populations. It would be interesting to determine if the proportion of sexes in the population is equalized as the season progresses.

There is a significant preoviposition period between the time adults emerge from hibernation and the time egg laying begins. This period lasted at least 20 days in laboratory cultures at 22–25° C. The probability that this period is not simply a result of delayed egg laying under unnatural conditions is indicated by the fact that no larvae were found in the field through at least May 3, 1984 when he last field sample was taken. Topp (1975a) noted that preoviposition of *Atheta fungi* (Gravenhorst) is temperature dependant but is also influenced by photoperiod. These factors probably also have a similar effect on specimens of *M. venustula.*

Developmental time of *M. venustula* averaged 15 days from oviposition to adult and is relatively short among known developmental times of aleocharine larvae. However, the larval period of 7.7 days is much longer than the 3.2 days of the mushroom inhabitating aleocharine, *Phanerota fasciata* (Say) (Ashe 1981). Among aleocharines which have more generalized habits, Topp (1971) found that preimaginal development of *Atheta sordida* Marsham required an average of 31 days at 23° C and (1975a) that *Atheta fungi* requires 40 days at 16° C. Topp also (1975a, 1975b) noted the purely temperature dependent relationship between development of eggs, larvae and pupae of athetine aleocharines. It is reasonable to expect that development of *M. venustula* is similarly temperature dependent. Adults, and also larvae later in the season, would certainly be living under much lower average, and probably lower maximum, temperatures than those which they experienced under laboratory conditions. If true, then preimaginal development as well as such temperature influenced physiological processes such as preoviposition period and oviposition rates, would be much slower under natural conditions than those reported here.

Topp (1975b) also noted a relationship between survival of larvae and temperature. He found that most athetine larvae developed with less mortality at 16° C than at higher temperatures. He also found that larvae of *Bolitochara lunulata* Paykull were consistently deformed if they emerged from eggs which had developed at 23°C, and suggested that they should be reared at lower temperatures. These results provide support for the suggestion presented above that the relatively high laboratory temperatures, with occasional fluctuations to near 30°C, was primarily responsible for decreased survival of larvae in this study.

It seems apparent that females of *M. venustula* mature only a single egg at a time. In laboratory cultures eggs were laid at an average rate of about 1 every other day per female, though rarely 2 eggs were produced by a single female in a 24 hour period. These averages were taken under the assumption that all females in the cultures were equally successful at maturing eggs, an assumption that cannot be evaluated further. However, eggs are relatively large (.45 mm average length compared to a maximum adult length of 2.2 mm). Therefore, a substantial investment of a female's energy resources are put into egg production, especially so when one considers that an average of 12.1 eggs were produced per female over a 26 day period (most in 17 days, see fecundity above). The fact that females were able to mature eggs at this rate suggests that they were receiving adequate nourishment from the food and fungal hyphae on which they fed. This is not to suggest, however, that these egg maturation rates can uncritically be assumed to represent those rates under natural conditions. Still, they must reflect natural oviposition rates at some level.

Time of oviposition, developmental rate of preimagos, and adult longevity suggest that *M. venustula* may be multivoltine with potential overlap of generations under natural conditions.

One of the most interesting findings of this study is that at least adults, and probably larvae also, will actively feed on fungus mycelium and appear to get a significant proportion of their nutrition from this resource. It is not possible to infer from available evidence that individuals of *M. venustula* are primarily fungus feeders under natural conditions. However, several lines of circumstantial evidence, in addition to observations of adults grazing on fungus mycelium, suggest that these beetles have feeding habits somewhat different from most other aleocharines. These include: 1) other aleocharine adults kept in culture under conditions similar to those of *M. venustula* showed no inclination to graze on fungus mycelium; 2) cannibalism of eggs or dead adults did not occur in cultures of *M. venustula* as it did in other cultures of aleocharines, suggesting that generalized predatory inclinations are not strongy devel oped; and 3) large amounts of fungus mycelium was present in guts of some adults and larvae.

Though structural characteristics of mouthparts of larvae and adults of *M. venustula* are not as highly derived in association with fungus feeding as are those of the mushroom inhabiting Gyrophaenina (see Ashe 1984 and In press), several features of mouthparts of adults and larvae are similar to those found among known fungus eating beetles. These also suggest that they have somewhat different feeding habits from many other aleocharines which are believed to be more general predators.

Mouthpart characteristics of larvae which suggest that observations of fungus feeding are not aberrent include the apically bifid mandibles which are broadly concave internally (Figure 3), the large dense patch of spines on the epipharynx (Figure 7) and perhaps the short broad ligula (Figure 8). Features of adults which suggest fungus feeding include the prominent ridge of distinct teeth with rows of smaller teeth more basally in the molar region of the mandible (Figure 18). Seevers (1978) and Ashe (1984) have suggested that such teeth in the molar region of mandibles of aleocharines are probably usually associated with fungus feeding. Preliminary observations of habits of several aleocharine species which have this characteristic (unpublished data) have supported this contention. However, it is interesting that maxillae of adults of adults of *M. venustula* (Figure 17) are not noticably modified from the generalized aleocharine condition. Among the fungus feeding Gyrophaenina it is the maxilla which is most strikingly developed in association with this habit. It is, however, important to note the different fungal resource that is being used by gyrophaenines, which feed on the hymenium layer of fruiting bodies of agarics, and members of *M. venustula* which apparently feed primarily on fungal hyphae. In any instance, these structural characteristics of adult and larval *M. venustula* are consistent with the habit of fungus feeding. However, they are also consistent with general omnivory or detritivory, and these habits cannot be eliminated as the generalized feeding mode in this species.

The weight of evidence suggests that both adults and larvae of *M. venustula* feed on fungus mycelium or fruiting structures which would be abundant in the wet vegetable litter in which they live. However, though they were able to effectively feed on fungus mycelium in laboratory cultures, they may eat it only facultatively under natural conditions.

Newton (1984) noted that species in several genera of aleocharines have been implicated as mycophagous. However, with the exception of the Gyrophaenina, fungus feeding by members of any aleocharine species had not been demonstrated. In general, this unexpected feeding habit of specimens of *M. venustula* suggests that fungus feeding, and perhaps other specialized feeding habits, may be more widespread within the Aleocharinae than has been expected in the past.

ACKNOWLEDGMENTS

I extend special thanks to Mr. James Day, an Antioch Work-Study student in the Division of Insects at the Field Museum during the spring and early summer of 1984, for his interest and commitment while caring for cultures of *Menonera venustula* and a number of other aleocharines. He initially made many of the observations reported here and maintained records of activities of the colony.

SUMMARY

Information about feeding habits, oviposition rate, developmental rate and longevity of adults of *Meronera venustula* (Er.) is provided based on colonies maintaned in the laboratory. Adults, and probably larvae, were found to actively feed on fungus mycelium and apparently received a substantial proportion of their nourishment from this resource. A preoviposition period of at least 20 days was followed by a burst of egg laying activity during which 104 eggs were laid by 10 females in 31 days. Average duration of the egg stage lasted 2.8 days, the first instar 1.8 days, the second instar 1.4 days and the third instar 4.5 days at temperatures of 22–25° C. Pupation occurred without production of a pupal cocoon, and the pupal stage lasted an average of 4.5 days. Development under natural conditions is expected to be slower than rates reported because of expected lower temperatures in the natural microhabitat of these beetles. Adults survived an average of 43.5 days and a maximum of 61 days from the time of collection.

Late instar larvae are described and illustrations of distinctive features are provided.

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ANTS FROM THE CRETACEOUS AND EOCENE AMBER OF NORTH AMERICA*

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The discovery of *Sphecomyrma freyi* in amber from New Jersey disclosed the existence of an extinct subfamily of ants (Sphecomyrminae) intermediate in some traits between modern ants and nonsocial wasps and dating as far back as the lower part of the Upper Cretaceous (Wilson *et al.*, 1967a, b). Subsequently Dlussky (1975, 1983) described a series of new genera from the Upper Cretaceous of the Taymyr Peninsula (extreme north-central Siberia), southern Kazakh S.S.R., and the Magadan region of extreme eastern Siberia. Among the various specimens assigned to these taxa (the genera are *Archaeopone, Armania, Armaniella, Cretomyrma, Cretopone, Dolichomyrma, Paleomyrmex, Petropone, Poneropterus,* and *Pseudarmania*), the ones well enough preserved to disclose subfamily-level diagnostic characters appear to fall within the Sphecomyrminae. Indeed it is difficult to find sound reasons for separating most of them from *Sphecomyrma,* providing we limit ourselves to the same criteria applied to contemporary genera and tribes. There seems to be little justification for placing them in a separate family, the Armaniidae, as suggested by Dlussky.

If this interpretation of the Russian material is correct, we have established that the most primitive known group of ants, the Sphecomyrminae, lived over much of the northern hemisphere during middle and late Cretaceous times. Other discoveries have revealed that by Eocene times, some 50 million years later, higher forms of ants had come into existence, but the evidence remains very scanty and ambiguous. *Eomyrmex guchengziensis,* described from amber in the Eocene coal beds of Fushun, Manchuria, appears from the description and illustrations to be a relatively primitive ponerine with traits reminiscent of the Sphecomyrminae (Hong *et al.,* 1974). Because of its possibly intermediate status, a further study of the single worker would be a valuable exercise. The giant *Eoponera*

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berryi of the Tennessee Eocene, long considered to be a ponerine, was recently placed in the horntail family Pseudosiricidae by Smith (1978) and by Rasnitsyn (1980). F. M. Carpenter, the original describer of this species, concurs with this placement (Carpenter, personal communication). Finally, a winged queen found in the mid-Eocene oil shales of Messel, Germany, has been placed in either the Dolichoderinae or Formicinae by Gahl and Maschwitz (1977). This is a reasonable approximation, but the specimen is so poorly preserved that an alternative subfamily assignment—even to some as yet unrecognized, extinct group—cannot be excluded.

It is clear, then, that in order to understand the key events of ant evolution the most crucial time frame in which to study fossils is the Upper Cretaceous to Middle Eocene. I report here two recent important finds: the first ants from the Cretaceous amber of Canada, representing a new species of *Sphecomyrma;* and a small sample of workers from the mid-Eocene amber of Arkansas, representing three of the most advanced subfamilies of ants (Myrmicinae, Dolichoderinae, Formicinae).

Sphecomyrma canadensis, new species
(Figs. 1, 2)

Diagnosis. Closely resembling *S. freyi* of the New Jersey amber (Magothy Formation, mid-Cretaceous) in most of its visible traits, differing in its smaller size (Head Width of holotype 0.66 mm as opposed to 1.00 mm in *freyi*), somewhat more robust alitrunk, and proportionately shorter third funicular segment (which is about as long as the second funicular segment, as opposed to slightly more than twice as long in *freyi*).

Holotype worker. Head Width 0.66 mm, Head Length 0.66 mm, Scape Length 0.50 mm, length of alitrunk 1.32 mm. A relatively well-preserved worker collected *in situ* in the Cretaceous "Canadian amber" deposits near Medicine Hat, Alberta. J. F. McAlpine, CAS 330, deposited in the Biosystematics Research Institute, Ottawa, Canada.

Paratype worker. Length of alitrunk 1.57 mm. A poorly preserved worker in the Medicine Hat amber provisionally placed in the same species as the holotype. J. E. H. Martin and J. F. McAlpine, CAS 205, deposited in the Biosystematics Research Institute, Ottawa, Canada.

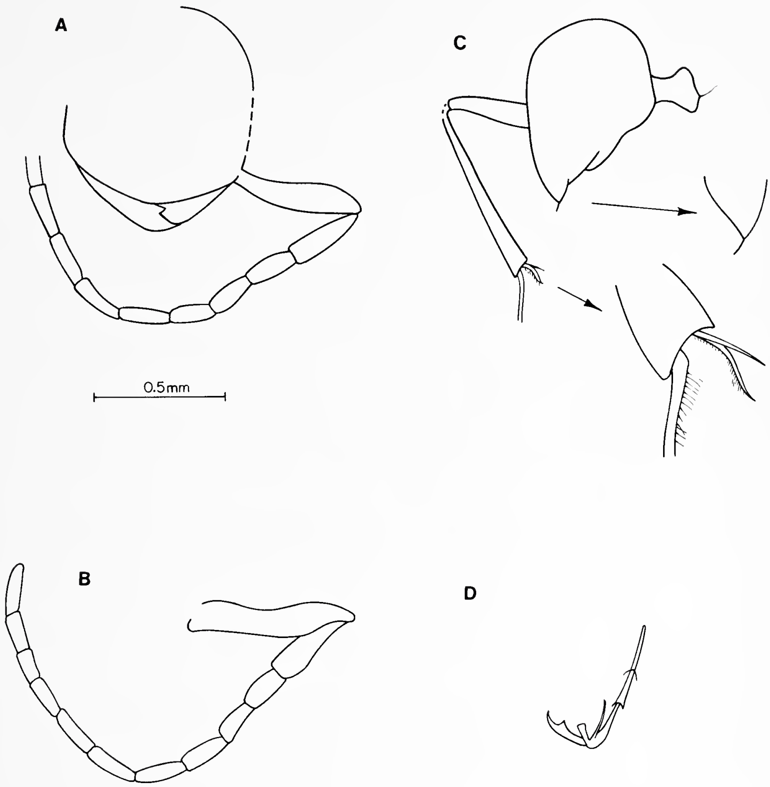

Fig. 1. *Sphecomyrma canadensis*, holotype worker: **A**, frontal view of head; **B**, left antenna, dorsal view; **C**, gaster, petiole, and left rear leg, with enlarged views of the rear-leg tibial comb and spur and tip of abdomen (showing the extruded sting); **D**, left front tarsus.

These are the first ants recorded from the Canadian amber, despite the fact that thousands of pieces containing large numbers of insects of diverse orders have been processed since the late nineteenth century (Carpenter *et al.*, 1937; Rice, 1980). The holotype (and by inference the paratype) is so close to *S. freyi* in key characters that it can be placed with certainty in the Sphecomyrminae and with reasonable confidence in *Sphecomyrma*, providing we use the same anatomical standards by which the modern subfamilies and genera of ants are distinguished. The resemblance is well marked,

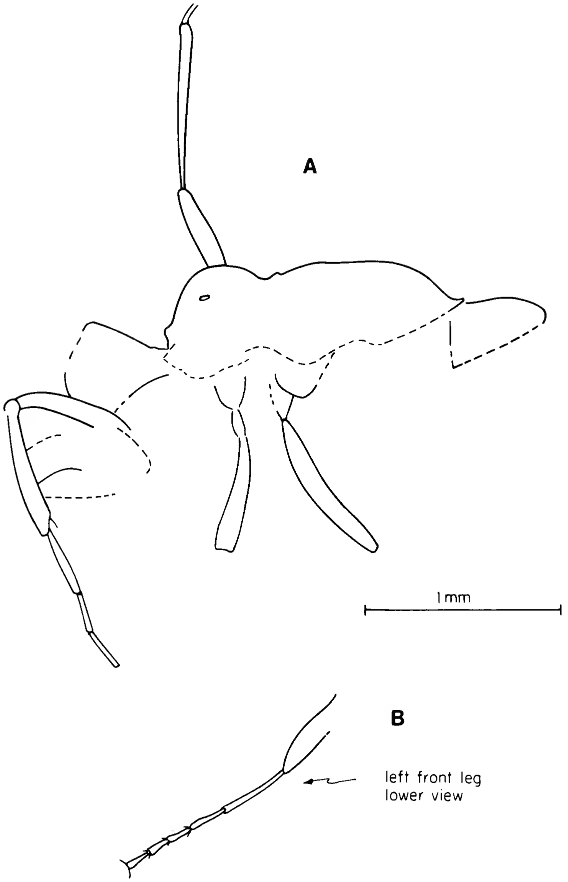

Fig. 2. *Sphecomyrma canadensis*, paratype worker: **A**, part of right side of body and head; **B**, left front leg.

for example, in the overall body form, including especially the distinctive petiole and head; in the unique short, 2-toothed mandibles; in the equally peculiar antenna, with its proportionately short scape and long, flexuous funiculus; and in the well-developed secondary median claw of the tarsus.

During late Cretaceous times the Alberta locality was close to the midpoint between New Jersey and Magadan, the easternmost of the Russian fossil sites. Thus the discovery of the Canadian specimens contributes new evidence that the most primitive known ant subfamily, the Sphecomyrminae, was widespread through the northern half of the world during the latter half of the Cretaceous Period.

Eocenidris, new genus

Diagnosis (*worker*). An Eocene myrmicine genus distinguished from all other known genera by the following combination of worker traits: very small size; relatively narrow mandibles with oblique masticatory border bearing 6 irregularly shaped teeth; smoothly and strongly convex promesonotum apparently undivided by transverse sutures; propodeum armed with short, stout spines; and incrassate femora and tibiae.

Type species: Eocenidris crassa.

Eocenidris crassa, new species

(Fig. 3)

Diagnosis (*worker*). Distinguished from other known ants by the combined traits just cited in the generic diagnosis.

Holotype worker. Head Width 0.40 mm; length of alitrunk from the anterior edge of pronotal collar to posterior edge of propodeal flange, 0.50 mm. Other visible features as shown in Fig. 3. The antennae and eyes are either missing or positioned in a way so as not to be made visible without endangering the specimen through fragmentation. Similarly, the posterior part of the abdomen could not be studied. In amber of the Middle Eocene (Claiborne) of Malvern, Arkansas. Collected by R. H. Mapes (see Saunders *et al.,* 1974). Deposited in the Museum of Comparative Zoology, Harvard University.

Eocenidris crassa is a typical myrmicine, possessing a set of traits that are advanced relative to those of *Agraecomyrmex* of the Baltic amber, the modern genera *Hylomyrma* and *Myrmica,* and other Myrmicinae considered primitive. Its existence demonstrates conclusively that a substantial amount of evolution had occurred within the subfamily, hence within the ants as a whole, by the middle of the Eocene.

E. crassa superficially resembles the species of the modern Neotropical genus *Oxyepoecus,* which are in some cases inquilines of *Pheidole* and *Solenopsis,* but it lacks ventral processes on either the

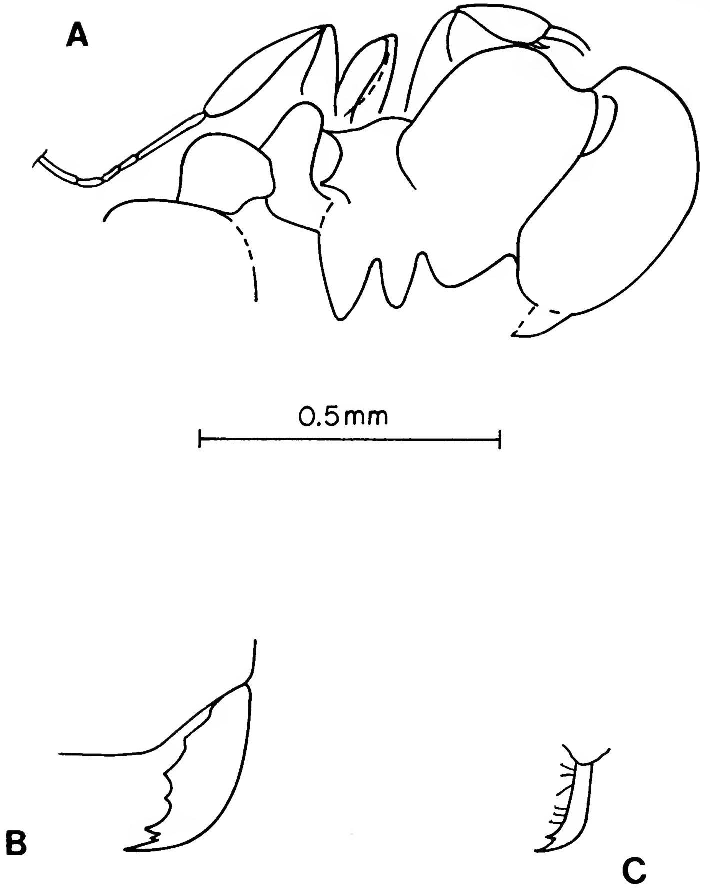

Fig. 3. *Eocenidris crassa*, holotype worker: **A**, oblique-dorsal view of head and part of body; **B**, left mandible and part of clypeus, full-face view; **C**, left mandible with masticatory border facing observer, revealing the row of vertical bristles on the inner surface.

petiole or postpetiole and possesses more uniform and numerous mandibular teeth (6 as opposed to 4 in *Oxyepoecus*). It also bears a general resemblance to some of the New World species of *Erebomyrma* (*eidmanni, longi, nevermanni,* and *urichi*), including its possession of stiff bristles along the inner mandibular surface and incrassate femora and tibia. It is easily distinguished from these ants, however, by its more convex promesonotum and more numerous and less evenly distributed mandibular teeth (4 in all *Erebomyrma* and 5 in the Old World species of the closely related genus *Oligomyrmex*).

Iridomyrmex mapesi, new species
(Figs. 4, 5)

Diagnosis (*worker*). An Eocene species tentatively assigned to *Iridomyrmex* on the basis of the overall habitus, antennal form, and structure of the mandibles, which fall within the limits of the living and fossil species placed within that genus. The preservation of the single type is not good enough to make a detailed comparison with all of the previously recognized forms of *Iridomyrmex,* but the following minimal characterization is possible. The worker of *mapesi* is larger and possesses fewer mandibular teeth than the living New World species and *I. hispaniolae* and *I. humiloides* of the Miocene Dominican amber. In these traits *mapesi* falls within the range of some of the contemporary members of the Indo-Australian *calvus, cordatus,* and *rufoniger* groups. Hence, in a purely technical sense it is not possible to separate *mapesi* from all other known ants, but on the combined basis of its age, geographical location, and morphology this form can be safely treated as a distinct species.

Holotype worker. Head Width 1.06 mm, Head Length 1.1 mm (measurable only to the nearest 0.1 mm), Eye Length 0.11 mm, Pronotal Width 0.62 mm. Other visible details as illustrated in Figs. 4 and 5. Deposited in the Museum of Comparative Zoology.

The species is named in honor of Royal H. Mapes, the discoverer of the Arkansas amber, who also collected the type specimen.

I. mapesi is the oldest verifiable record of the subfamily Dolichoderinae. The following note may be of additional, ecological significance: a small segment of leafy liverwort (Hepaticae) is embedded close to the head of the *I. mapesi* worker. According to Alice F. and Rolla M. Tryon, who kindly identified the fragment, the presence of these plants indicates a mesic habitat, presumably either swampland or mesic forest.

Protrechina, new genus

Diagnosis (*worker*). A small Eocene formicine close to *Paratrechina* in habitus, differing from that genus in its lack of a circlet

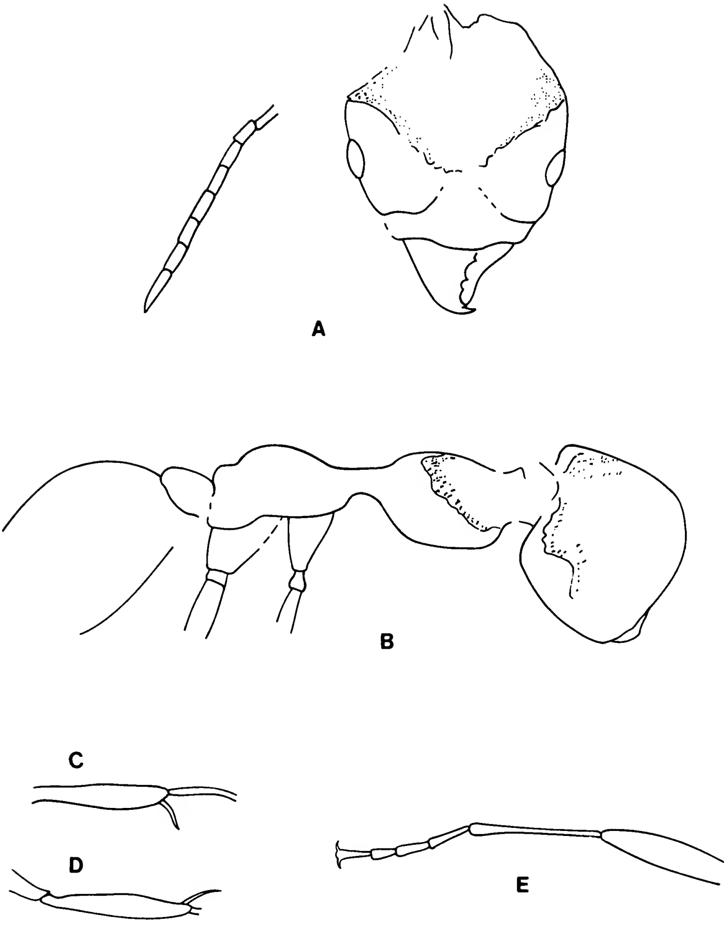

Fig. 4. *Iridomyrmex mapesi,* holotype worker: **A,** frontal view of head and part of right antenna; **B,** right side of part of head and body; **C,** left hind tibia and metatarsus; **D,** left front femur and tibia; **E,** middle right tibia and tarsus.

of hairs surrounding the acidopore (*Paratrechina* and most other formicine genera possess the circlet) and in the absence of the upraised paired bristles on the alitrunk (possessed by *Paratrechina* and some species of *Acantholepis* and *Brachymyrmex*).

Type species: Protrechina carpenteri.

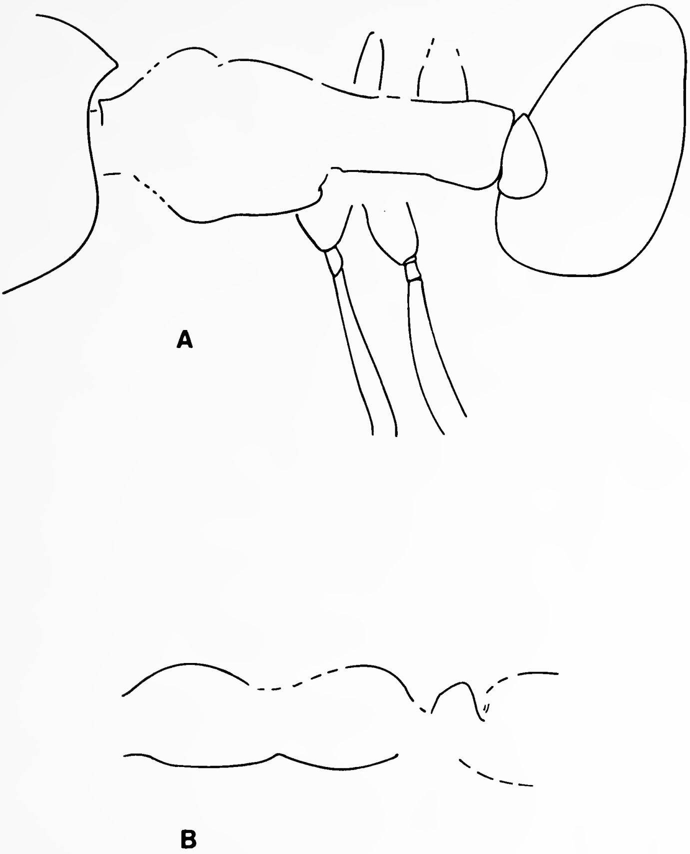

Fig. 5. *Iridomyrmex mapesi,* holotype: **A,** dorsal view of part of head and body; **B,** left side of alitrunk and petiole.

Protrechina carpenteri, new species
(Fig. 6)

Diagnosis (*worker*). Distinguished from all other known formicine ants by the characteristics just cited for the genus *Protrechina.*

Holotype worker. Head Width 0.23 mm, Scape Length 0.48 mm, Pronotal Width 0.23 mm. Ocelli absent. Mandibles folded, evidently short, and hidden from view. Body surface smooth to weakly shagreened, and feebly shining. Upper surface of head and

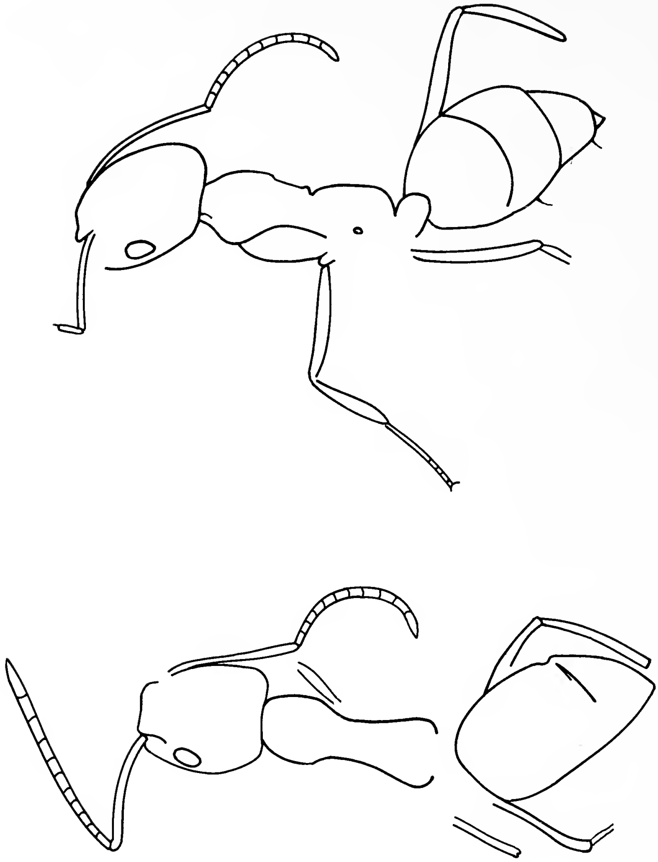

Fig. 6. *Protrechina carpenteri,* holotype: two views of entire body.

body devoid of hairs. In amber of the Middle Eocene (Claiborne) of Malvern, Arkansas. Collected by R. H. Mapes (see Saunders *et al.,* 1974). Deposited in the Museum of Comparative Zoology.

The species is named for Frank M. Carpenter in recognition of his pioneering work on the fossil ants of North America.

Two comments on the generic diagnosis are required. First, the conical shape of the last gastric segment as seen from two obliquely dorsal views leaves little doubt that the *Protrechina carpenteri* holotype possessed an acidopore, the most distinctive trait characterizing the Formicinae as a whole. Unfortunately, while grinding the amber piece along a new plane in order to see the opening of the acidopore, I shattered and lost the rear part of the abdomen before this opening came into view. Hence I cannot be certain that the ant possessed a typically circular formicine acidopore. Additionally, the absence of a circlet of hairs at the tip of the abdomen and paired bristles on the alitrunk, on which the generic diagnosis rests, could be the result of postmortem deterioration. However, I doubt that such is the case, because the body form as a whole and the entire dorsal cuticular surface were preserved in excellent shape, without the kind of distortion and rupturing usually accompanying severe decay in amber specimens. Also, at least two well-preserved hairs were present on the ventral surface of the gaster, as depicted in Fig. 6.

To ascertain the status of *Protrechina* I surveyed representatives of all of the living genera of Formicinae with reference to the two characters in pilosity. In only two genera, *Oecophylla* and *Camponotus* (and only in a few species of the latter), is the circlet of acidopore hairs lacking. Conversely, only some of the species of *Acantholepis* and *Brachymyrmex* share the *Paratrechina* trait of coarse paired setae on the alitrunk dorsum. Thus *Protrechina* is not unique among the Formicinae in its possession of the two character states that distinguish it from *Paratrechina.*

Protrechina carpenteri, if I have interpreted its morphological features correctly, is the first member of the Formicinae recorded from a definitely dated Eocene deposit.

SUMMARY

(1) The first ants from the Canadian amber are described as *Sphecomyrma canadensis,* providing a record of the primitive Cretaceous subfamily Sphecomyrminae geographically intermediate between the New Jersey and Siberian collections recorded earlier.

(2) The first specimens of Eocene ants definitely assignable to higher subfamilies have been discovered in amber from Malvern, Arkansas: *Eocenidris crassa* (Myrmicinae), *Iridomyrmex mapesi* (Dolichoderinae), and *Protrechina carpenteri* (Formicinae).

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INTER-NEST INTERACTIONS, NEST AUTONOMY, AND REPRODUCTIVE SPECIALIZATION IN AN AUSTRALIAN ARID-ZONE ANT, *RHYTIDOPONERA* SP. 12

By P. Pamilo,[1,2] R. H. Crozier,[1] J. Fraser[3]

Introduction

Rhytidoponera sp. 12 ANIC is a large Australian ponerine ant which lacks a morphologically-differentiated queen caste. As is the case for many other Australian species in this genus, some of the workers mate and assume the egg-laying role. As has been inferred for species in the *R. metallica* complex (Haskins and Whelden, 1965) and observed for *R. maniae* (another large arid-zone species) and species in the *R. impressa* complex (Ward, 1981), colony-founding under this life-pattern is probably usually accomplished by fission ("hesmosis"), in which one colony divides into two. Unlike the situation where nest-founding follows a dispersive mating flight, colony fission is likely to lead to the new nest being located close to the parent one, leading to a population structure in which neighboring nests are genetically related. A large study of the apportionment of genetic variation in a population of *R.* sp. 12 (Crozier et al., 1984) found that neighboring nests are indeed more similar genetically than expected by chance—they are related.

The finding (Crozier et al., 1984) that neighboring nests are related raises the question of colony boundaries. Does each nest represent a separate colony, or do daughter-nests remain socially connected after fission, forming polydomous (multi-nest) colonies? The two alternatives are not, of course, completely clear-cut, in that intermediates could occur between single-nest colonies and truly

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integrated polydomous colonies. Thus, there could be differing degrees of tolerance between the workers of neighboring nests, and various levels of worker exchange between nests.

Our study on intra-population genetic variation in *R.* sp 12 is a continuing one, the results for which will be reported elsewhere (Crozier et al., 1984, and in prep). In this paper we report observations on colony maintenance and inter-nest interactions, made with the intention of furthering our understanding of the extent of the reproductive division of labor within colonies, and the degree of nest autonomy in natural populations.

Rhytidoponera sp. 12 ANIC has also been referred to as *R. mayri* (Crozier et al., 1984) and as *R.* sp. B (Davidson and Morton, 1981). The acronym "ANIC" refers to provisional species recognised, but not yet named, by Dr. R. W. Taylor and held by the Australian National Insect Collection, maintained by the CSIRO Division of Entomology in Canberra (see Imai et al., 1977).

METHODS AND RESULTS

Study site.

The population studied is in Conservation Paddock of the University New South Wales Arid Zone Research Station, north of Broken Hill, New South Wales, and is further described by Crozier et al. (1984).

The dominant ant with respect to competitive interactions in the study site is *Iridomyrmex viridiaeneus,* a colony of which is associated with a grove of *Acacia victoriae* in the center.

The observations reported here were made during September 17–28 and November 9–15, 1983, although preliminary observations have been made over a number of years in connection with the relatedness studies.

Reproductive state

The ant nests are in hard clay soil and data from a number of excavations indicate that the lowest gallery reaches a depth of about 1 m below ground level. We excavated two nests completely; one of these was a mature nest (excavated on November 15), in that it went down to the usual depth, whereas the other was an incipient colony (we observed it being established and it only achieved a depth of ca. 16 cm) excavated on September 21.

Ants were taken from the mature nest in two groups which were kept separate. The excavation took place during the middle of the day, with surface temperatures in excess of 45 C, so that no ants would have been expected to be absent foraging. We first extracted ants by "fishing" them from the nest entrance using straws. When no more ants could be obtained by this method, we dug the nest up, carefully checking all the side tunnels for ants as we went. Fishing yielded 192 ants and digging 245. The excavated ants consisted of 107 mature ants and 138 young ones (as determined by their exoskeletons being soft and them lacking abdominal white or yellow bodies). We also found 243 cocoons and 11 larvae. Of the cocoons, 235 contained worker pupae, one contained a male pupa, and seven had unclassifiable larvae or prepupae.

The adult ants were dissected and checked for ovarian status and whether or not the spermatheca (sperm storage device) contained sperm. All of the young ants were found to be non-inseminated upon dissection, and also lacked corpora lutea. Their ovaries were either quite undeveloped, or very poorly developed in terms of possessing oocytes in the ovarioles. The results of dissecting the old ants are shown in Table 1. Inseminated ants occurred significantly more often among the ants obtained by digging than those obtained by fishing ($G = 37.26$ (Yate's correction), $p < 0.001$). The one inseminated worker caught by fishing was unusual for an inseminated worker in having no empty ovarioles, but this state is the predominant one among uninseminated workers. We therefore tentatively discount this ant as an established egg-layer, leading to an estimate of 22 egg-layers, or 7.4% of the worker force.

Pooling empty-ovariole classes 1–5 reveals marked differences in ovarian status between the various categories of ants shown in Table 1. Thus there is a significant difference among the uninseminated ants between those collected by fishing and those collected by digging ($X^2 = 14.6$, $p < 0.001$), and, among the ants collected by digging, between those inseminated and those not ($X^2 = 74.7$, $p < 0.001$). The uninseminated ants collected by digging had, on average, less-developed ovaries than the uninseminated ants collected by fishing. The inseminated ants are characterised by belonging to the classes with intermediate (1–5) numbers of empty ovarioles, and also had an intermediate number of oocytes per ovariole.

The incipient colony examined was discovered through carrying being observed to it from an established nest about 5 m away. The

Table 1. Reproductive status of inseminated and non-inseminated ants from a mature colony in terms of the number of ovarioles per ant which lacked oocytes. Ants were further classifiable into those collected before the nest was dug up (by "fishing") and those collected during excavation.

	Number of empty ovarioles							
	0	1	2	3	4	5	6	Total
Non-inseminated								
fished	111	8	7	2	3	7	53	191
excavated	68	1	0	1	0	0	15	85
Inseminated								
fished	1	0	0	0	0	0	0	1
excavated	3	1	10	6	1	1	0	22

ants collected from it were packed tightly into the limited gallery space available. We dissected 230 ants from the incipient colony; about 30 more died before they could be dissected. None of the ants dissected were inseminated. The distribution of empty ovarioles for these individuals is shown in Table 2; it resembles that of the uninseminated ants collected by digging from the mature colony (Table 1), although it should be remembered that these two nests were collected almost two months apart. We found no eggs or larvae in the incipient colony, although partial excavations of mature colonies at that time yielded small larvae.

Foraging interactions

The nests in the study area are overdispersed (Crozier et al., 1984), suggesting that there is foraging competition (Levings and Traniello, 1981). Given the relatedness between neighboring nests, and this *a priori* evidence for competition, investigation of various aspects of foraging behavior that pertain to these factors was carried out.

We studied the foraging characteristics of one nest (number 54 in our system) in both September and November. The vegetation in the study area, chiefly herbaceous, was considerably more abundant in September than in November, with plants of *Tetragonia tetragonioides* (New Zealand Spinnache) being numerous in September but largely absent in November. This plant appeared to be particularly significant as a food plant for caterpillars, a major prey item. Even in September, however, the overall cover was not thick, with 33.7% of the ground bare, 58.1% covered by sparse herbs, 6.7% with a

Table 2. Reproductive status of ants from an apparent incipient colony, in terms of the number of ovarioles per ant lacking oocytes. No inseminated ants were found during dissections from this group.

Number of empty ovarioles							
0	1	2	3	4	5	6	Total
166	17	12	16	10	6	3	230

medium cover, and 1.5% with a relatively dense herbaceous cover.

We determined the foraging area of nest 54 by following individual foragers and marking the points at which they turned back for the nest (whether they had obtained a food item or not). The distributions (Table 3) of these most-distant points of foraging trips differed significantly ($X^2 = 9.59$) between September and November, with the trip-distances in November being longer. This difference may be due to differences in the success rates of foraging trips: although we did not record successes and failures, it was readily apparent that a majority of trips in September resulted in collection of a food item, whereas most November trips ended with ants returning unladen. Most food items were brought back to the nest by individual workers, but very rarely large items such as large (ca. 5 cm long) crickets were retrieved by groups; the mechanism of recruitment is unknown but may involve short-range communication via the powerful stridulation mechanism these ants possess.

The extent of the overlap between the foraging areas of adjacent nests cannot be quantified in the absence of data, such as in Table 3, collected for adjacent nests simultaneously, but it is clearly considerable, in that many ants walked beyond the edge of the figure described around their home nest by its neighbors (figure 1).

To determine the extent to which individual workers show fidelity in foraging direction over several trips we marked individual foragers from two nests (54 and 6) and subdivided the nest environs into eight equal-sized radial sectors. We recorded the sectors in which each marked individual foraged. The extent of fidelity can then be

Table 3. Most distant points reached during individual foraging trips from nest 54 during the two observation periods.

	0–5 m	5–10 m	10–15 m	>15 m	Total
September	6	20	10	2	38
November	6	16	22	13	57

measured by the distribution of sector-numbers pertaining to the trips observed. The difference between two successive foraging trips is zero if the ant selects the same sector each time (showing perfect fidelity), four if she takes opposite sectors, and on average two if she selects foraging sectors at random. We obtained records of three or more trips for some individuals, but, for simplicity of analysis, only used two in our calculations, using the first and the last where several data were available for one individual. The mean difference for nest 6 was 1.57 (based on seven foragers) and 1.24 (based on 25

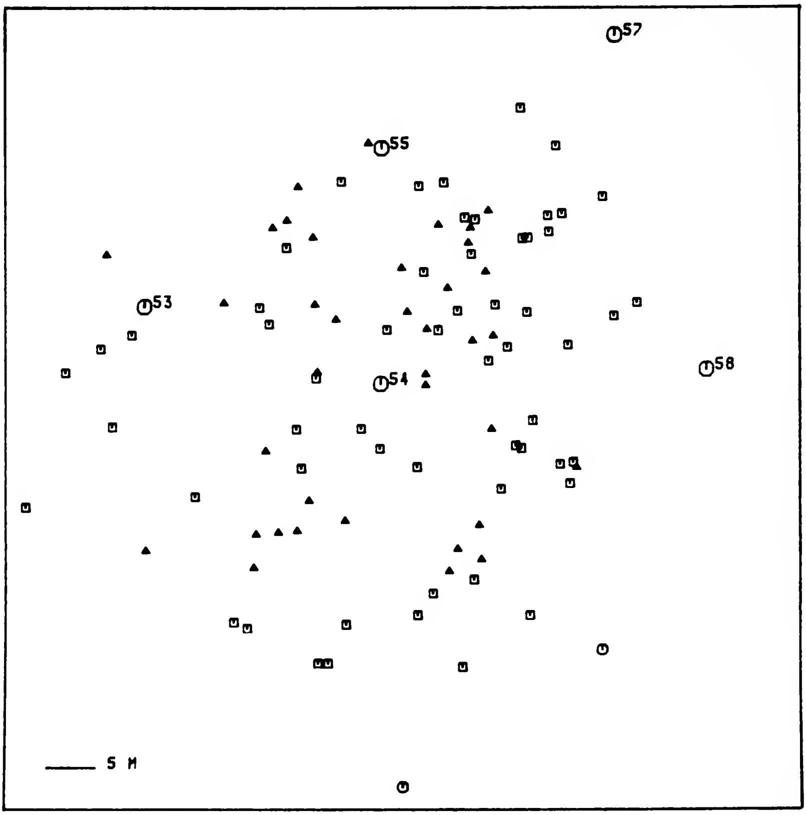

Fig. 1. Furthest points reached by foraging ants from nest 54 during the September (closed triangle) and November (open square) observation periods. Octagons denote active nests, with numbers referring to those given in the relatedness study (Crozier et al., 1984).

foragers) for nest 54. For both nests we calculated the expected mean sector-difference according to random expectation using the actually-observed distribution of trips between sectors (because some sectors were visited more than others). In both cases, the mean sector-difference observed was significantly less, at the 95% level, than that under random expectation. These findings indicate short-term foraging-direction fidelity, but we do not know how long this fidelity persists, or if it occurs at other times of the year, nor whether the success or failure of a foraging trip influences the sector chosen subsequently.

We observed several instances in which foraging ants from different nests encountered each other in the field. In each case they reacted with apparent alarm or hostility to such ants, but not to nestmates. Foragers from different nests often ran away from each other, but on occasion fought, using their mandibles and stings. Seized ants stridulated. When such encounters occurred close to one or other nest, the ant from that nest was sometimes joined by a nest-mate. In that case, the two ants sometimes dragged the third further away before releasing it, but at other times dragged it into the nest. Ants dragged into an alien nest are not necessarily killed: we observed that one ant (not necessarily alien) was dragged out of one nest and released 2 m away.

Inter-nest movements.

We observed ants moving between nest sites in three sections of the study area. Two of these instances involved the establishment of a new nest, one of which was dug up and the ants dissected, as reported above; the third involved movement between old, inhabited nests. In each case, many ants were carried between nests by others; such ants moved in pairs, one carrying the other over its head, grasped by the mandibles. We concentrated our observations on the case involving the movement between long-established nests. To speed our subsequent discussion, and following established practice, we will term this phenomenon "carrying", and distinguish the ant carrying the other as the "carrier", and the ant being transported as the "recruit". Such carrying has been described for other *Rhytidoponera* species (Möglich and Hölldobler, 1974; Ward, 1981).

We first observed carrying occurring from nest 59 to nest 60 on September 17, and this activity continued at a high level for the entire September observation period (11 days) and was also seen in

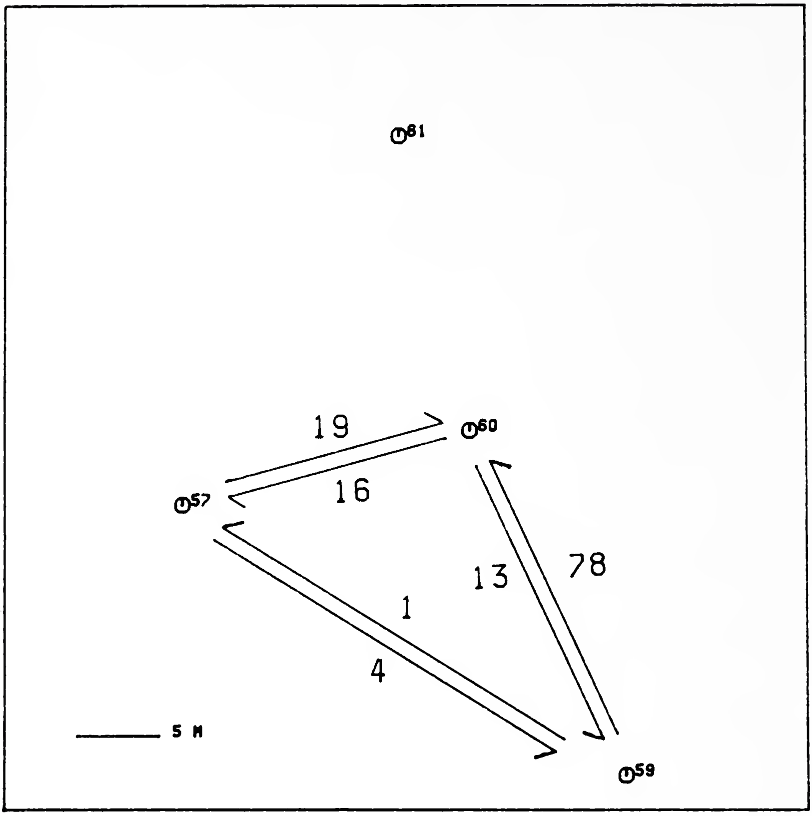

Fig. 2. Positions of nests involved in internest transfers in September. The arrows give the direction taken by observed carrier/recruit pairs, and the figures beside the arrows the numbers of such observations. Thus, most activity involved nest 60, with 60% of all observed carrier-recruit pairs moving to it from nest 59.

November. It soon became clear that carrying was occurring between nests 59, 60 and 57, and such movements occurred in each of the possible directions. But the predominant direction remained, as shown in figure 2, from nest 59 to nest 60 (involving 60% of all observations of carrying). The fidelity of carrying direction was high; during our observation periods we saw only one carrier change the nest it used as a destination. While it is likely that carrying started before we first observed it, it is our impression that it started first with nests 59 and 60, with nest 57 becoming involved later.

We used model paints to mark ants distinctively according to the nest in which they were caught, and could thus trace the flow of ants during inter-nest movements and evaluate the degree of mixture of ants from different (original) nests. Table 4 shows that this mixture was very considerable, and also reflects the fact that most ants in the three nests had moved into nest 60 by the end of the second observation period.

Carrying was also observed during our November visit to the study site, although it did not appear to be as frequent as in September. In November we observed ants being carried from nests 59 and 57 to nest 60, and also observed ants moving between these nests without carrying or being carried. Transport of brood was also seen, once in September. Although, in September, the ants of nest 61 were markedly hostile to ants from nests 57, 59 and 60, marked ants from all of these nests were found in nest 61 during November.

Carrying took place at times of high activity of ants outside the nests (i.e., during foraging sessions). These times, during our observation periods, were in the morning and late afternoon. At times, carrying became an activity rivaling foraging, with many ants emerging from nest 60 and heading towards the neighboring nests. These carriers mostly brought ants back from the other nests; seldom did they take ants to them.

Marking of carriers and riders showed that these two categories

Table 4. Mark-recapture observations on nests 57, 59 and 60. Ants were marked with paint dots according to whether they were found in nest 57 (O = orange), 59 (W = white), or 60 (G = green). At the end of the September observation period, as many ants as possible were captured from each nest, and the colors of the marked ants noted before all ants were returned to the nests they were last captured in. The decline in the number of marked ants in November is mostly due to loss of the marks rather than to mortality . The numbers in the table are of the ants recaptured; percentages of the total captured in each nest for each color are shown beneath each number.

	Sept. 20			Sept. 28			Nov. 14		
Nest	O	W	G	O	W	G	O	W	G
57 (O)	39	0	1	14	2	5	1	0	0
	97.5	0	2.5	65	10	25			
59 (W)	0	82	5	6	29	3	0	0	0
	0	94	6	16	76	8			
60 (G)	3	11	47	20	64	41	2	13	5
	4	18	78	16	51	33	10	65	25

are distinct: carriers form a specialized group. For example, we observed 11 carriers make 40 transport trips from nest 59 to 60. The differences between carriers and recruits extended to physiological state, with carriers having relatively poorly-developed ovarioles (Table 5).

Fukumoto and Abe (1983) found recruits to be indoor, and carriers to be outdoor, ants in the ponerine *Diacamma rugosum,* but the observation in *Formica* suggest that the carriers have an intermediate position between the two groups (Rosengren, 1971). We therefore attempted to demonstrate differences in the laboratory between carriers and recruits of *Rhytidoponera* sp. 12 in their preferences for darkened as against lit conditions. Ten ants from each group were individually placed into chambers made of two test tubes connected at their openings. One test tube was shaded using foil, and the other left uncovered. Each ant was allowed to select the dark or the light section of the chamber, and nine readings were made on each ant at half-hour intervals changing which end was shaded after each reading. The difference between the carriers and recruits is in the direction expected although ranking the two series of ants does not quite reveal a statistically significant result (the value of the Mann-Whitney test statistic comparing the two distributions from Table 6 is 72.5; whereas the value for the 5% level of a one-tailed test is 73, and for the 10% level it is 68).

Hostility tests.

Although ants from different nests often fight when they meet as foragers, the carrying phenomenon indicates that there must be considerable variation in the degree of hostility depending on the nests involved. We attempted to quantify the degree of hostility between different nests by moving ants between them.

Trials in previous years using mutton baits had been highly successful in moving ants between nests with minimal disturbance. This method, however, proved hard to quantify and had to be aban-

Table 5. Ovary development in carrier versus recruit ants collected during movements between colonies.

	Number of empty ovarioles							
	0	1	2	3	4	5	6	Total
carriers	2	1	1	1	1	0	9	15
recruits	23	1	3	0	0	1	4	32

Table 6. Behavioral comparison of carrier and recruit ants collected during internest movement: number of observation periods (out of nine) that ants were seen in the lit halves of choice chambers. Each series of observations on 10 individual ants in the two categories has been ranked.

	Ant rank									
	1	2	3	4	5	6	7	8	9	10
Carriers	0	4	6	7	7	8	8	8	9	9
Riders	1	1	2	2	4	5	5	6	8	9

doned in 1983 anyway because the ants showed no interest in mutton baits during our visits then. We chose not to use the method described by Haskins and Haskins (1983) for tests with *R. metallica,* in which individual ants from different nests are placed together in glass containers, because in that case both ants have been removed from their natural surroundings. Instead, we picked up an ant from one nest, grasping it by a mid-femur using forceps, and held it in the entrance of a target nest until four residents had examined it. If any of these attacked the transferred ant, the result was taken as a rejection of this ant. Five ants in all were used sequentially for each test, and, wherever allowed by the numbers of ants available, tests were made reciprocal. Because our method creates an artificial situation and the response at the nest entrance can be largely induced by the introduced ant, we also tested the method by making a control test at each nest, returning ants to their home nest: these ants were never attacked.

During any one test, results were usually fairly unequivocal. Even when ants attacked the forceps vigorously, they often ignored the transferred ant. However, we found a high degree of variation between replicates (Table 7), which may reflect differences in the responsiveness of the ants under varying environmental conditions (which we could not readily control). Nevertheless, some patterns do emerge. Thus, nest 61 was markedly more hostile to the "carrying" nests in September than in November, reflecting the significant turnover of ants between those times. Similarly, nest 60 shows elevated acceptance levels compared to other nests.

The results at nest 55 may have been affected by the fact that the mound was destroyed by some animal (probably a kangaroo) at the beginning of our experiments in September and the ants were busy rebuilding it.

Table 7. Hostility test results. Five ants in turn were taken from one nest to another and held by a mid-femur with forceps in the entrance of the "host" nest. An ant was considered "accepted" if at least three ants from the host nest contacted it without attacking it. The figures are the number of ants out of each set of five which were thus "accepted". Slashes separate results from repeated tests. The tests were carried out first in September and then repeated, where possible, in November. Dashes indicate tests that could not be done because of a shortage of ants at the surface of the nest of origin.

		Nest of Origin								
Host		54	55	57	58	59	60	61	63	64
September	54	5	5/1	0/3/2	0	–	1	2	1	0
	55	5	5	–	4	–	4	4	5	4
	57	5/0	–	5	–	3	5	5/0	–	–
	58	0	1	–	5	–	1	3	1	3
	59	–	–	–	–	5	5	–	–	5
	60	5	5	4	4	5	5	4	4	4
	61	0	3	1/0	1	–	1/0	5	5/1	4/2
	63	2	1	–	0	1	0	3	5	0
	64	0	0	–	4/0	0	1	1	2	5
November	54	5	4	5	1	–	5	4	4	4
	55	0	5	2	2	–	1	3	5	3
	57	3	1	5	3	–	5	5	2	5
	58	0	2	4	5	–	1	0	3	3
	60	4	2	5	1	–	5	5	3	5
	61	0	0	5	–	–	5	5	–	–
	63	2	1	5	2	–	5	1	5	5
	64	1	0	1	1	–	1	0	0	5

DISCUSSION

Of the ants we excavated from the mature colony, 299 were old ants and 138 had emerged relatively recently. The number of true egg-layers was 22, yielding estimates of these being 7.4% of the mature ants, or 5.0% of the total worker force. Whelden (1957) dissected 274 ants of a relatively closely-related species, *R. violacea*, and found 22 of these to be inseminated. Unfortunately, Whelden does not record the numbers of mature versus callow ants, although he does mention the presence of some of the latter. His figure of 8.0% of the workers being inseminated is therefore not directly comparable to our estimates, because his collection was made in May (a late autumn month in Australia) whereas ours was made in November, an early summer month.

The average relatedness level of 0.158 (± 0.037, 95% confidence limits) for this *R.* sp. 12 population (Crozier et al., 1984) would suggest that the average number of egglayers per nest yielding workers would be 5.8 (with 95% confidence limits 4.6–7.9), according to the formulas of Pamilo and Varvio-Aho (1979) and under the assumptions that these egg-layers are as closely related as workers on average, that they mate once and to unrelated males, and that they contribute equally to the next generation. The figure of 22 we observed requires confirmation by further excavations but, if confirmed as typical, would indicate that one or more of these assumptions are violated. If 22 mated workers did contribute to the next generation under these assumptions, then the mean relatedness level would be below 0.05.

Data are also available for *Rhytidoponera* species with life-patterns differing to that of sp. 12 with regard to the observed proportions of mated workers. Haskins and Whelden (1965) found 5.4% of the workers to be inseminated in *R. metallica* and 2.3% in *R. inornata,* both species that habitually lack differentiated queens in their colonies, but in which winged queens do occasionally occur. Ward (e.g., 1981, 1983) found that species in the *impressa* group have colonies of two kinds: those with a single differentiated queen each, and those lacking such queens but in which the reproductive role is taken over by some mated workers, as in sp. 12. Figures reported by Ward (1983) for 33 colonies of the latter type in *confusa* and *chalybaea* yield an estimate of 3.7% of the workers being inseminated. While the various *Rhytidoponera* species *may* differ in the percentages of workers per colony that are inseminated, little can be inferred from the figures so far, because it is likely that the percentage varies with age and size of colonies, and with the time of the year collections are made, and these data are imperfectly recorded in the literature.

The occurrence of oocytes in the ovarioles of most ants, mated or not, is striking. Whelden (1957) mentions that many workers in *violacea* have oocytes, and that the occurrence of oocytes is not linked to that of sperm in the spermatheca, but he gives no figures. Ward (1983) found much smaller percentages of unmated workers to have oocytes in *impressa*-group colonies. We suggest that the eggs of uninseminated workers are probably trophic eggs, eggs laid only to be eaten. Nutrient transfer by this means is common in the colonies of ants and other social Hymenoptera, and has its precursors in presocial insects (Wilson, 1971: 279–281). However, the oocytes of unmated sp. 12 workers did not appear different morphologically to those of inseminated individuals, whereas in some ant species at least trophic eggs differ in size, consistency, or both, from reproductive eggs (Wilson, 1971: 279–281).

The life pattern of *Rhytidoponera* species such as sp. 12 and *violacea,* in which the differentiated queens regarded as normal among ants are replaced by mated workers, is paralleled in many other ants. Wheeler and Chapman (1922) provided the first such observation, for the ponerine *Diacamma rugosum,* Haskins and Zahl (1971) showed that another ponerine, *Dinoponera grandis* is very similar, and a further ponerine, *Ophthalmopone berthoudi,* has recently been examined intensively (Peeters, 1982; Peeters and Crewe, 1984). Whereas the ponerine workers all resemble each other closely, those of another ant with mated workers, the myrmicine *Harpagoxenus sublaevis,* vary in size and thoracic development, and only about 4% of them possess a spermatheca: the mated workers form a majority of this 4% (Buschinger and Winter 1975, 1978). True queens also occur in *H. sublaevis;* whether a female larva has the capacity to develop as a queen or as a worker is determined genetically (Buschinger 1978). Workers lack spermathecae in *Harpagoxenus canadensis* and in *H. americanus* (Buschinger and Alloway 1977, 1978), preventing the evolutionary replacement of true queens by mated workers in these species; in all three species unmated workers may also oviposit. A major difference between the ponerine mated worker system and that of *H. sublaevis* is that *H. sublaevis* colonies possess only one mated egg-layer each, whether a worker or a true queen, whereas the ponerines can have many such individuals per colony. The polymorphism of mated egg-layers in *Rhytidoponera* species such as *metallica* and *confusa,* and in *Harpagoxenus sublaevis,* and the apparent morphological identity of all workers, mated or not, in the ponerines, indicates that the mated workers are fundamentally different in evolutionary origin and present-day caste-determination dynamics to the ergatoid queens of genera such as *Myrmecia* and *Dorylus,* with ergatoids differing morphologically from workers in the direction of true queens and representing intergrades. Wilson's (1971: 138–139) distinction between queens (as fully-developed reproductive females with functional though deciduous wings) and ergatogynes (queen-worker intermediates) is useful as a description of significantly-different biologies for the egg-layer role, and the mated workers we have discussed represent a third important type. We concur with the felicitous term of *gamergate* proposed for them by Peeters and Crewe (1984).

The factors leading a *Rhytidoponera* worker to become a gamergate or not are unknown. Peeters and Crewe (1984) found percentages of gamergates much higher for *Ophthalmopone* (up to 63%) than reported for *Rhytidoponera,* and suggested that the wide variability of this percentage during the year indicates that the determination of gamergates in *Ophthalmopone* is purely a matter of whether or not males are available during a crucial period during the early period of a worker's life. This idea remains to be tested for *Rhytidoponera,* but a major difference between the two genera is already known: a majority of *Rhytidoponera* workers have ovarian activity, whereas only gamergates possess oocytes in *Ophthalmopone.* Gamergates in both genera, however, are similar in being found in the nest and not outside.

Foraging appears to be a rudimentary type-II type in the classification of Oster and Wilson (1978: 248–251): workers diffuse out from the nest and mostly act individually, but are capable of at least short-range recruitment when difficult food items are located. Concerted defense of territory is lacking, although a kind of "defense in depth" operates: the further workers penetrate into the foraging areas of neighboring colonies, the more likely they are to encounter workers from these colonies and undergo potentially-deadly combat. However the density of ants is not high enough to make such contact invariable, and this is reflected in the fact that many foraging trips approach or exceed the line subtended by neighboring nests. Nevertheless, we would expect that workers would tend to avoid areas heavily patrolled by hostile ants, although the data are not numerous enough to test this hypothesis.

The finding that foragers tend to choose the same direction in repeated trips is consistent with our expectation that the worker force would tend to avoid areas patrolled particularly heavily by those of neighboring nests, in that such a capacity for recollection is needed for the avoidance mechanism to operate. Foraging direction fidelity of the same kind as in *R.* sp. 12 has also been demonstrated in the myrmicine harvesters *Pogonomyrmex barbatus, P. maricopa* (Hölldobler 1976), and *P. mayri* (Kugler, 1984); another myrmicine harvester, *Pheidole militicida* (Hölldobler 1976; Hölldobler and Möglich 1980), and various formicines such as *Formica* species (Rosengren, 1971: 7–57), show route fidelity: tendency of workers to exit along the same trunk route in successive trips. It is possible that foragers of these species and of *R.* sp. 12 not only forage in the same direction in successive trips, but also visit the same areas in the foraging grounds, as has been demonstrated for foragers and aphid-tenders of the formicines *Cataglyphis bicolor* (Harkness and Harkness 1976), *Formica obscuripes* (Herbers 1977), *Formica yessensis* (Higashi 1978), *F. subnuda, F. subsericea* and *Camponotus noveboracensis* (Ebbers and Barrows 1980): the phenomenon of *ortstreue* (Oster and Wilson 1978: 152).

Among ponerines, carrying has also been implicated in nest-moving in *Diacamma rugosum* (Fukumoto and Abe, 1983), *Bothroponera tesserinoda* (Maschwitz et al., 1974; Möglich and Hölldobler, 1974), and *Ophthalmopone berthoudi* (Peeters, 1984). However, *D. rugosom* also employs tandem running and in *B. tesserinoda* tandem running is the chief method used.

The extensive "carrying" between nests indicates that, although considerable hostility can be demonstrated both between foraging workers and by our "hostility tests", such internest hostility is not invariable. We are uncertain at present whether certain groups of nests are linked as multinest colonies, or whether the situation might not be more complex. It is possible, for example, that the fundamental selection unit above that of the individual in populations such as that of the observed *R.* sp. 12 and of some *Formica* species (Scherba 1964) is not the nest but the matriline or sibship. Nests would contain cooperating matrilines, and carrying may represent attempts to maintain nests at adequate strength via the antnapping of outsiders. The rather confused nature of carrying, with workers making trips in several different directions, is consistent with the matriline-selection hypothesis, but is also observed in some other ants during nest-moving when scouts "choose" different destinations (Möglich and Hölldobler 1975; Rosengren and Pamilo 1983), and such multi-directional carrying can be likened to a voting system for choosing the best nest-site (Rosengren, 1971: 21; Wilson, 1971: 224). The observation of ants marked in the 57–59–60 system in nest 61 in

November, whereas ants from nest 61 had been uniformly hostile to such ants in September, is not, however, consistent with the hypothesis of a multinest colony. That moving in *R.* sp. 12 rests on the pronota of elite movers is consistent with observations from other ants (Möglich 1978; Möglich and Hölldobler 1974, 1975), as is the observation of reduced ovarian activity in these mover workers (Möglich and Hölldobler 1975). Carrier ants may not, of course, be acting in the "interests" of those carried: carrying in *Formica aquilonia* (Rosengren and Pamilo 1983) can represent the robbing of workers by one nest of another (closer to true slavery than is dulosis).

If carrying is an "amicable" activity, then it might be expected to occur between nests more closely related than the average. The analyses so far available (Crozier et al 1984) cannot yield that information, because the relatedness estimates are regression coefficients pertaining to the population as a whole. But the determination of genetic distances between colonies, based on further data, may overcome this lack.

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SUMMARY

We report studies on the reproductive and foraging biology of *Rhytidoponera* sp. 12, a large ponerine ant which lacks a morphologically-differentiated queen caste.

Based on dissections of 437 ants from an established colony, about 7.5% of the mature workers are mated egglayers (equivalent to the gamergates of Peeters and Crewe, 1984). These mated workers are concentrated in the lower regions of the nest, or move preferentially to them during disturbance. Workers taken from the upper regions of the nest had low levels of ovarian activity whereas unmated workers from the lower regions had high such levels;

mated workers showed intermediate activity. We suggest that the oocytes of unmated workers may be destined to become trophic eggs.

None of the 230 ants dissected from an apparently incipient colony was inseminated; the level of ovarian activity in such individuals was high.

Foragers from different nests were not indifferent to each other after contact, usually running away but sometimes fighting. Despite this antagonism between foragers, the foraging area for two nests studied intensively extended beyond the figure subtended by neighboring nests. Foraging trips extended significantly further in November than in September, probably due to a decline in the food supply.

Foragers had a strong and statistically significant tendency to take the same direction in successive foraging trips, i.e., they show foraging-direction fidelity.

We saw ants carrying others from one nest to another in three regions of our study area, and studied their behavior in one of these areas intensively. In this region, we saw this carrying take place in September in each of the possible six directions between three nests. But most traffic was into one of them, nest 60. The resulting intermixture of ants between nests was considerable, as shown by marking experiments. Tests for worker hostility to ants from other nests showed nest 60 to be the least hostile, with the adjacent nest 61, not one of the three nests linked by carrying, showing a high level of intolerance to strangers. In November, however, nest 61 included ants originally marked in the other three nests.

"Carrier" ants had less ovarian activity than those they carried, and, from the additional fact that the same carriers made repeated trips, seem to form a relatively small group within the colonies.

It is uncertain whether the nests linked by internest movements represent multi-nest colonies, or whether such activity can potentially involve any neighboring nests.

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THE ORIENTAL LEPIDOSTOMATIDAE (TRICHOPTERA) DESCRIBED BY BANKS AND HAGEN[1]

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Introduction

There are 14 Oriental and 1 eastern Palearctic (Japan) species of Lepidostomatidae described by Banks and Hagen (Fischer 1970). Unfortunately, the original descriptions of these species are not very useful for identification purposes today, because neither author relaxed and cleared the genitalia of these species. This technique reveals important characters of caddisfly genitalia and is now a standard method in Trichopterology. Hence, the redescription of these species is a desired prerequisite for further contributions to the Oriental lepidostomatids. Fortunately, syntypes of all these species have been located; most were at the Museum of Comparative Zoology (MCZ), Harvard University, Massachusetts and a few were at the British Museum (Natural History), London.

Banks and Hagen rarely indicated where all syntypes of their new species were deposited. Judging from the collection of Trichoptera at the MCZ, I infer they exchanged specimens, including syntypes, with their colleagues. Most of their syntypes are at the MCZ, but many are also in several other museums. For example, Ulmer (1951) mentioned that a few lepidostomatid types of Banks were in the "Museum Selangor" (probably the National Museum of Malaysia, Kuala Lumpur) and for this work I found male syntypes of two species only at the British Museum.

Also, Banks and Hagen did not label unique species types as holotypes. Banks' Trichoptera syntypes at the MCZ, that I have examined, have red type labels of two varieties. The first and older kind of label is glossy red obverse and white reverse, reading "Type"

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on the first line and with a species specific number on the second line. All of Hagen's syntypes examined bear MCZ labels of this variety. The second kind of type label is on nonglossy red paper, reading "M.C.Z." on the first line, "Type" or "Paratype" on the second line and with a species specific number on the third line. Also, the first syntype of the series with the red label reading "Type" has an additional label of determination that has "type" written in the lower left corner; other syntypes have red labels reading "Paratype," but usually not have larger determination labels. The change in type labels of Banks' species took place sometime after MCZ type no. 16500 of *Goerodes grandis* (Banks 1931c), but before type no. 20182 of *Goerodes medius* (Banks 1934).

Lectotypes have been designated for all species examined, even when only one syntype was available, because of the possibility that additional syntypes might exist at other institutions. For each species I have selected as lectotype the first specimen in the type series which bears a separate determination label. Ross (1938) described the important details of Hagen's and Banks' type labels and I have followed his procedure for selecting lectotypes, which was recommended to him by Banks.

In this work, the bibliography following each species lists selected references. In the examined material cited, the institutions or persons holding the specimens are indicated in parentheses and are abbreviated as follows: British Museum (Natural History), BMNH; Canadian National Collection, CNC; Museum of Comparative Zoology, MCZ; Smithsonian Institution, National Museum of Natural History, USNM; and the collections of Hans Malicky, HM; and the author, JSW. Also, known collectors are abbreviated as follows: Baumann and Cross, B&C; C. S. Clagg, CSC; Davis and Rowe, D&R; O. S. Flint, Jr., OSF; M. R. Henderson, MRH; K. V. Krombein, KVK; and H. M. Pendlebury, HMP.

LEPIDOSTOMATIDAE

Goerodes abruptus Banks
(Fig. 1)

Goerodes abrupta Banks 1931b: 391, ♀, fig. 40.
Goerodes abruptus, Fischer 1970: 17.

Male. Unknown.

Female. Wings brown, fore wing 6.2 mm long. Genitalia (Fig.

1), spermathecal sclerite trapezoidal with posterolateral corners extended, in ventral view.

Material Examined. *Lectotype* ♀, "Type 16473," MALAYSIA, PERAK, Batang Padang, Jor Camp, 1800 ft, 10 III 1924, HMP, (MCZ).

Goerodes apoanus (Banks)
(Figs. 2, 3, 4)

Goerinella apoana Banks 1937: 155, ♂♀, pl. 5 figs. 49, 51.
Goerodes apoanus, Fischer 1970: 17.

Male. Scape 1.2 mm long, not highly modified, cylindrical, mesal surface concave. Maxillary palp 1.0 mm long, similar as in *G. conjunctus* (Fig. 6B). Fore wing (Fig. 2) 8.7 mm long, modified with narrow anterior costal fold. Genitalia (Fig. 3).

Female. Genitalia (Fig. 4); spermatheca ovoid, microtrichia with a conspicuous pattern, short and dense in anterior 1/3, fewer and larger in middle 1/3, sparse and short in posterior 1/3.

Material Examined. PHILIPPINES, *MINDANAO: Lectotype* ♂, "M.C.Z. Type 22049," Mt. Apo, 6000 ft, Mainit Riv., 22 IX, CSC, (MCZ). Paratypes, "M.C.Z. Paratype 22049:" same data as lectotype, 6 ♂, (MCZ); same place, 1 ♂, 10 IX: 1 ♂, 24 IX: 1 ♀, 21 X; 1 ♂, 23 X, (MCZ); Mt. Apo, Galog Riv., 6000 ft, 1 ♀, 1 ♂, 26 IX; 1 ♂, 18 X, 2 ♂, 1 ♀, 19 X; 1 ♂, 21 X; 1 ♀, 6 XI, CSC, (MCZ); Mt. Apo., Sibulan Riv., 7–8000 ft, 1 ♂, 6 IX, CSC, (MCZ). Nontypes: Mt. Apo., Galog Riv., 6000 ft, 1 ♀, 1 IX; 1 ♀, 8 X; 1 ♀, 18 X; 3 ♀, 19 X; 1 ♂, 21 X; 1 ♀, XI; 1 ♂, 4 XI, CSC, (MCZ); Mt. Apo, Mainit Riv., 6000 ft, 1 ♀, 22 IX, CSC, (MCZ); Mt. Apo, Sibulan Riv., 7–8000 ft, 1 ♂, 1 ♀, 6 IX, CSC, (MCZ); Mt. Mayo, Davao, 4–5000 ft. 1 ♀, 26 I; 1 ♀, 30 I, CSC, (MCZ).

Goerodes bicolor (Banks)
(Fig. 5)

Goerinella bicolor Banks 1937: 155–6, ♀, pl. 5 fig. 45.
Goerodes bicolor, Fischer 1970: 18.

Male. Unknown.

Female. Scape 1.7 mm long, cylindrical. Fore wing brown, 12.0 mm long. Eyes dark brown, rest of body orangish brown. Genitalia (Fig. 5), spermatheca with a few microtrichia, lacking any conspicuous pattern.

Material Examined. *Lectotype* ♀, "M.C.Z. Type 22050," PHILIPPINES, *MINDANAO,* La Lun Mts., Davao, 4 VII, CSC, (MCZ).

Goerodes conjunctus (Banks)

(Figs. 6, 7, 8)

Goerinella conjuncta Banks 1934: 574–5, ♂♀, figs. 10, 20.
Goerodes conjunctus, Fischer 1970: 18–9.

Male. Color brown. Scape (Fig. 6B) 1.7 mm long, mesal surface concave with modified setae and lobes. Maxillary palps (Fig. 6A), basal segment curved, apical segment flexible and setose. Fore wing (Fig. 6C) 9.2 mm long. Genitalia (Fig. 7).

Female. Scape 1.2 mm long. Fore wing 8.6 mm long. Genitalia (Fig. 8).

Material Examined. *Lectotype* ♂: MALAYSIA, *SABAH,* Kinabalu, Lumu Lumu, 5000 ft, 16 IV, (BMNH); "Allotype," Lumu Lumu, 5500 ft, 1 ♀, 16 IV 1929, (BMNH).

Goerodes grandis (Banks)

(Figs. 9, 10, 11)

Goerinella grandis Banks 1931c: 420, ♂♀, figs. 1, 3, 4, 9.
Goerodes grandis, Fischer 1970: 20–1.

Male. Color brown. Scape (Fig. 9B) 2.0 mm long, with mesal surface modified. Maxillary palp 2.0 mm long, similar as in *G. conjunctus* (Fig. 6B). Fore wing (Fig. 9A) 13.5 mm long. Genitalia (Fig. 10).

Female. Color brown. Scape 1.5 mm long. Fore wing 14.0 mm long. Genitalia (Fig. 11).

Material Examined. MALAYSIA, *SABAH:* *Lectotype* ♂, "Type 1650," Pakka, Mt. Kinabalu, 10000 ft, 23 III 1929, HMP, (MCZ); "CNC No. 12359 Paratype," same place: 1 ♂, 20 III 1929, HMP, (CNC); 1 ♀, 23 III 1929, HMP, (MCZ); 2 ♀, 22 III 1929, HMP, (MCZ).

Goerodes medius (Banks)

(Figs. 12, 13, 14)

Goerinella media Banks 1934: 574–5, ♂♀, figs. 11, 17, 18, 22.
Goerodes medius, Fischer 1970: 21–2.

Male. Color brown. Scape 0.9 mm long, not highly modified. Maxillary palp 0.5 mm long, curved in front of frons. Fore wing (Fig. 12) 8.0 mm long. Genitalia (Fig. 13).

Female. Scape 1.0 mm long. Fore wing 6.5–7.5 mm long. Genitalia (Fig. 14).

Material Examined. MALAYSIA, *SABAH: Lectotype* ♂, Mt. Kinabalu, Lumu Lumu, 5500 ft, 10 IV, HMP, (BMNH); "Allotype," same place, 1 ♀, 14 IV 1929, HMP, (BMNH); "M.C.Z. Type 20183," "Paratype," same place, but 7000 ft, 1 ♀ w/o head and abdomen, 3 IV 1929, HMP, (MCZ); same place, but 5500 ft, 1 ♀, 17 IV 1929, HMP, (BMNH); same data, 1 ♀, (MCZ).

Goerodes minor (Banks)
(Figs. 15, 16)

Goerinella minor Banks 1931a: 67, ♂, pl. 5 fig. 6.
Goerodes minor, Fischer 1970: 22.

Male. Color brown. Scape 0.9 mm long, cylindrical, not highly modified. Maxillary palp 0.5 mm long, curved in front of frons, similar as in *G. conjunctus* (Fig. 6B). Fore wing (Fig. 15) 8.0 mm long. Genitalia (Fig. 16).

Female. Unknown.

Material Examined. *Lectotype* ♂, "Type 16418," PHILIPPINES, *LUZON,* Mt. Mekiling, no date, Baker, (MCZ).

Goerodes piscinus (Hagen)
(Fig. 17)

Mormonia piscina Hagen 1859: 208.
Goerodes piscina, Mosely 1949: 784–5, ♂♀, figs. 167–71.
Goerodes piscinus, Fischer 1970: 23.

Male. Color brown, cf. (Mosely 1949: figs. 167–71). Scape 1.3 mm long, not highly modified. Maxillary palp 0.8 mm long.

Female. Scape 1.2 mm long. Fore wing 9.1 mm long. Genitalia (Fig. 17).

Material Examined. SRI LANKA: *Lectotype* ♂, "Type 10946," no date, (MCZ); 1 ♂ syntype, (MCZ); 1 ♀ (Hagen and Mosely det. as *ursina*) with BMNH type label, (BMNH); N. E. DIST.: Kanda-ela, Resevior, 5.6 mi. SW Nuwara Eliya, 6200 ft, 5 ♂, 1 ♀, 10–21 II 1970, D&R, (USNM); 2 ♂, 1 ♀' 1–5 X 1970, OSF, (USNM); 1 ♂, 31 V–2 VI 1976, KVK *et al.,* (USNM); Great Western Est. nr Talawalele, 4200 ft, 1 ♂, 1 ♀, 5 X 1970, OSF, (USNM); Pattipola, 1 ♂, V 1911, J. C. Fryer, (BMNH); Pattipola, 6100 ft, 2 ♂, 2 ♀, 3–6 X 1970, OSF, (USNM); Horton Plains, Agrapatana Rd., 6600 ft, 5 ♂, 4 ♀, 4 X 1970, OSF, (USNM); same place, but 7000 ft, 1 ♂, 20 III 1973, B&C, (USNM); same place, but 6000 ft, 1 ♂, 2 ♀, 21 III 1973, B&C,

(USNM); Lovers Leap Creek, 7000 ft, 5 ♂, 15 III 1973, B&C, (USNM); Moon Plains, 1635 ft, 11 ♂, 13 ♀, 18 VIII 1973, Ginter Ekis, (USNM); Nuwara Eliya, 1 ♂, 25 VII 1924, (BMNH); 2 ♂, 1 ♀, 24 IX 1975; 1 ♂, 2 ♀, 26–27 IX 1975, D. M. Davis *et al.,* (USNM); 1 ♂, 27–29 V 1975, D. H. Messersmith *et al.,* (USNM); Nuwara Eliya, Galway Reserve, 2 ♀, 28 IX-1 X 1973, KVK *et al.,* (USNM); Hakgala, Botanic Garden, Circuit Bung., 1 ♂, 1 ♀, 5–8 II 1979, KVK *et al.,* (USNM); Botanical Gardens, 6000 ft, 3 ♀, 6–8 X 1976, G. F. Hevel *et al.,* (USNM).

Goerodes posticatus (Banks)
(Figs. 18, 19)

Goerinella posticata Banks 1931b: 393, ♂, figs. 35, 37, 38.
Goerodes posticatus, Fischer 1970: 23.

Male. Color brown. Scape 1.3 mm long, with basomesal lobe. Maxillary palp 1.2 mm long. Fore wing (Fig. 18) 7.7 mm long, with long posterior marginal fold. Genitalia (Fig. 19).

Female. Unknown.

Material Examined. MALAYSIA: *Lectotype* ♂, "Type 16471," *PAHANG,* Cameron's Highlands, Tahan Padang, 4500 ft, 13 VI 1924, MRH, (MCZ); Cameron's Highlands, 4–5000 ft, 1 ♂, 10 VI 1935, HMP, (MCZ); *SELANGOR,* Bnkit Kutu, 3500 ft, 1 ♂, 14 III 1931, HMP, (MCZ).

Goerodes ursinus (Hagen)
(Fig. 20)

Mormonia ursina Hagen 1858: 484.
Goerodes ursina Mosely 1949: 782–3, ♀, fig. 166.
Goerodes punda Mosely 1949: 785, ♂, figs. 172–7, NEW SYNONYM.
Goerodes punda, Fischer 1970: 23.
Goerodes ursinus, Fischer 1970: 25.

Male. Color brown, cf. (Mosely 1949: figs. 172–7). Scape 1.1 mm long, not highly modified. Maxillary palps 0.7 mm long. Fore wing 6.0–7.4 mm long.

Female. Scape 1.0 mm long. Fore wing 7.0–8.5 mm long. Genitalia (Fig. 20). Spermatheca ovoid, microtrichia in anterior 1/4 dense and stout, having reticulate pattern, in middle 1/2 long, in posterior 1/4 short and sparse.

Material Examined. SRI LANKA: *Lectotype* ♀, "Type 10943," (MCZ); 1 ♀ syntype, no date, (MCZ); 1 ♀, (MCZ); BAD. DIST.:

Koslanda, Diyaluma Falls, 3000 ft, 6 ♂, 7 ♀, 19 III 1973, B&C, (USNM); COL. DIST.: Pudukka, 300 ft, 1 ♂, 16 XI 1970, OSF, (USNM); Tunmodera, 200 ft, 2 ♂, 17 XI 1970, OSF, (USNM); GAL. DIST., Sinharaja Jungle, Kanneliya sec., 1 ♂, 13–16 July 1978, KVK *et al,* (USNM); KAN. DIST.: Polpitiya, Kelani Ganga, 400 ft, 1 ♂, 24 IX 1970, OSF, (USNM): Laksapana, 1200 ft, 1 ♀, 23–29 IX 1970, OSF, (USNM); MATE. DIST.: Elkaduwa, Hunas Falls, 3000 ft, 6 ♂, 6 ♀, 5 IV 1973, B&C, (USNM); RAT. DIST.: Belihul Oya, 2000 ft, 1 ♂, 12 X 1970, OSF, (USNM); same place, 3 ♂, 2 ♀, 22 III 1973, B&C, (USNM); Uggalkaltota, 350 ft, irrigation bungalow, 1 ♂, 21 I-8 II 1970, D&R, (USNM); Uggalkaltota, 1♂, 23–26 VI 1978, KVK *et al.*, (USNM).

Goerodes venularis (Banks)
(Figs. 21, 22, 23)

Goerinella venularis Banks 1931b: 392, ♂, figs. 34, 36.
Goerodes continuata Banks 1931b: 391–2, ♀, fig. 39, NEW SYNONYM.
Goerodes continuatus, Fischer 1970: 19.
Goerodes venularis, Fischer 1970: 25.

Male. Color brown. Scape 1.0 mm long, not highly modified. Maxillary palps 0.6 mm long. Fore wing (Fig. 21) 7.0–7.5 mm long. Genitalia (Fig. 22).

Female. Scape 1.0 mm long, cylindrical. Fore wing 7.5 mm long. Genitalia (Fig. 23). Spermatheca with two chambers: main chamber with microtrichia sparse, auxiliary chamber smaller, with microtrichia dense, stout, in reticulate pattern.

Material Examined. MALAYSIA, *PAHANG: Lectotype* ♂, "Type 16474," "*Goerinella venularis* type," Cameron's Highlands, 4800 ft, 21 VI 1923, HMP, (MCZ); 1 ♂ syntype, same place, but Tahan, 4500 ft, 12 I 1924, MRH, (MCZ); same place as lectotype, 1 ♂, 6 VI 1935, HMP, (MCZ); same place, 1 ♂, 6 VII 1935, HMP, (MCZ); same place, but 45–5000 ft, 1 ♀, 14 VI 1935, HMP, (MCZ); same place, but 45–4800 ft, 3 ♀, 16 VI 1935, HMP, (MCZ); same place, 4700 ft, 2 ♂, 12 V 1939, HMP, (MCZ); Ginting Kial, 5200 ft, 1 ♂, 25 VI 1938, HMP, (MCZ). *Lectotype* ♀, "Type 16472," "*Goerodes continuata* type," Cameron's Highlands, Tahan, 4500 ft, 12 I 1924, MRH, (MCZ); 4 ♀ syntypes: same place, but 4800 ft, 1 ♀, 12 X 1923; 1 ♀, 13 X 1923; 1 ♀ 12, III 1924, HMP, (MCZ); Sungai Ranglat, 3–500 ft, 1 ♀, 10 III 1925, HMP, (MCZ). INDONESIA, *SUMATRA:*

Brastagi, 1200 m, 1 ♀, 11 XII 1969; 1 ♂, 26 XII 1971, (HM); Bukit Tinggi, 9 ♀, 24 VIII 1974, (HM); Dairi, 1600 m, 2 ♂, 3 ♀, 30 VIII 1970; 4 ♂, 3 ♀, 2 IX 1970; 8 ♂, 13 ♀, 8 XI 1970; 1 ♂, 27 XII 1970; 8 ♂, 25 IV 1971; 6 ♂, 6 V 1977; 1 ♂, 1 ♀, 28 VIII 1979, (JSW); Dolok Merangir, 1 ♀, 27–31 XII 1969; 1 ♀, 1–22 VI 1970; 2 ♂, 20 VI–17 VII 1971; 3 ♂, 1 ♀, 24 III–22 IV 1972; 1 ♂, 3 II–19 III 1972; 1 ♂, 20 XI 72–5 I 1973; 1 ♀, 10 I–3 III 1973; 1 ♂, 1 ♀, 7 VI–6 X 1974; 1 ♂, 3 ♀, 22 XII 73–27 I 74; 1 ♂, 21 VIII 1976; 1 ♂, VI 1981, (HM); Mt. Kerinei, 1800 m, 2 ♂, 1 ♀, 21–24 II 1976, (HM); Mts. Daior, 5 ♂, 6 ♀, 17 VIII 1977, (HM); Paritokoa, 1 ♀, 22 II 1981, (HM); Prapat, 1200 m, 1 ♂, 1 ♀, 20 IV 1974; 4 ♂, 2 ♀, 24 III 1974; 1 ♂, 3 ♀, 25 XI 1973, (HM); Sitahoan, 1400 m, 1 ♂, 7 ♀, 2 IX 1981, (HM); Tele, 1400 m, 6 ♂, 7 ♀, 4 VI 1973, (HM).

Dinarthropsis picea Ulmer
(Figs. 24, 25)

Dinarthropsis picea Ulmer 1913: 91–2, ♂♀, figs. 9, 10, 12, 13, 15.
Dinarthrodes niger Banks 1913: 142–3, ♂, pls, 8–9 figs. 4, 5, 13, NEW SYNONYM.
Dinarthropsis picea, Ulmer 1951: 10, 14, 22, 25, 491–4, ♂♀, figs. 773–89.
Dinarthropsis nigra, Fischer 1970: 4.
Dinarthropsis picea, Fischer 1970: 4–5.

Male. Color brown. Scape 1.5 mm long, with two mesal lobes and modified setae. Maxillary palps curved in front of frons. Wings (Fig. 24); fore wing 8.7 mm long; hind wing with discal cell open. Genitalia (Fig. 25).

Female. Cf. (Ulmer 1913, 1951).

Material Examined. *Lectotype* ♂, "*Dinarthrodes niger* type," "Type 11780," JAVA, no date, Batavia, (MCZ); same data as lectotype, 2 ♂, (MCZ).

Dinarthrodes albicorne (Banks) new comb.
(Fig. 26)

Crunoecia albicornis Banks 1906: 109, ♀, pl. 3 fig. 11.
Crunoecia albicornis, Fischer 1970: 71.

The hind wing of this species has a closed discal cell and thus, it should be removed from *Crunoecia*. It is tentatively placed in the genus *Dinarthrodes*, because in the female the scape is relatively long and the wings are not broad.

Male. Unknown.

Female. Color dark brown. Scape 2.0 mm long. Fore wing 9.0 mm long. Hind wing with open discal cell. Genitalia (Fig. 26).

Material Examined. *Lectotype* ♀, "Type 11830," JAPAN, Hiko-san, Buzen, no date, (MCZ); same data as lectotype, 1 ♀, (MCZ).

GOERIDAE

Goera mustellina (Hagen) new comb.

Mormonia mustellina Hagen 1859: 209.
Goerodes mustellinus, Fischer 1970: 22.

I have not examined any syntypes of this species. However, Oliver S. Flint has informed me that it is another species of *Goera.*

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SUMMARY

The Oriental Lepidostomatidae described by Banks and Hagen are redescribed and lectotypes are designated, including: *Goerodes abruptus* Banks, *G. apoanus* (Banks), *G. bicolor* (Banks), *G. conjunctus* (Banks), *G. grandis* (Banks), *G. medius* (Banks), *G. minor* (Banks), *G. piscinus* (Hagen), *G. posticatus* (Banks), *G. ursinus* (Hagen) *G. venularis* (Banks). Two new combinations: *Goera mustellina* (Hagen), removed from *Goerodes*: and *Dinarthrodes albicorne* (Banks), removed from *Crunoecia.* Three new synonyms: *Goerodes continuatus* Banks, junior synonym of *G. venularis* (Banks); *G. punda* Mosely, a junior synonym of *G. ursinus* (Hagen); and *Dinarthropsis nigra* (Banks) a junior synonym of *D. picea* Ulmer.

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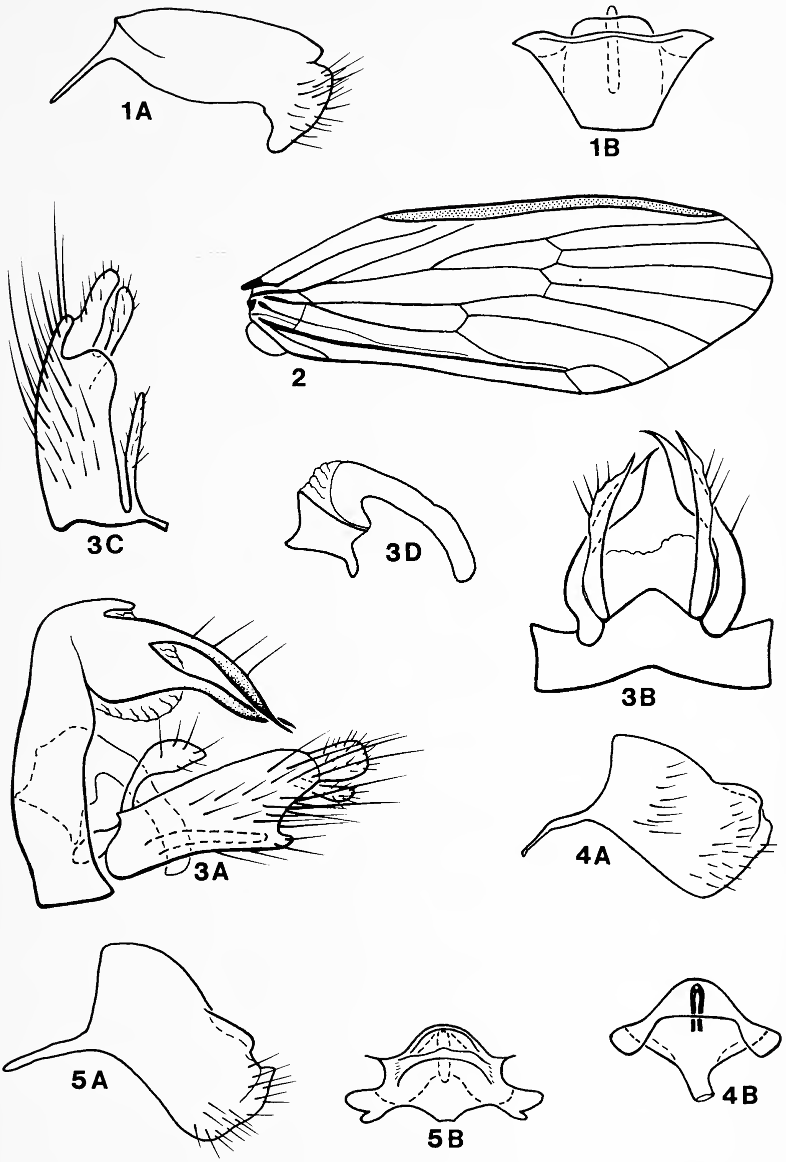
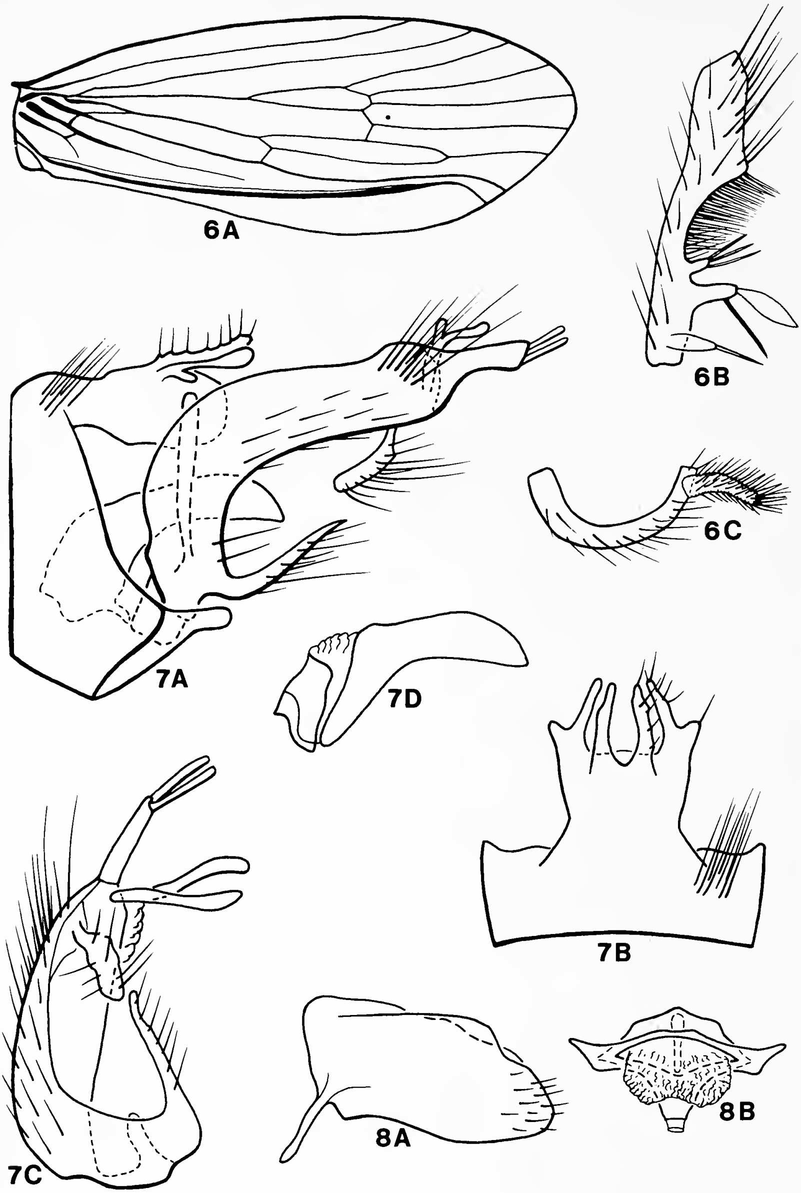
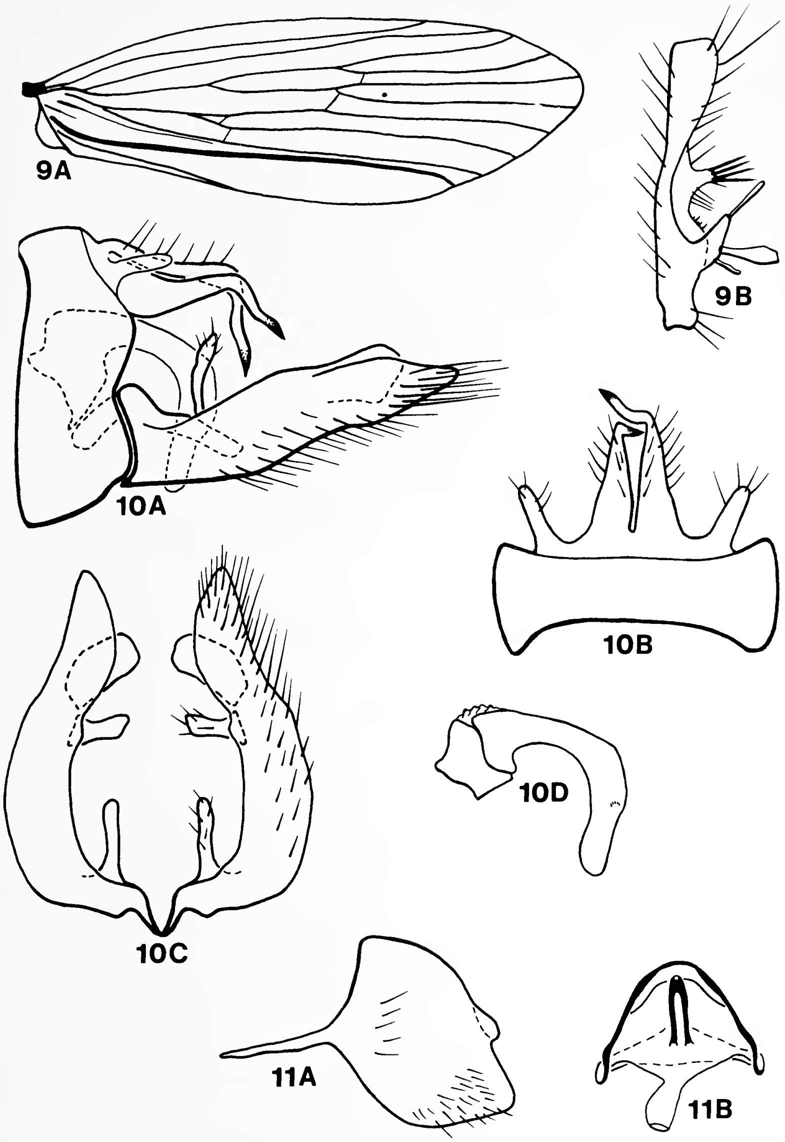


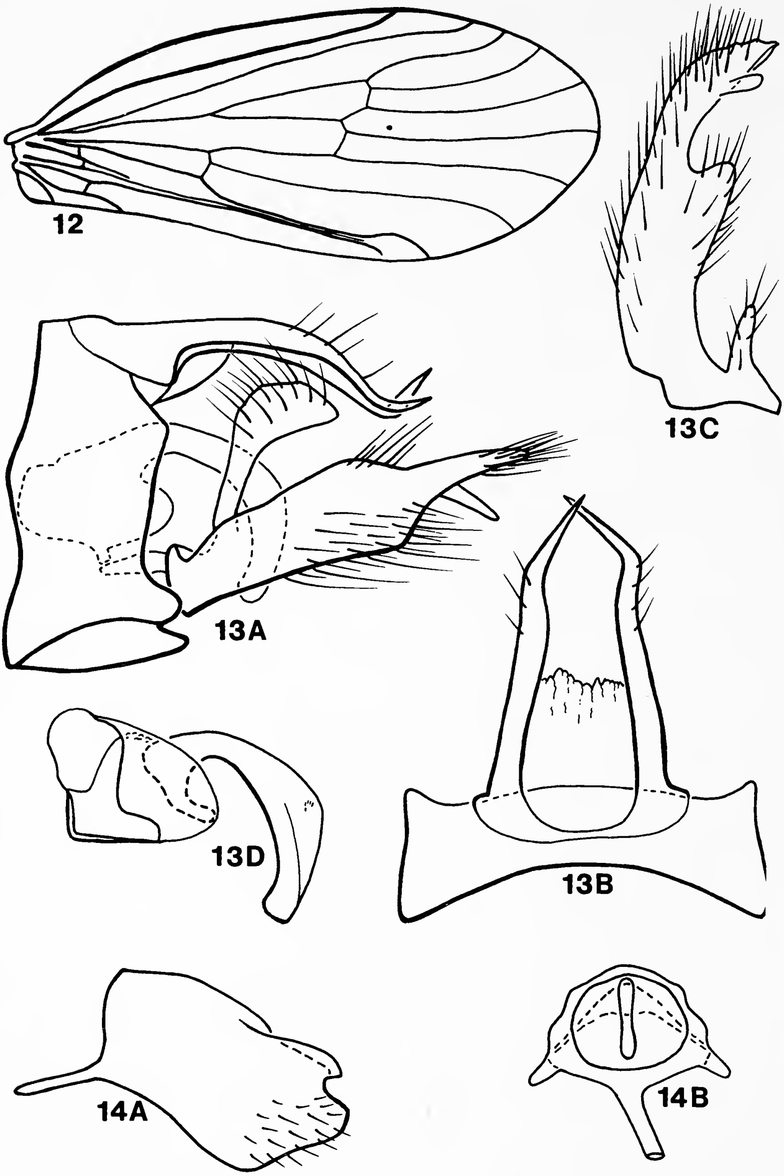
Figs. 1–5. 1. *Goerodes abruptus,* ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral. 2–4. *G. apoanus:* 2. ♂ fore wing. 3. ♂ genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendage, ventral; D. phallus, lateral. 4. ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral. 5. *G. bicolor,* ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral.



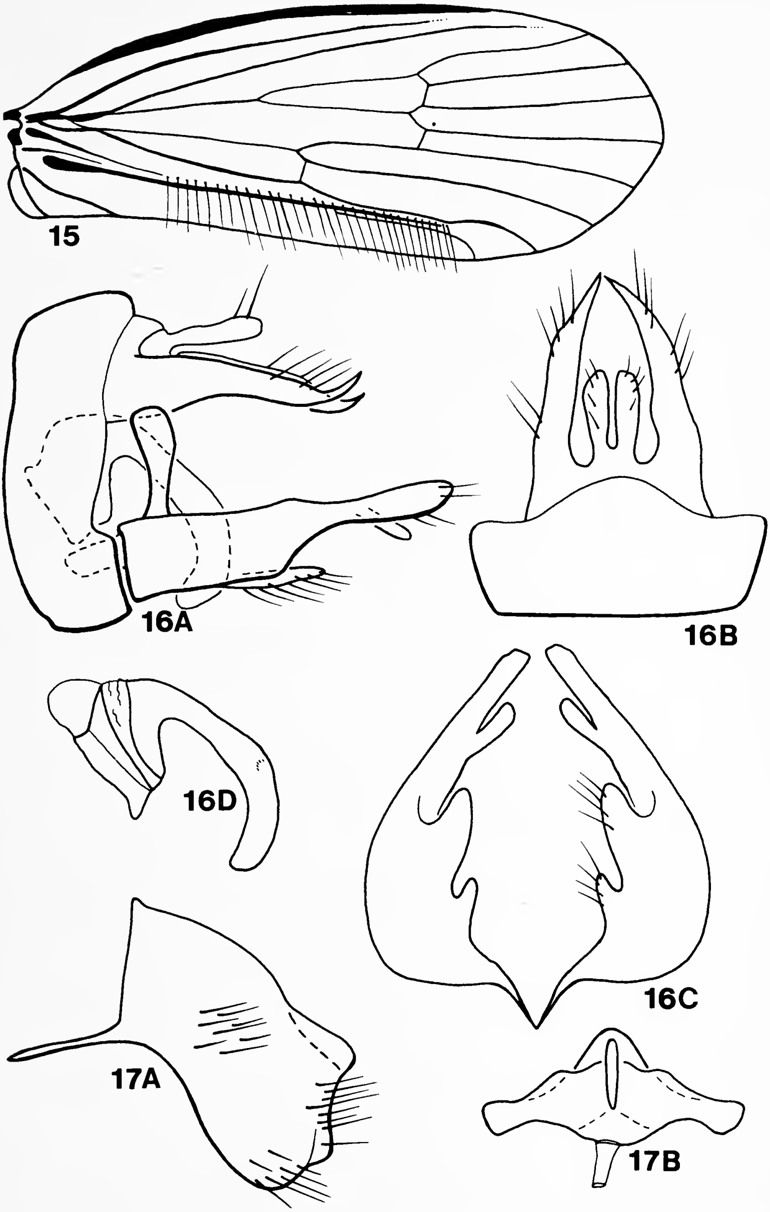
Figs. 6–8 *Goerodes conjunctus:* 6. ♂, A. fore wing; B. scape, left, dorsal; C. maxillary palp, left, mesal. 7. ♂ genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendage, ventral; D. phallus, lateral. 8. ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral.



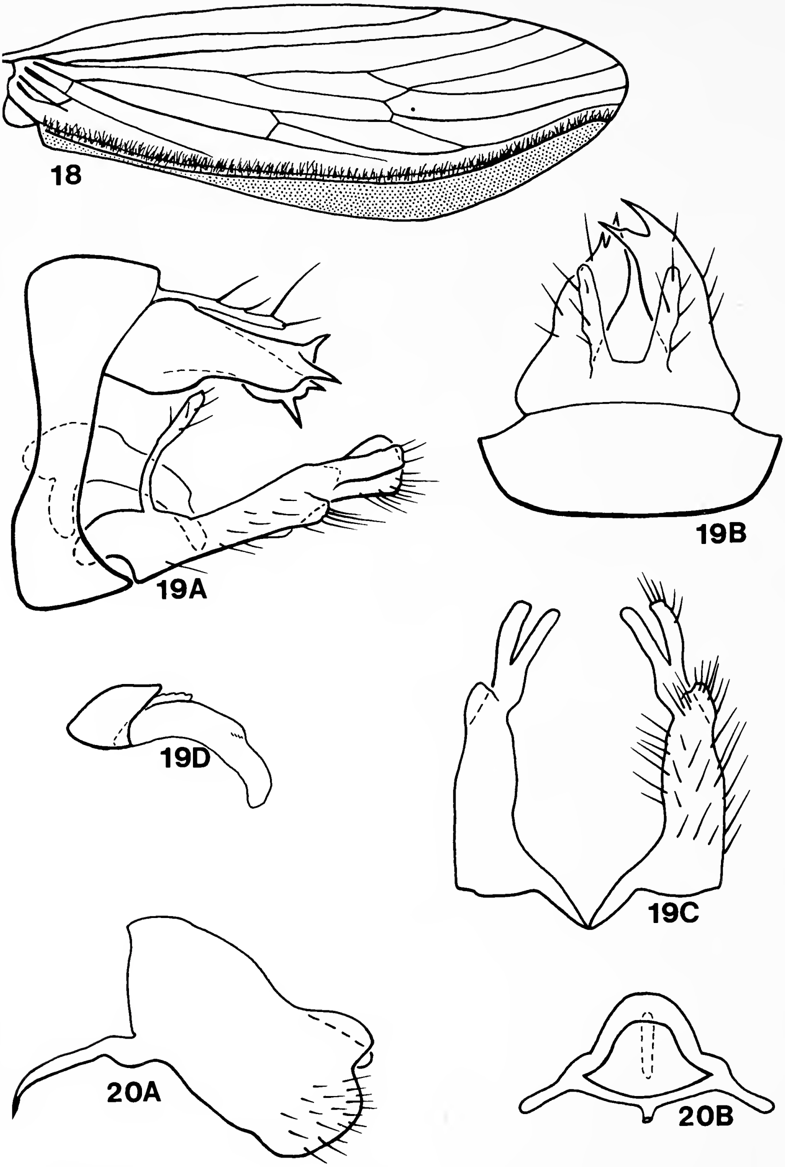
Figs. 9–11. *Goerodes grandis:* 9. ♂, A. fore wing; B. scape, left, dorsal. 10. ♂ genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendages, ventral; D. phallus, lateral. 11. ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral.



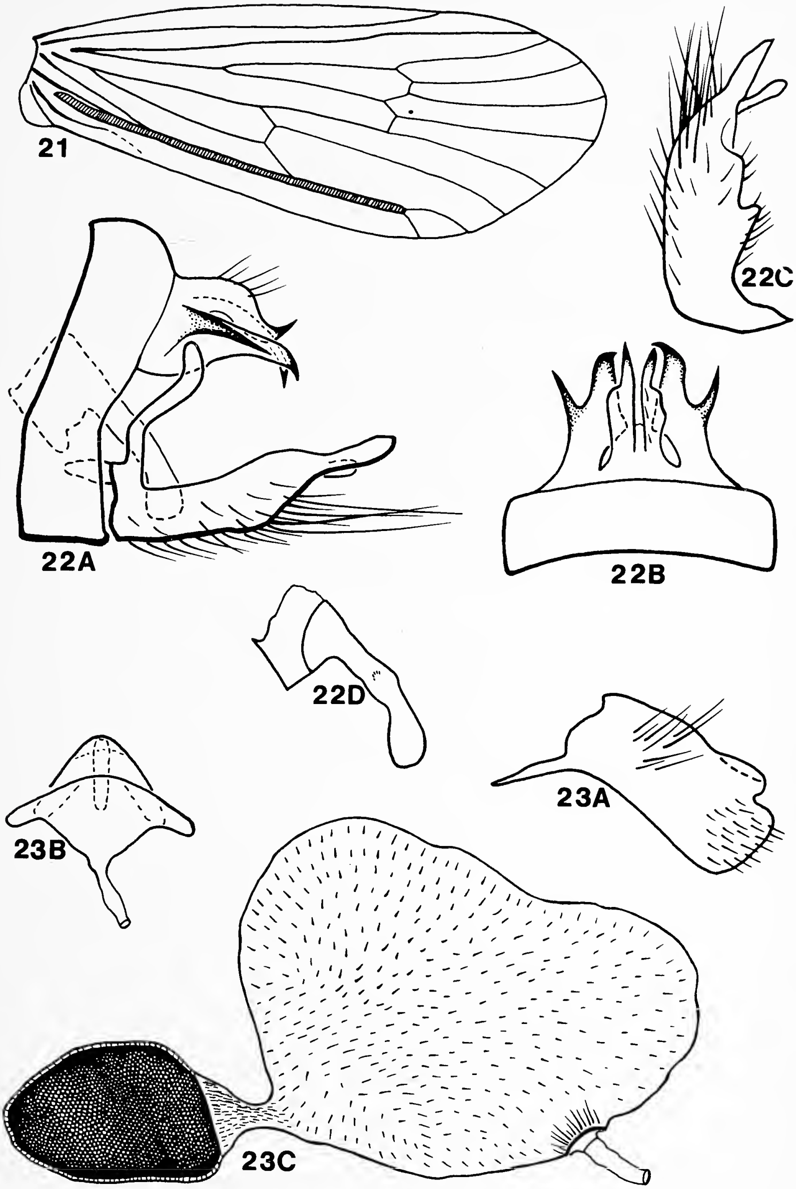
Figs. 12–14. *Goerodes medius:* 12. ♂ fore wing. 13. ♂ genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendage, ventral; D. phallus, lateral. 14. ♀ genitalia, A. segment IX; B. spermathecal sclerite, ventral.



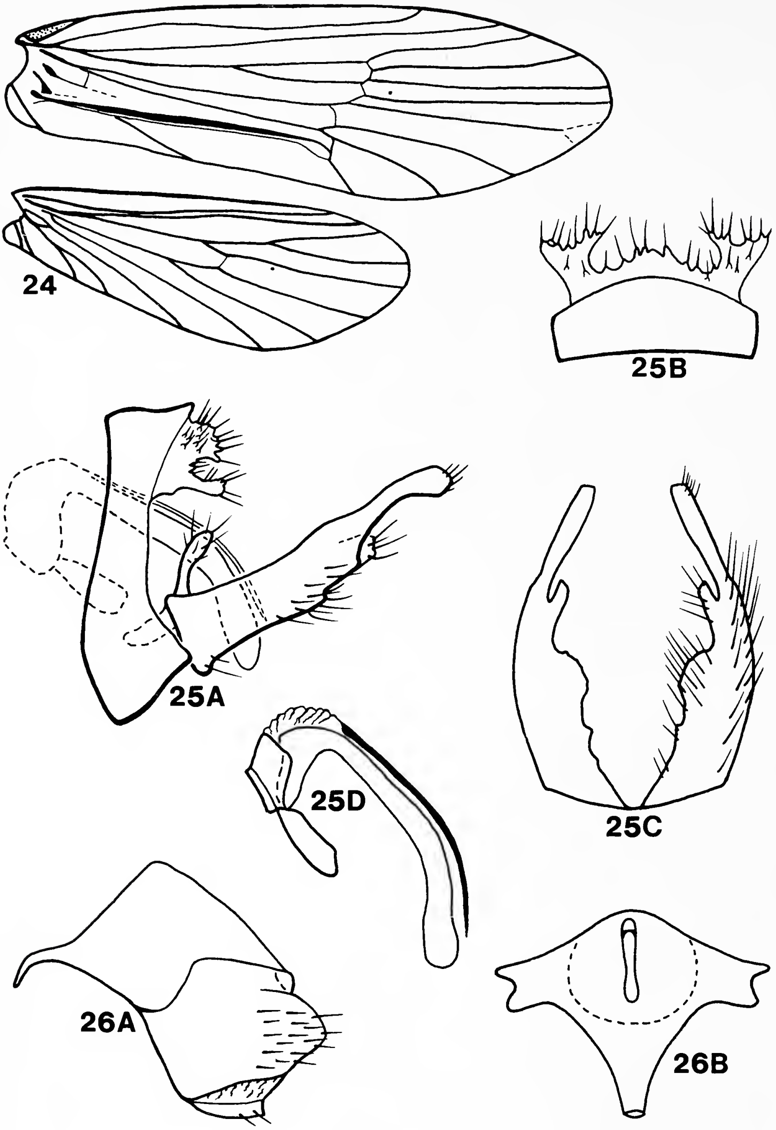
Figs. 15–17. 15–16. *Goerodes minor,* ♂: 15. fore wing. 16. genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendages, ventral; D. phallus, lateral. 17. *G. piscinus,* ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral.



Figs. 18–20. 18–19. *Goerodes posticatus*, ♂: 18. fore wing; 19. genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendages, ventral; D. phallus, lateral. 20. *G. ursinus*, ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral.



Figs. 21–23. *Goerodes venularis:* 21. ♂ fore wing. 22. ♂ genitalia, A. lateral; B. segments IX and X; C. inferior appendage, lateral; D. phallus, lateral. 23. ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral; C. spermatheca, lateral.



Figs. 24–26. 24–25. *Dinarthropsis picea,* ♂: 24. wings. 25. genitalia, A. lateral; B. segments IX and X, dorsal; C. inferior appendages; D. phallus, lateral. 26. *Dinarthrodes albicorne,* ♀ genitalia, A. segment IX, lateral; B. spermathecal sclerite, ventral.

AN EXPERIMENTAL STUDY OF THE ATTRACTIVENESS OF ARTIFICIAL PERCH TERRITORIES TO MALE TARANTULA-HAWK WASPS, *HEMIPEPSIS USTULATA* (HYMENOPTERA: POMPILIDAE)*

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Introduction

Males of the tarantula-hawk wasp *Hemipepsis ustulata* (Dahlbom) defend perch sites on the highest points of prominent hills and ridges in central Arizona (Alcock 1979, 1981, 1983). A territorial male permits no other male to alight in his plant, be it a palo verde (*Cercidium microphyllum*), jojoba bush (*Simmondsia chinensis*), creosote bush (*Larrea tridentata*), saguaro cactus (*Carnegia gigantea*), or cholla cactus (*Opuntia* spp.). Receptive females sometimes visit a territory site; mating occurs when the resident male captures the female in flight and the pair descends to the ground for a brief copulation. Because defended plants contain no food or oviposition resource for females nor any nests from which virgin females may emerge, males of *H. ustulata* appear to practice lek territoriality (Alcock 1981); they defend areas whose only value to females is the presence of a mating partner.

A striking feature of male behavior is the consistency with which individuals of different generations select certain perch trees from year to year. In one study site many dozens of palo verdes grow on the ridge and yet, every year over five flight seasons the same two trees have been most frequently occupied by territorial wasps (Alcock 1984). A few other trees are almost as popular while some are usually claimed for only a few days of the 2–3 month flight season. The wasps completely ignore the many other trees on the ridge.

We have analyzed the properties of natural territories in order to determine why some trees are so much more likely to be defended than others (Alcock 1984). Males only defend palo verdes growing

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on or very near the backbone of the ridge, not those growing on the slopes. Moreover, the frequency with which males claim a tree is primarily a function of (1) its altitude on the ridge backbone, with trees closer to the peak favored over trees farther down the ridge, and (2) the width of the tree, with large bulky trees preferred over smaller ones.

These results suggest that visual conspicuousness is an important attribute of a preferred territorial perch site for male wasps. They appear to be drawn to large targets clearly outlined against the sky rather than small trees or shrubs whose forms are obscured by a hillside. In order to test this hypothesis we designed experiments in which male tarantula hawks were offered two artificial landmarks in sequence. This gave the wasps a chance to choose between perch sites that differed in their height, size, or contrast. If visual conspicuousness is a key property of a perch site, then male tarantula hawks should inspect and perch on taller, larger, darker targets more often than lower, smaller, and paler landmarks. Our report discusses the response of male wasps in these choice experiments.

MATERIALS AND METHODS

The experiments were carried out near Usery State Park, Mesa AZ (see Alcock 1979 for a description of the study site) and at South Mountain Park, Phoenix AZ from late March to mid-May 1981 and 1982. Both areas have vegetation typical of the Sonoran Desert of central Arizona.

The experimental landmarks consisted of a pole composed of aluminum tubing supported by a base of metal slats and tubes; the entire structure was painted flat black mottled with tan (Fig. 1). At the top of the pole targets of various sorts were mounted upon which male wasps might perch. Totally artificial perch materials were used to eliminate any effects of familiarity with perch substrates on male choices. The height of the pole could be adjusted by adding or subtracting units of tubing. Each experimental trial consisted of two trials with first one artificial landmark offered to a male after which the landmark was altered and presented again for the same period (either 12 or 15 min, depending on the experiment). The experimental apparatus was erected between 2.5 and 3.0 m from a natural perch site occupied by a territorial male. This wasp and others patrolling the ridge could investigate or land upon the landmark during the two trials after which the apparatus was moved to a new site. We recorded each "approach" and the total perching time at the various artificial landmarks. An "approach" was scored when a male tarantula hawk flew directly toward the target on the pole and came within 1 m of it. Thus, if a male in a palo verde left his perch and flew close to the perch target, then circled back around his tree and returned to the target (after having traveled at least 2.5 m from the artificial landmark) two approaches were recorded. Perching time consisted of the period from first landing on the artificial landmark until the male left and did not return or until the trial was terminated.

In order to test the effect of landmark height on male tarantula hawks, one experimental perch was set to be about as high (± 0.2 m) as the nearby tree, the other extended by the insertion of more aluminum tubing to be 1.25 m (± 0.2 m) higher. The order of presentation of the two types was established randomly. The same perch target was used in any given set of experiments; in one series of 14 paired presentations, the target consisted of four semicircular pieces of green cardboard, mottled black and tan, fastened onto thin strips of aluminum painted flat black. In another 24 trials, the perch material consisted of green plastic ferns, about 0.5 m long, mounted in an aluminum tube that fitted onto the pole (Fig. 1). Ten of the 24 experiments were conducted in 1981 using four ferns as the target in trials that lasted 12 min each; the remaining choice experiments were carried out in 1982 using five ferns as the perch target in trials that lasted 15 min each.

In order to test the effect of perch size, two landmarks the same height but with different perch targets were placed near occupied territories ($N = 14$ paired trials). Four semicircular pieces of green plastic mesh were fastened at right angles to one another with flat black aluminum strips and mounted on top of the pole. The larger mesh target had pieces 0.5 m × 0.55 m (total area about 0.45 m^2 and total volume about 0.4 m^3); the smaller target was composed of pieces 0.3 m × 0.35 m (total area about 0.2 m^2, with a volume of about 0.09 m^3). Otherwise the shape and structure of the two targets was the same; each was positioned about 1.25 m higher than the nearby natural perch. Again the sequence of presentations of the small and large targets was random, and each trial lasted 15 min during which time approaches and perches were tallied.

Fig. 1. The artificial landmark with plastic ferns attached to the top of the aluminum pole as a target-perching site for males of *H. ustulata*.

The same procedure was followed in testing the effect of perch contrast. Here, mesh targets were also used, with the same dimensions as the larger target employed in the preceding experiment, but one target composed of plastic mesh was painted green while the other wire mesh target was painted flat white.

After each pair of presentations, the artificial landmarks were moved to a different tree so that no one resident male was given more than one opportunity to respond to a particular pair of landmarks.

Means are expressed ± 1 S.D.

RESULTS

The Effect of Height on Landmark Perch Attractiveness

When given a choice between approaching or perching on two targets, one of which was elevated 1.25 m above the other, male wasps clearly preferred the higher target (Table 1). When the perching material was cardboard, the wasps approached the taller landmark significantly more often ($W = 284.5$, $p < 0.0001$; Wilcoxon two-sample test). The same result applied to the two experiments in which plastic ferns were employed as a perch target (1981: $W = 147.5$, $p = 0.0022$; 1982: $W = 282.5$, $p = 0.0005$). Although for some reason males refused to take up residence upon the cardboard perch, they regularly did so when the target consisted of artificial ferns, but only on the taller of the two available landmarks ($X^2 = 26.32$, $p < 0.0001$, for the combined 1981 and 1982 results). Of the 17 individuals that claimed artificial landmark perches, 12 were residents in a nearby tree that abandoned their territories to move to the higher but completely unnatural perch sites. The other five

Table 1. The effect of height of artificial perches on the frequency with which male tarantula hawks approached and perched on them during 15-min trials.

Perch Material	Perch Height	Number of Paired Trials	Mean Approaches	Mean Perching Time (min)	Number of Males Perching
Cardboard	High	14	15.1 ± 11.2	0	0
	Low		3.1 ± 4.0	0	0
Plastic Ferns (1981)[a]	High	10	17.9 ± 11.1	5.3 ± 5.6	7
	Low		4.5 ± 4.9	0	0
Plastic Ferns (1982)	High	14	22.2 ± 13.5	5.4 ± 5.2	10
	Low		4.9 ± 5.7	0	0

[a] 1981 trials lasted 12 min each.

males had been patrolling the ridge but stopped in order to perch in and defend the experimental landmarks.

The Effect of Size and Contrast on Perch Attractiveness

The larger of two mesh targets was approached significantly more often than the smaller one (W = 270.0, $p < 0.005$, Wilcoxon two-sample test; Table 2). The same was true for the darker of two targets when the choice was purely between a dark and a pale perch target (W = 298.0, $p < 0.0001$; Table 3). However, there were no significant differences with respect to perching times because flat vertical perches, whether constructed of cardboard or of plastic mesh proved ineffective in inducing male wasps to land. This was probably not due to an aversion to plastic mesh per se because a perch target constructed of five pieces of plastic mesh cut, curled into cones, and mounted on a pole top in such a way as to resemble the artificial ferns attracted 11 perching males in 16 trials. These flexible cones of plastic moved in the wind, as did the plastic ferns, perhaps providing a more attractive visual stimulus than the immobile flat mesh targets.

DISCUSSION

The results of the experiments show that males of *H. ustulata* are clearly attracted to objects that are tall and large, and that stand out against the sky. Their readiness to investigate tall, large, and dark artificial landmarks, which do not resemble any natural perch substrates, demonstrates that certain visual properties are inherently attractive to the wasps. Indeed a substantial number of males abandoned their perch trees and shrubs in order to take up residence on the aluminum and plastic landmarks, provided only that the artifi-

Table 2. The effect of size of artificial perches on the frequency with which male tarantula hawks approached and perched on them during 15-min trials.

Perch Material	Target Size	Number of Paired Trials	Mean Approaches	Mean Perching Time (min)	Number of Males Perching
Plastic	Large	14	16.2 ± 6.5	0.62 ± 1.4	4
Mesh	Small		8.1 ± 4.5	0.05 ± 0.2	3

Table 3. The effect of visual contrast of artificial perches on the frequency with which male tarantula hawks approached and perched on them during 15-min trials.

Perch Material	Target Contrast	Number of Paired Trials	Mean Approaches	Mean Perching Time (min)	Number of Males Perching
Plastic	Dark	14	10.7 ± 4.6	0.4 ± 1.5	2
Mesh	Pale		1.6 ± 1.7	0	0

cial landmark was taller than the natural one and that flexible, structurally complex perching materials were available at the top of the pole. Perch switches occurred even though the natural sites often had a total volume much greater than the artificial ones. The results then are consistent with the hypothesis that males of *H. ustulata* prefer high, conspicuous points on the skyline as territories.

We can speculate briefly on the adaptive significance of this preference. We begin by dismissing the possibility that males are attracted to certain perches because these are the best sites from which to release pheromonal odor plumes. Although it might appear that males at the highest point would be able to generate the longest odor trail, heated air rising off the hillsides creates thermal updrafts that would carry the pheromonal signal upwards, rendering it ineffectual. Instead, we believe that males select the tallest perches at the highest points in order to inspect their surroundings with a minimum of visual obstruction, and this may help them detect approaching females. If, in addition, receptive females more easily perceive tall, large, and dark objects outlined against the sky and therefore approach these objects more often, then male wasps perched in conspicuous landmarks should gain more opportunities to mate. The competition that occurs among males for preferred perches could then arise as individuals attempt to secure a clear view of incoming females and to advertise their presence to mate-searching females.

To the best of our knowledge this is the first study to identify experimentally what makes a potential territory site attractive to males of a lekking species. Although it is well-established that certain perch-display sites are more attractive than others in such animals as the white-bearded manakin (Lill 1974), the hammer-headed bat (Bradbury 1977), and sage grouse (Wiley 1973), it is unclear precisely what stimuli are critical in male territorial decisions. There are many lek territorial insects (Thornhill and Alcock 1983), and perhaps these animals offer better opportunities to explore the proximate factors that underlie perch site selection in lek-forming species.

SUMMARY

Males of the tarantula-hawk wasp *Hemipepsis ustulata* defend mating territories centered on individual plants of various species growing on ridges and peaktops in central Arizona. Males will leave their natural territories to investigate plastic and cardboard perch targets placed on top of aluminum poles, preferring higher to lower targets and large targets of high contrast to smaller targets of low contrast presented at the same height. A resident male will abandon his natural territory altogether in order to perch upon an artificial landmark, provided that the landmark is structurally complex and is taller than the shrub or tree that the male has been defending.

ACKNOWLEDGMENTS

We thank Uta Matthes-Sears for her help in carting artificial perches through the desert. Jerry Waldvogel provided useful information on odor plumes on hilltops. This work was supported in part by National Science Foundation grant BNS 821 9791.

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NAME CHANGES FOR SOME SPECIES OF MYOPSOCIDAE (PSOCOPTERA)*

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Mockford (1982) pointed out the problems raised by inadequate definitions of some of the genera of the Myopsocidae. After examining the type specimen of *Myopsocus unduosus* Hagen he listed the species which should be included in *Myopsocus* (= *Phlotodes* Enderlein, = *Rhaptoneura* Enderlein) and *Lichenomima* Enderlein, leaving six species as *incertae sedis* which cannot be assigned until they have been re-examined. Some relevant, described species were, however, not mentioned. This short paper is an attempt to place as many of these as possible in their appropriate genera and is thus a supplement to Mockford's very useful paper. The species omitted by him are dealt with here in groups according to the history of their nomenclature.

A. Species which should now be placed in *Myopsocus.*

1. Species originally assigned to *Phlotodes.*

longicauda New 1975, Nigeria. Dr New, *in lit.,* informs me that this species should be placed in *Myopsocus* as Rs and M in the hind wings are fused for a length.

medleri New 1973, Nigeria. See comment under *longicauda.*

nigeriensis New 1975, Nigeria. See comment under *longicauda.*

ornata New 1973, Nigeria. See comment under *longicauda.*

sagitta Smithers and Thornton, 1979, New Hebrides.

tropica Smithers 1975, Queensland. This species has some characters which suggest close association with *Lophopterygella* Enderlein but was retained in *Phlotodes* at the time of description on the basis of characters of hind wing venation.

longigena Enderlein 1926, Java. At the time of description Enderlein considered *Phlotodes* have Rs and M fused in the hind wings and *Lichenomima* to have these veins joined by a crossvein. As he

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placed *longigena* in *Phlotodes* it probably has Rs and M fused and should be in *Myopsocus.*

2. Species originally assigned to *Psocus* Latreille then to *Phlotodes.*

hermosus Banks 1920, Singapore (see Smithers 1979).
luteolus Banks 1920, Singapore (see Smithers 1979).
pulchellus Banks 1920, Singapore (see Smithers 1979).

3. Species originally assigned to *Myopsocus* or to *Psocus* then to *Myopsocus* and best left in *Myopsocus* until they can be re-examined, as in the case of the six species listed as *incertae sedis* by Mockford (1982).

loriai Ribaga 1908, New Guinea.

B. Species which should now be placed in *Lichenomima.*
Originally assigned to *Myopsocus:*

pattoni Datta 1966, India. Dr. Datta has kindly provided a sketch of the wing venation of this species. In the hind wing Rs and M are joined by a crossvein, as in species of *Lichenomima.*

virginianus Banks 1900, North America. Mr. Vogt has kindly examined Banks' material in the Museum of Comparative Zoology and has informed me that Rs and M in the hind wing are joined by a crossvein, not fused, as in *Lichenomima.*

C. Additional comments.

It should be noted that *Myopsocus novaezealandiae* Kolbe and *M. griseipennis* (McLachlan) are listed separately by Mockford (1982). Both are synonyms of *M. australis* (Brauer) (Smithers, 1975a). *Phlotodes inocellata* Smithers and Thornton has been transferred to *Mouldsia* Smithers (Smithers 1978).

SUMMARY

An attempt is made to place thirteen species of Myopsocidae in appropriate genera following a redefinition of *Myopsocus* Hagen and *Lichenomima* Enderlein by Mockford (1982).

ACKNOWLEDGEMENTS

I would like to thank Dr. New and Dr. Datta for providing additional information on the species described by them and Mr. Charles Vogt for information on Banks' material.

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DISTINCTION OF THE '*NEOCHRYSIS*' GENERA AND DESCRIPTION OF NEW SPECIES (CHRYSIDIDAE, HYMENOPTERA)*

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The subgenera of *Neochrysis* comprise 4 distinct groups of species in the Chrysidinae (Chrysididae), which were discussed by Kimsey and Bohart (1980). Subsequent reevaluation of these subgenera indicates that they have sufficiently discrete diagnostic characteristics to justify their elevation to genera. *Ipsiura* is the most divergent group and is being elevated by Bohart (1985).

The relationships of these groups to other genera of Chrysidinae are obscure. Although they have been placed in the Euchroeini, based on the widely open marginal cell and long radial sector (Kimsey 1983), no sister group within this tribe is yet apparent and further study is necessary. However, these 4 taxa are closely related to each other, based on the characteristics given in table I, particularly those of the apical external sterna, RS vein and hindfemoral pit.

A number of abbreviations have been used, some of which are illustrated in fig. 1: T = gastral tergum, S = gastral sternum, F = flagellomere, MOD = midocellus diameter, LID = least interocular diameter.

In each list of included species an asterisk indicates that the type has not been seen.

Specimens have been borrowed from the following institutions: CURITIBA—Departmento de Zoologia, Universidad de Federal do Parana, Curitiba, Brazil; DAVIS—Bohart Museum of Entomology, University of California at Davis; MANHATTAN—Department of Entomology, Kansas State University, Manhattan; NEW YORK—Department of Entomology, American Museum of Natural History, New York; TUCUMAN—Instituto Miguel Lillo, Tucuman, Argentina, and WASHINGTON—Department of Entomology, U. S. National Museum, Washington, D. C.

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Key to the Genera Elevated from *Neochrysis*

1. Pronotum with sharp, protruding and nearly straight lateral carina (fig. 7); male S-IV large and usually metallic, two-thirds or more as long as S-III (fig. 12); female S-III longer than II (fig. 13); face with frontal carina extending up to and around midocellus .... *Ipsiura* Linsenmaier
   Pronotal carina absent or punctate and irregular (fig. 6), not protruding; male S-IV only exposed fringelike beyond S-III (fig. 10), except in 4 species of *Pleurochrysis*; female S-III variable in length; facial carina present or absent......................2
2. Head with elongate fovea along genal carina (fig. 2), metanotal lobe digitate and protruding (fig. 4), propodeum with medial tooth; female S-III longer than II (fig. 11) ...*Exochrysis* Bohart
   Head without genal fovea, metanotal lobe subtriangular, not protruding (fig. 5); propodeum without medial tooth, except *Pleurochrysis alfkeni*; female S-III subequal in length to II (fig. 9) 3
3. Hindfemur without basal pit; pronotal declivity with 2 deep submedial pits (fig. 3); T-III pit row pits large and deep and/or pit row depressed, often with prepit swelling (fig. 6)........... .... *Pleurochrysis* Bohart
   Hindfemur with small circular or linear anterobasal pit; pronotal declivity without 2 deep submedial pits (rarely 2 pits apparently present); T-III pit row absent or only indicated by slight lateral depression or small pits, no prepit swelling (fig. 8) .... *Neochrysis* Linsenmaier

Exochrysis Bohart, N. Stat.

Exochrysis Bohart 1966: 141. Type: *Chrysis panamensis* Cameron 1888:464. Monobasic and orig. desig.

Discussion. The most distinctive features of *Exochrysis* species are the genal fovea, a long slender depression along the ventral side of the genal carina (fig. 2), and the shape of the lateral metanotal tooth, which is digitate and protrudes away from the propodeal tooth (fig. 4). In addition *Exochrysis* species have a distinctive basomedial tooth on the propodeum, which is only found in *Exochrysis* and one species of *Pleurochrysis, alfkeni,* and have a hindfemoral pit. All *Exochrysis* have four apical teeth on T-III. The black spots on S-II are sexually dimorphic, tending to be much smaller and farther apart in females.

Table I. Generic Characteristics of *Exochrysis, Ipsiura, Neochrysis* and *Pleurochrysis.*

Characteristic	*Exochrysis*	*Ipsiura*	*Neochrysis*	*Pleurochrysis*
Pronotal carina sharp and protruding	−	+	−	−
Male S-IV exposed	−	+	−	−
Male S-IV two-thirds or more as long as III*	−	+	−	+−
Female S-III longer than II*	+	+	+	+
Head with genal fovea*	+	−	−	−
Metanotal lobe digitate and protruding*	+	−	−	−
Hindfemur with basal pit*	+	+	+	−
Pronotal declivity with 2 pits	−	−	−	+
Propodeum with medial tooth	+	−	−	+−
T-III without depressed pit row	−	−	+	−
RS sigmoid, curving away from costal margin	+	+	+	+
T-I anterolateral corners sharp	+	+	−	+−

*Characteristics unique to these genera.

Exochrysis is the sister group of *Ipsiura.* Both have a well-developed facial carina that extends up to the midocellus, T-I generally has sharp anterolateral corners and the female S-III is much longer than II. A number of *Exochrysis* species, including *imperforata* and *leucostigma* have a well-developed pronotal carina, although it is not as highly modified and sharp as in *Ipsiura.*

Included Species: *alabamensis* (Mocsáry) 1914, *imperfecta* (Gribodo) 1879, *lemniscata* Kimsey new species, *leucostigma* (Mocsáry) 1889, *panamensis* (Cameron) 1888, *silvanus* Kimsey new species, *spinigera* (Spinola) 1838.

Key to the Species of *Exochrysis*

1. Scapal basin up to and including transverse frontal carina highly polished and impunctate except narrow band of minute punc-

tures and sparse setae along ocular margin; propodeal medial projection longer than 1 MOD in dorsal view .... *imperfecta* (Gribodo)
Scapal basin covered with dense small punctures and silver setae, with at most a narrow polished, impunctate stripe; propodeal medial projection usually 1 MOD long or shorter in dorsal view (may be longer in *spinigera*) 2
2. T-III without basolateral pale spot 3
T-III with large whitish or transparent basolateral spot.......4
3. Sternum II spots about as far apart as wide in females and twice or more as far apart in males ....*panamensis* (Cameron)
Sternum II spots at least twice as far apart as wide in females, and as far apart in males..............*alabamensis* (Mocsáry)
4. Malar space longer than 1 MOD.............*silvanus* Kimsey
Malar space equal to or, more usually, shorter than 1 MOD 5
5. T-III lateral margin between base and tooth strongly convex; S-II spots elongate ovoid in males, and 1.5 times or more as far apart as wide in females .... *lemniscata* Kimsey
T-III lateral margin between base and tooth concave, straight or only slightly convex basally; S-II spots round in males and less than 1.5 times as far apart as wide 6
6. T-III pits deep and larger than adjacent punctures, except medial pair; pit row wide and exposed; prepit swelling microsculptured between pits .... *spinigera* (Spinola)
T-III pits small, subequal in size to adjacent punctures, except medial pair; pit row obscured by prepit swelling; prepit swelling polished between punctures .... *leucostigma* (Mocsáry)

Exochrysis lemniscata Kimsey, new species
(Fig. 10)

Holotype male. Body length 9 mm. Scapal basin with narrow impunctate polished medial stripe and dense fine punctures and silvery pubescence along ocular margin; frontal carina an exaggerated W shape, extending up to and nearly enclosing midocellus; malar space 0.7 MOD long; LID 1.3 times eye width; subantennal distance 1.0 MOD long; F-I length 2.1 times width; F-II 1.1 times; F-III as long as wide; F-V 0.6 times; pronotum without lateral carina, medially depressed; mesopleural carina with one posterior

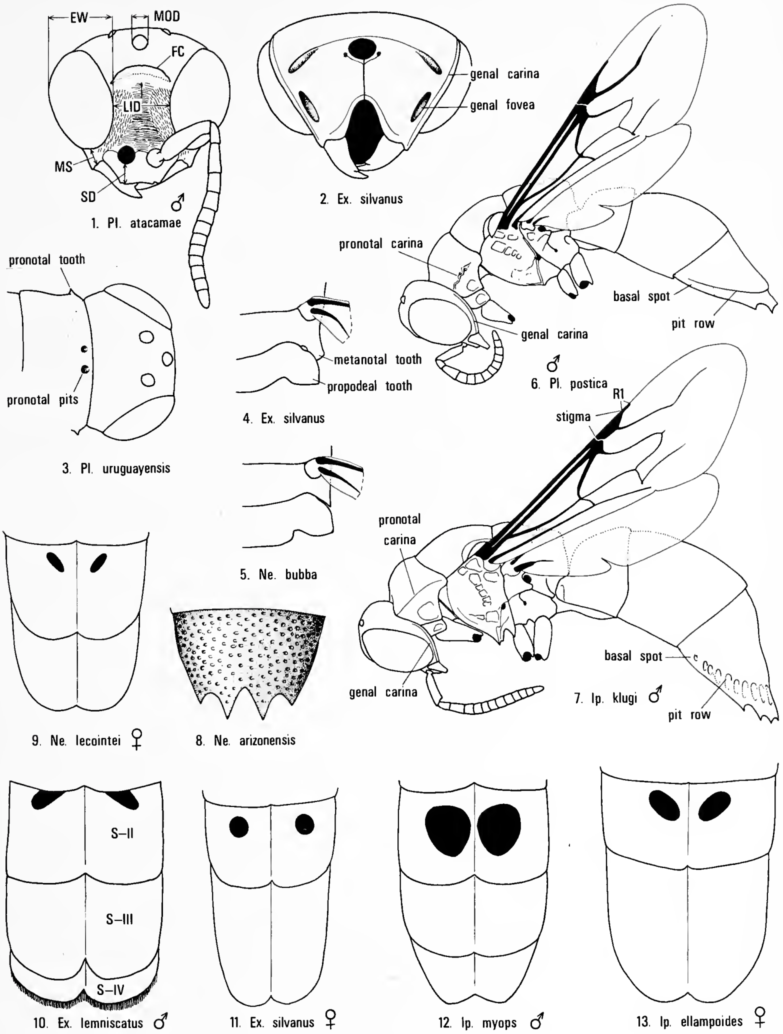

Fig. 1. Head, front view; eye width (EW), frontal carina (FC), least interocular distance (LID), midocellus diameter (MOD), malar space (MS), subantennal distance (SD). Fig. 2. Head, posterior view. Fig. 3. Head and pronotum, dorsal view. Figs. 4–5. Right side of metanotum and propodeum, dorsal view. Figs. 6–7. Body with legs removed, lateral view. Fig. 8. Tergum III, dorsal view. Figs. 9–13. Sterna II-III (females) and IV (males). Ex. = *Exochrysis*, Ip. = *Ipsiura*, Ne. = *Neochrysis*, and Pl. = *Pleurochrysis*.

and two ventral lobes or teeth; propodeal median tooth about 1 MOD long; R1 length about two-thirds stigmal length; T-I punctures about twice as large as on III, anterior corners sharp knoblike; T-III pit row sunken beneath prepit swelling, pits small and deep; S-II spots oblong and slender, about as far apart as long (fig. 10). Body generally blue green with purplish transverse stripes on T-I-III; propodeum purple, except lateral teeth; black on vertex, anterior face and medial and sublateral pronotal stripes, medial and sublateral scutal stripes, and scutellum anteromedially; T-II lateral edge transparent; T-III with large transparent basolateral spot.

Female. Same as male, except S-II spots about 1.5 times as far apart as wide.

Holotype male: BRAZIL: São Paulo, 1 January 1965, V. N. Alin (DAVIS). Paratype female: BRAZIL: Minas Gerais, Ibiraci, October 1961, C. Elias.

Discussion. The differences between *Exochrysis* species are often subtle, involving details on the pronotum and T-III, and the shape of the spots on S-II. *E. lemniscata* most closely resembles *panamensis* and *leucostigma* and all three are sympatric throughout much of their distributions. It can be distinguished from these species by the elongate spots on the male S-II and medium-sized, round ones in females (about 1.5 times as far apart as wide), and T-III with a white basolateral spot and small to tiny submedial pits.

Exochrysis silvanus Kimsey, new species
(Figs. 2, 4, 11)

Holotype male: Body length 9 mm. Scapal basin with narrow impunctate polished stripe, laterally with dense fine punctures and silvery pubescence; frons without transverse carina but with two vertical carinae extending back to midocellus; malar space 0.9 MOD long; LID 0.9 times eye width; subantennal distance 0.7 MOD long; F-I 1.5 times as long as wide; F-II as long as wide; F-III 0.8 times; F-V 0.6 times; pronotum with lateral carina and depressed medially; mesopleuron with three knobs or teeth on posterior carina; metanotum not strongly spiculate, elevated medially; propodeal medial tooth small, 1 MOD long; R1 subequal to stigmal length; T-I punctures about twice the size of those on II and III; T-III lateral margin convex, pit row depressed, sunken beneath prepit swelling, and two large pits located submedially; S-II spots large, ovoid and about twice as far apart as wide (fig. 11). Body greenish blue ventrally, becoming bluer laterally and purplish black dorsally, with black spots on vertex medially and sublaterally on pronotum and scutum, scutellum medially, transverse submedial stripe on T-I-II; T-III purple with whitish basolateral spot.

Female. Same as male except 1 specimen much greener.

Holotype male. COSTA RICA (DAVIS). Paratypes, two females: PANAMA: Zona del Canal, Barro Colorado Is., 5 September 1981; BRAZIL: Amapa, 24 October 1978.

Discussion. This species most closely resembles *leucostigma* and *alabamensis* based on the strongly flattened male flagellum, T-III with a transparent basolateral spot, the long malar space, and T-III with two large submedial pits. It can be distinguished by the indefinite transverse facial carina, presence of a pronotal carina, a small medial propodeal tooth, and convex lateral margin of T-III.

Ipsiura Linsenmaier

Ipsiura Linsenmaier 1959:74. (4 spp.). Type: *Chrysis marginalis* Brullé 1846. Orig. desig.

Discussion. *Ipsiura* is the most distinctive of these four taxa, and is being elevated to genus by Bohart (1985). The pronotal carina is so enlarged that the pronotum almost appears winged in some species. The gastral sterna are distinctive in both sexes. In males S-IV is large and visible externally; it is two-thirds or more as long as III (fig. 12), and is metallic colored. Female S-III is much longer than II (fig. 13). In males and often females the spots on S-II are large and only narrowly separated (fig. 12). Tergum III is also quite diagnostic; the pits are shallow and elongate or only indicated by long, vague depressions (fig. 7), and there are two to six apical teeth.

Included Species: *affinissima* (Ducke) 1903 NEW COMB., *bisulcata* (Ducke) 1902, *brevispina* (Ducke) 1911, *ellampoides* (Ducke) 1902, *friesiana* (Ducke) 1902, *genbergi* (Dahlbom) 1854*, *goeldi* (Ducke) 1907, *klugi* (Dahlbom) 1854, *leucobasis* (Mocsáry) 1889, *leucocheila* (Mocsáry) 1889, *leuchocheiloides* (Ducke) 1903, *longiventris* (Ducke) 1907, *marginalis* (Brullé) 1846, *myops* (Buysson) 1904, *neolateralis* (Bohart) 1963, *obidensis* (Ducke) 1903, *pilifrons* (Cameron) 1888.

See Bohart (1985) for a key to species and descriptions of new species.

Neochrysis Linsenmaier

Neochrysis Linsenmaier 1959:73. Type: *Chrysis punctatissima* Spinola 1840, nec Villers 1789 (=*Chrysis carina* Brullé 1846). Monobasic and orig. desig.

Discussion. *Neochrysis* and *Pleurochrysis* are closely related and may be difficult to separate. *Neochrysis* lacks a distinct pit row on T-III; pits may or may not be present but there is never a depression or prepit swelling, and it does have a hindfemoral pit. The spots on S-II are sexually dimorphic; in males they are large and narrowly separated (as in fig. 12), and in females these spots are small, often oblong and widely separated (fig. 9). In both genera the female S-III is subequal in length to S-II (fig. 9) and male S-IV protrudes only as a narrow fringe (fig. 10). All *Neochrysis* species have four apical teeth on T-III, except *jenseni*, with six to eight teeth.

Included Species: *argentina* (Brèthes) 1908 NEW COMB., *arizonensis* Kimsey 1982, *bubba* Kimsey new species, *cameroni* (Buysson) 1900, *carina* (Brullé) 1846, *confusa* (Ducke) 1911 NEW COMB., *deuteroleuca* (Mocsáry) 1912, *inseriata* (Mocsáry) 1902, *jenseni* (Buysson) 1906 NEW COMB., *lecointei* (Ducke) 1906, *montezuma* (Cameron) 1888, *paraensis* (Ducke) 1903, *tysis* Kimsey new species.

Key to the Species of *Neochrysis*

1. Metanotum with medial carina and strongly protruding medially in lateral view 2
   Metanotum without medial carina and broadly rounded in lateral view 3
2. T-III pit row indicated by broad impunctate stripe; S-II spots round in both sexes .... *cameroni* (Buysson)
   T-III pit row not indicated by impunctate stripe; S-II spots tiny and comma-shaped in males and linear in females .... *carina* (Brullé)
3. T-III with six or more apical teeth or angles .... *jenseni* (Buysson)
   T-III with four apical teeth or angles 4
4. Pronotum, scutum and scutellum covered with transverse striae; anterior pronotal declivity with broad impunctate stripe .... *typsis* Kimsey
   Thoracic dorsum without transverse striae, anterior pronotal declivity without broad impunctate stripe 5

5. R1 and stigmal lengths subequal 6
R1 two-thirds or less as long as stigma .8
6. S-II spots large and round much closer together than wide in both sexes; frons with irregular boxlike transverse carina. . . . . *confusa* (Ducke)
S-II spots absent or tiny and round, and much farther apart than wide; frons without transverse carina 7
7. F-I less than twice as long as broad, T-III lateral margin between base and lateral tooth straight or only slightly convex . . . . *inseriata* (Mocsáry)
F-I twice or more as long as wide, T-III lateral margin between base and lateral tooth strongly convex . . . . *montezuma* (Cameron)
8. T-III with large basolateral transparent amber or whitish spot 9
T-III without basolateral spot, although may have narrow translucent edge 10
9. Male F-I and II with long ventral fringe of silvery setae; female S-II spots round and slightly farther apart than wide; T-III apical teeth long and pronglike, medial notch deeper than wide apically . . . . *arizonensis* Kimsey
Male F-I and II without fringe; female S-II spots subtriangular and much closer than wide; T-III apical teeth short and broad, medial notch as broad or broader than deep . . . . *paraensis* (Ducke)
10. F-I twice or more as long as wide, large species 7–9 mm long. 11
F-I 1.5 times as long as wide or less, small species 5–6 mm long 12
11. S-II spots large and teardrop-shaped, much closer together than wide in females; male unknown . . . . *bubba* Kimsey
S-II spots small and ovoid, twice as far apart as wide in females, small and slightly ovoid and 5 or more times as far apart as wide in males . . . . *lecointei* (Ducke)
12. Frons with irregular transverse carina and 2 or more irregular carinae extending from it toward vertex. . . *argentina* (Brèthes)
Frons without carinae . . . . *deuteroleuca* (Mocsáry)

Neochrysis bubba Kimsey, new species
(Fig. 5)

Holotype female. Body length 10 mm. Scapal basin shallow with narrow impunctate and polished medial stripe, laterally with dense small punctures and silver pubescence; no frontal carina; malar space 0.6 MOD long; LID 0.7 times eye width; subantennal distance 0.7 MOD long; F-I 2.4 times as long as wide; F-II 1.1 times; F-III 0.8 times; F-V 0.7 times as long as wide; gena between ocular margin and carina polished and impunctate; mesopleuron rounded ventrally, carina without posterior teeth or lobes, punctures 0.5-1 puncture diameter apart with tiny punctures between; metanotum evenly rounded; propodeum flat and vertical in lateral view; costal length beyond stigma subequal to stigmal length; S-II spots large and ovoid, barely separated medially; T-I punctures larger than those on scutum and T-II, which are subequal; T-III lateral margin slightly convex, pit row faintly depressed laterally with small deep pits about as large as adjacent punctures, without transparent basolateral spot or edge. Body bluish green ventrally becoming bluer laterally and darker dorsally, blackish dorsomedially.

Male. Unknown.

Holotype female: BRAZIL: Santa Catarina, Nova Teutonia, February 1974, F. Plaumann (DAVIS). Paratypes, one male, one female: BRAZIL: Parana, Curitiba, 19 January 1968, A. Sakakibara (one male); BRAZIL: Parana, Piraquara, 13 January 1968, Moure and Laroca (one female).

Discussion. The most distinctive feature of *bubba* is the large spots on S-II, which serves to immediately distinguish this species from the two it most closely resembles, *lecointei* and *montezuma*. *N. bubba* can be distinguished from other *Neochrysis* species by having no frontal carina, either transverse or vertical; no white spots on T-III, and an evenly rounded metanotum.

Neochrysis tysis Kimsey, new species

Holotype female. Body length 7 mm. Scapal basin shallow with narrow impunctate and polished medial stripe, laterally with dense small punctures and silver pubescence; no frontal carina; malar space 0.4 MOD Long; LID 1.1 times eye width; subantennal distance 0.6 MOD long; F-I 1.4 times as long as wide; F-II and III 1.1 times;

F-IV 0.6 times; gena polished and impunctate for most of area between ocular margin and carina; pronotal anterior face with broad, polished and impunctate stripe, with lateral pronotal carina; dorsum of head and thorax strongly striate, punctures flattened and striatiform; mesopleuron relatively rounded ventrally, carina without teeth or lobes, punctures separated by 0.5–1.0 puncture diameter; metanotum evenly rounded; propodeum flat and vertical in lateral view; R1 slightly shorter than stigma; S-II spots large and ovoid, barely separated medially; abdominal punctures flattened and oblong; T-III pit row only indicated by faint lateral depression, lateral margin slightly convex basally. Body bluish green, becoming purplish on T-III, T-III with large whitish transparent basolateral spot.

Male. Unknown.

Holotype female: VENEZUELA: Aragua, Ocumare de la Costa, 12 June 1976, Menke and Vincent (WASHINGTON). Paratype female: COLOMBIA: Antioquia, Medellin, May 1982, I. D. Correa (DAVIS).

Discussion. *N. tysis* can be distinguished from other *Neochrysis* by the impunctate stripe on the pronotum, striatiform dorsum and lack of a projection on the metanotum. This species most closely resembles *paraensis* based on the shape and coloration of T-III, the evenly rounded metanotum and the pronotal carina.

Pleurochrysis Bohart

Pleurocera Guèrin 1842:355. Nec Rafinesque 1818. Type: *Pleurocera viridis* Guèrin 1842 (=*Chrysis bruchi* Brèthes 1903).

Pleurochrysis Bohart 1966:144. N. name for *Pleurocera* Guèrin 1842.

Discussion. *Pleurochrysis* contains a relatively heterogeneous group of species characterized by their lack of derived characteristics. The two features diagnostic for *Pleurochrysis* are the presence of 2 pits on the anterior face of the pronotum (fig. 3), and the lack of an anterobasal pit on the hindfemur. Unfortunately, the presence of pronotal pits is not a characteristic unique to *Pleurochrysis* and rare individuals of *Neochrysis* may have these pits as well. *Pleurochrysis* may be paraphyletic but the species it contains are clearly related; further study is needed.

Pleurochrysis species vary in a number of characteristics: The frontal carina is present or absent and may even enclose the midocellus in *fasciifera* and *leucophris*. The pronotum has an irregular lateral carina in *postica* and *alfkeni* but not in the other species. One species, *alfkeni*, has a medial propodeal tooth, which is particularly well-developed in some individuals. S-IV is generally narrow and fringelike in male *Pleurochrysis* (as in fig. 10), except in *cavifrons, bruchi, leucophris* and *uruguayensis*, where it is large and usually metallic green as in *Ipsiura* (fig. 12). A few species have a metanotal projection. Two characteristics are unique in this genus, but unfortunately do not occur in all species. The first is the presence of a small lateral tooth on the pronotum as seen in dorsal view (fig. 3). Second, a number of males have highly modified antennae. The most extreme case can be seen in *bruchi* where the flagellomeres are strongly flattened and flabellate. Typically, though, the male flagellum is yellowish and somewhat flattened. Finally, there is little sexual dimorphism in the spots on sternum II, in most species these spots are round and about as far apart as wide in both sexes. Only one species, *bruchi*, has six apical teeth on T-III, the rest have four.

Included Species: *acuta* (Brèthes) 1908, *alfkeni* (Ducke) 1902*, *ameghinoi* (Brèthes) 1903, *ancilla* (Buysson) 1898, *atacamae* Kimsey new species, *bruchi* (Brèthes) 1902, *cavifrons* (Brullé) 1846, *charruana* (Brèthes) 1903, *chilicola* (Mocsáry) 1914, *fasciifera* (Bischoff) 1910, *imbecilla* (Mocsáry) 1889 NEW COMB., *lagopus* (Buysson) 1891 NEW COMB., *leucophris* (Mocsáry) 1889 NEW COMB., *lynchi* (Brethes) 1903, *postica* (Brullé) 1846, *simulator* Kimsey new species, *sur* Kimsey new species, *uruguayensis* Kimsey 1985 new species, *ypirangensis* (Buysson) 1904.

Key to the Species of *Pleurochrysis*

1. T-III with six apical teeth, male flagellum unusually flattened and basal segments flabellate .... *bruchi* (Brèthes)
   T-III with four apical teeth, male flagellum variously shaped but not flabellate 2
2. Pronotum with lateral tooth 3
   Pronotum without lateral tooth 8
3. T-III pre-pit swelling large usually obscuring pits, LID 0.6 times eye width, R1 0.2–0.3 times stigmal length.... *alfkeni* (Ducke)
   T-III prepit swelling usually small or absent but never obscuring pits, pits large and clearly defined; LID 0.8 times eye width or wider; R1 0.9 or more times as long as stigmal length 4

4. Metanotum with large medial projection .... *imbecilla* (Mocsáry)
   Metanotum without medial projection 5
5. Malar space longer than 1 MOD ....*cavifrons* (Brullé)
   Malar space less than or equal to 1 MOD in length 6
6. Scapal basin with polished and impunctate medial stripe as wide or wider than lateral finely punctate area ....*acuta* (Brèthes)
   Scapal basin without impunctate medial stripe or stripe much narrower than width of lateral finely punctate area .... *uruguayensis* Kimsey, new species
7. Scapal basin with fine transverse cross-ridging 8
   Scapal basin without cross-ridging 9
8. T-III lateral edge concave between lateral tooth and base, male flagellum yellow .... *atacamae* Kimsey, new species
   T-III lateral edge slightly to strongly convex, male flagellum brown .... *chilicola* (Mocsáry)
9. T-II lateral edge transparent, T-III basolateral margin transparent or with large basolateral whitish, amber or transparent spot 10
   T-II and III without lateral transparent, amber or whitish spot or edge...13
10. T-III pit row obscured by prepit swelling, pits barely visible as small flattened ovals 11
    T-III pit row broad and well-developed, pits large and round or oval, not obscured by pre-pit swelling 12
11. Malar space less than 1 MOD long, T-III narrow and tapering apically in dorsal view including rim, face without transverse frontal carina .... *postica* (Brullé)
    Malar space more than 1 MOD long, T-III broad and rim flared apically in dorsal view, face with traces of transverse frontal carina ....*ypirangensis* (Buysson)
12. Face with strong carina enclosing midocellus, metanotum with large medial projection, T-III medial pits subequal to sublateral ones .... *leucophris* (Mocsáry)
    Face without carina enclosing midocellus, metanotum without large medial projection, T-III medial pits much larger than sublateral ones .... *charruana* (Brèthes)
13. Subantennal distance at least 1.4–1.5 MOD long 14
    Subantennal distance not more than 1 MOD long; S-II spots as

far apart as wide, except closer in female *simulator* 15

14. S-II spots 0.5 or less as far apart as wide, T-III margin between lateral tooth and base strongly convex .... *lynchi* (Brèthes)
S-II spots as far apart as wide or further apart, T-III margin between lateral tooth and base nearly straight or only slightly convex .... *lagopus* (Buysson)

15. Face without clearly defined carinae on brow 16
Face with clearly defined transverse, and in *simulator*, vertical carinae on brow 17

16. Malar space less than 0.5 MOD long and shorter than subantennal distance; male flagellum yellowish and broadly flattened, F-II as long as wide; male basitarsus dilated .... *ameghinoi* (Brèthes)
Malar space and subantennal distance equal and both more than 0.5 MOD long; male flagellum reddish brown and cylindrical, F-II length 1.3 times width; male basitarsus unmodified .... *fasciifera* (Bischoff)

17. Transverse frontal carina with 2 carinulae extending back around midocellus, male flagellum cylindrical and blackish ... . *simulator* Kimsey
Transverse frontal carina linear or an inverted C-shape, without carinulae extending back toward midocellus; male flagellum flattened and yellowish 18

18. T-III lateral margin concave, with a basal angle; male LID narrower than eye width .... *sur* Kimsey
T-III lateral margin straight or somewhat convex, male LID as wide as or wider than eye width............ *ancilla* (Buysson)

Pleurochrysis atacamae Kimsey, new species
(Fig. 1).

Holotype male. Body length 6.5 mm. Scapal basin with dense fine transverse ridges (fig. 1), outer two-fifths with dense silvery setae; brow with strong transverse carina; malar space 1 MOD long; least interocular distance 0.8 times eye width; subantennal distance 1.5 MOD long; F-I 2.4 times as long as wide; F-II 1.5 times; F-III and V as long as wide; pronotum rounded, without medial projection; R1 as long as stigma; S-II spots small and circular, about as far apart as wide; Abdominal segments coarsely punctate, punctures as large as those on thorax and nearly touching; T-II with low impunctate medial welt extending about two-thirds of length; T-III with strong medial carina extending through pit row, pit row only slightly depressed, pits subequal in size to punctures but deeper, apical teeth clustered medially. Head blue, except face greenish blue; thorax purplish blue, abdomen greenish blue; scape, pedicel, F-I and part of F-II blue, rest of flagellum yellowish red except apical segment brown.

Female. Body length 6–7 mm. Same as male, except scapal basin without silvery setae; antenna blackish; F-I 2.2 times as long as wide; F-II length 1.7 times width; F-III 1.4 times as long as wide, and T-V with fine apical ridges.

Holotype male: CHILE, Atacama Prov., 40–60 km s Copaipo, 18–20 October 1969, L. E. Peña (DAVIS). Paratypes, five males, two females: CHILE, Atacama Prov.: two males, one female: same data as type; one male, one female: 26 mi s Copaipo, 19 October 1969; one male: 14 km s Vallenar, 13 October 1969; Canto del Agua, 21 October 1969; one male: La Junta, 15 October 1969.

Discussion. Although very closely related to *chilicola, atacamae* differes in the strongly convex lateral margin of T-III and the yellowish male flagellum. Both species have a finely cross-ridged scapal basin, a characteristic not found in other *Pleurochrysis*.

Pleurochrysis simulator Kimsey, new species

Holotype male. Body length 6 mm. Scapal basin almost completely clothed in silvery setae, somewhat sparser medially; brow with strong transverse carina; malar space and subantennal distance 1 MOD long; LID equal to eye width; F-I 1.8 times as long as wide; F-II 1.5 times. F-III as long as wide; F-V 0.8 times width; pronotum without lateral tooth or carina; metanotum rounded; propodeum slightly projecting basomedially; R1 two-thirds stigmal length; S-II spots elongate, about as far apart as wide; T-II with irregular medial welt, without translucent edge; T-III without basal spot, prepit row swelling slight, pit row slightly sunken, pits large and deep. Body green, with purple on vertex, tegulae, along notauli, T-I and III basally, and II basally and subapically; flagellum only slightly paler than scape.

Female. Body length 4.5–6.0 mm. Same as male except scapal basin with wider impunctate medial stripe.

Holotype male: BRAZIL: Bahia, Vitoria da Conquista, 25–27

May 1961, F. M. Oliveira (DAVIS). Paratypes, six males, seven females: VENEZUELA: Zulia, 6 km w La Concepcion, 18 June 1976 (one female, one male); BOLIVIA (one female); ARGENTINA: Buenos Aires: Moreno (one male); Misiones: Puerto Iguazu, 3 March 1945 (one male); Salta: n Cafayate, Yacochuya, 2 December 1970 (one male); Santiago del Estero: Termas de Rio Hondo, 28 May 1972 (one male); Catamarca: 6 km n Belen, 1–15 December 1968 (one female); Entre Rios: Feliciano (one female); La Rioja (one female); Rio Negro: Lamarque (one female); BRAZIL: Paraiba: Joazeirinho, 28 October 1955 (one female).

Discussion. *Pleurochrysis fasciifera* and *simulator* are quite close structurally; both have similar facial and antennal dimensions and lack a pronotal tooth or carina and whitish basolateral spot on T-III. *P. simulator* can be distinguished from *fasciifera* by the cylindrical brown male flagellum, male scapal basin with a broad medial impunctate stripe, and the presence of a strong transverse facial carina in both sexes. This carina in *simulator* is either single, particularly in females, or a rough, elevated, rectangular structure. In addition, individuals of *simulator* tend to be greener than those of *fasciifera*.

Pleurochrysis sur Kimsey, new species

Holotype male. Body length 6 mm. Scapal basin narrow, with broad zone of fine dense punctures and dense silvery setae along ocular margins and subtriangular impunctate and polished medial zone; brow protruding with strong transverse carina; malar space 0.6 MOD long; least interocular distance 0.7 times eye width; subantennal distance 0.7 MOD long; flagellum somewhat flattened: F-I 1.4 times as long as wide; F-II 1.1 times; F-III 0.8 times; F-V 0.7 times as long; pronotum without anterolateral tooth or lateral carina; metanotum and propodeum evenly rounded; R1 subequal to stigmal length; S-II spots round, about as far apart as wide; abdominal punctures about as large as those on thorax; T-III with large prepit row swelling, lateral margin strongly convex, pit row pits large and deep. Body greenish blue, becoming purplish dorsally and black on middle of metanotum and propodeum, anterior margin of T-II and III and in submedial transverse band on T-II; tarsi yellowish; flagellomeres yellow with brown lateral edges; T-III without transparent or whitish lateral rim or basolateral spot.

Female. Body length 6–7 mm. Similar to male except least interocular distance 1.2 times eye width, F-I twice as long as wide, F-II 1.6 times, F-III and V as long as wide, and body green with purplish markings.

Holotype male: ARGENTINA: La Rioja, C. S. Reed (SAN FRANCISCO). Paratypes, two males, three females: ARGENTINA: La Rioja, E. Giacomelli (one female); Icaña, E. R. Wagner (one male, one female); Santiago del Estero, Rio Salado, Icana (one female); Tucuman, Leales los Gomez, 28 March 1948 (one female).

Discussion: Most closely resembling *ancilla, sur* can be distinguished by the narrower scapal basin in the male, narrower subantennal distance and malar space, very deep pit row with very large deep pits, a large prepit swelling, and the lateral margin of T-III concave. This species can be distinguished from other species of *Pleurochrysis* by the lack of a pronotal, metanotal or medial propodeal tooth, no transverse facial carina and no transparent or whitish edge or spot on T-III.

Pleurochrysis uruguayensis Kimsey, new species
(Fig. 3)

Holotype male. Body length 5 mm. Scapal basin densely clothed with silver setae; brow without transverse carina; malar space 0.5 MOD long; least interocular distance 0.7 times eye width; subantennal distance 0.6 MOD long; F-I 2.3 times as long as wide; F-II slightly longer than wide; F-III as long as wide; F-V 0.8 times width; pronotum with small lateral tooth (fig. 3) and no lateral carina; metanotum pointed and strongly projecting medially; R1 as long as stigma; tarsi yellowish; S-II spots round and slightly less far apart than wide; T-II and III with vague, impunctate medial stripe; T-III pit row slightly sunken, no prepit row swelling, pits large and deep. Body bluish green, flagellum blackish.

Female. Body length 5.0–5.5 mm. Same as male except scapal basin with wider polished medial stripe, about one-fifth area, and T-I with fine apical ridges.

Holotype male: URUGUAY: Dept. Rio Negro, 15 km s Paysandu, 27 December 1962 to 6 January 1963, R. G. Van Gelder (NEW YORK). Paratypes, one male and three females: same data as type.

Discussion. *P. uruguayensis* is a small species with a well-developed pronotal tooth, no transverse facial carina, an elevated and acute metanotum, yellowish tarsi, and no basolateral spot on T-III. This combination of characteristics distinguishes *uruguayensis* from other species of *Pleurochrysis*.

SUMMARY

The remaining 2 subgenera of *Neochrysis* Linsenmaier, *Pleurochrysis* and *Exochrysis*, are elevated to genus. A key to these 2 taxa plus *Neochrysis* and *Ipsiura* is provided as well as diagnostic characteristics and a list of and keys to included species for each. In addition 2 new species of *Exochrysis, lemniscatus* and *silvanus*, 2 new *Neochrysis, bubba* and *tysis*, and 4 new *Pleurochrysis, atacamae, simulator, sur* and *uruguayensis* are described.

ACKNOWLEDGMENT

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SWARMING IN A BALLOON-CARRYING EMPIDID (EMPIDIDAE: *HILARA*)[1]

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INTRODUCTION

Swarms are perhaps the most spectacular of insect mating aggregations. Usually groups of males fly at particular stations or markers where females come to locate mates (Sullivan 1981). Swarming behavior is particularly common in Diptera, the flies. In one family, the Empididae, it is especially well known because swarming males often carry gifts of prey which are presented to females during copulation (i.e. nuptial feeding, Downes 1969). The gift-giving has become ritualized in some empidids and "balloons" made of glandular secretions produced by males are transferred to females at coupling (Kessel 1955). Balloon flies are found among three genera of empidids (*Empimorpha, Empis, Hilara*).

Though a large and diverse group of flies, few species of empidids have been extensively studied in the field (Alcock 1973, Chvala 1976). In North America only five balloon-carrying species have been studied (Kessel 1959) and all occur in western United States and Canada. This report is the most extensive of the field studies of the swarming and mating behavior of a single species of balloon fly and is the first detailed study of a balloon fly from the eastern U.S.

MATERIALS AND METHODS

The study site was the edge of a 50 × 100 m wooded area adjacent to cultivated fields at Green Acres Farm, Dept. of Agronomy, University of Florida (NE 1/4, sec. 27, tp. R18E, T9S). Adult season in Gainesville lasts about 2 weeks during late March or early April. I

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[1] Dr. Paul H. Arnaud, Jr. has examined specimens and determined this to be a new species of balloon fly. Voucher specimens have been deposited at the California Academy of Sciences, San Francisco and the Florida State Collection of Arthropods, Gainesville.

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found males swarming in early April 1981, and specific observations were made during the three following springs. I was at the study site each evening 30 min. prior to daily swarming.

Male activity. Male swarming periods were monitored on 12 days (1982 n = 9, 1983 n = 3). The start of swarming was noted when the first male was seen constructing a balloon at a swarming station and three more males were seen during the next minute. At the start of activity, light intensity was indexed by estimating the percent (nearest 10%) of the sky occluded by clouds. Temperature and wind speed at a height of 1 m were also taken. Activity period stopped when no males were found at swarming stations monitored that evening. All swarms of a given evening broke up within a 3 min. period.

Swarm station, height, size. Each swarming station was marked with a numbered wooden stake put into the ground below the swarm. Height of swarms was measured to the nearest .1 m with a 2.5 m pole marked at .1 m intervals. Measurement was taken from ground level beneath swarms to swarm center.

White balloons carried by males made them conspicuous and the number of males in a swarm (size of swarm) was estimated by counting balloons. Since females and possibly some males do not carry balloons, only displaying males were counted. Because of movement by males in swarms and difficulty in counting balloons, swarms with more than 10 males were estimated to the nearest 5 males.

Mating behavior. During swarming considerable effort was made to locate and watch pairs as they coupled and mated. As some pairs formed in the swarm they were collected. Uncoupled members of the swarm were also captured. The sizes of females, coupled males and uncoupled males were measured to investigate whether or not large males were more likely to mate with females. Size was determined by measuring with a ocular micrometer the lengths of a wing and hind femur of each individual.

RESULTS

Both sexes were found on leaves near swarming stations 15–30 min. prior to swarming activity. During this time males flew from leaf to leaf and walked along the leaf margins from the base to tip and then back again, possibly searching for females.

At about sunset swarms formed beneath branches of broadleaf trees (*Quercus, Prunus, Myrica*). Particular branches (stations) were used from 1 to 8 nights during a season and swarming occurred at some stations all four years (1981–1984). Average height of swarms was 1.7 m (range 0.5–4.5 m, Fig. 1). Most swarms contained fewer than 5 males but some swarms had over 20 males in a space of less than 25 × 25 × 25 cm (Fig. 2).

Swarming started about sunset and continued for 20 minutes (Fig. 3A). High winds (gusts > 10 kmph) often delayed or halted swarming and swarms never formed at temperatures below 13° C, even though individuals were seen on leaves prior to the activity period. The starting and stopping of swarming was negatively correlated with cloud cover ($r = -.81, -.90$, respectively; $p < .05$). That is, when greater percent of the sky was covered by clouds swarming started and ended earlier in the evening (Fig. 3B).

Males in the swarms carried a 2–3 mm spherical, white, silken balloon below them while they flew. The balloons were hollow, did not contain prey, and were constructed with silk from tarsal glands while in flight. Male movement in swarms was easily followed by watching the white balloons against a background of foliage or males silhouetted against the sky. Males generally flew side-to-side in swarms and often males (balloons) collided. Twice a male was

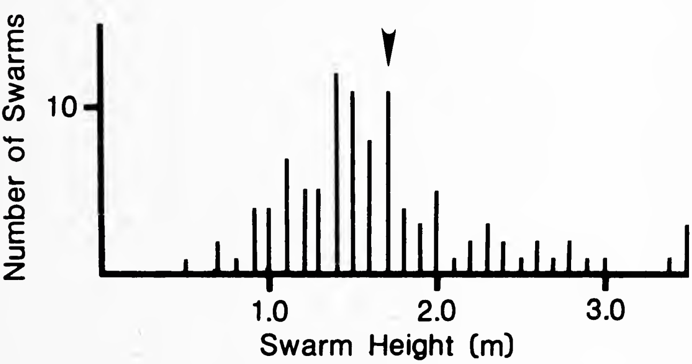

Figure 1. Frequency distribution of height of *Hilara* n. sp. swarms (n = 103, during spring 1982 & 83) at Green Acres Farm, Dept. of Agronomy, Gainesville, Fla. Two swarms at heights of 3.7 and 4.5 m are shown at 3.5 m. Arrow represents mean height.

seen flying from a swarm with his balloon trailing by a silken thread. Upon landing on nearby vegetation the balloons were lost and never retrieved. These balloons were probably dislodged during a collision with another male in the swarm. It is not known whether these two males constructed new balloons and returned to a swarm that evening. Some individuals left a group, joined another more than 1 m away, and sometimes returned to their initial swarm, but in general males remained at the same station for the entire swarming period.

Females perched on vegetation near swarms and flew into swarms where coupling occurred. Pairs were easily distinguished from the more erratic flight of uncoupled males. Mating (coupling) occurred during the last 8 min of the activity period (n = 22 pairs, range 1–19 min.). When couples were captured, males were mounted atop

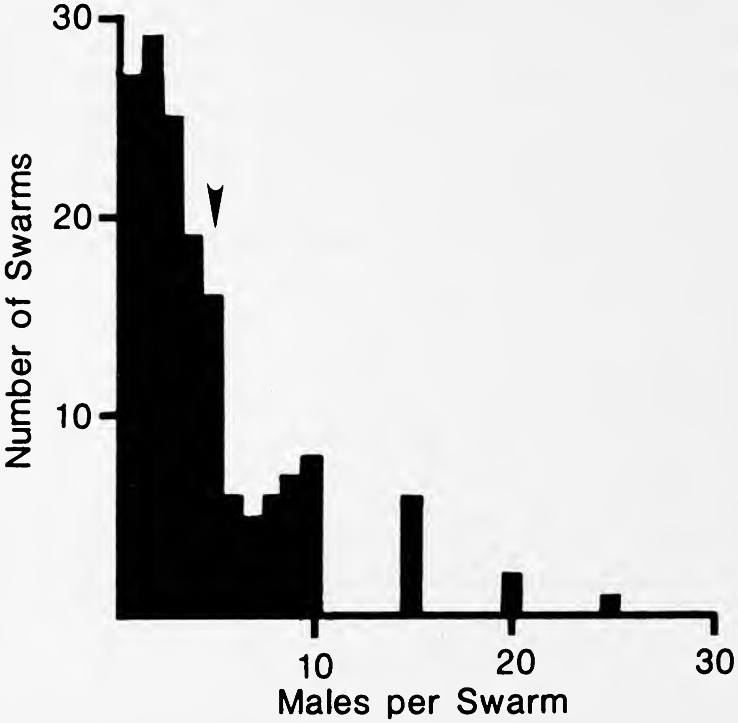

Figure 2. Distribution of swarm size as measured by counting the number of balloons in 156 *Hilara* swarms (spring 1982 & 83). Swarms with more than 10 males were estimated to the nearest 5 males. Arrow shows mean size of swarms.

females that now held but did not eat the balloons. Males held females by the thorax with their enlarged forelegs. Pairs kept in vials remained coupled for 2–6 min.

Some couples left swarms and hovered at the edge of the woods. Once swarming ceased, more pairs were found flying near the wood's edge. Due to failing light pairs could not be followed for more than a couple of minutes during which time pairs never separated or landed.

Females are significantly smaller than males in both wing length and hind femur length. However, males that were captured while mating did not differ significantly in femur length but had signifi-

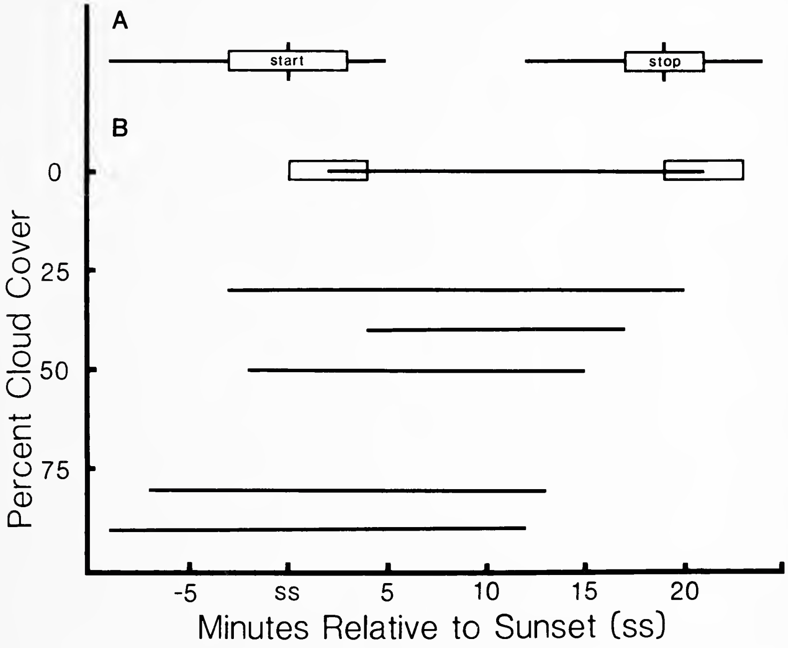

Figure 3. A. Average starting and stopping times of swarming for 12 nights (1982 and 1983). Vertical lines are means, horizontal lines are ranges, and bars represent 95% confidence intervals of means. Average duration of swarming is time between average start and stop. B. Daily duration of swarming for 12 nights in 3A relative to cloud cover at the beginning of swarming. Duration shown for clear days (0% cloud cover) is the average for 7 nights. Note the correlation between cloud cover and start and stop of swarming (r = −.81, −.90, respectively).

cantly shorter wing lengths than uncoupled males captured in swarms (Table 1).

DISCUSSION

Kessel (1955), expanding on Hamm's (in Poulton 1913) and Melander's (1940) classification, recognized eight stages in the evolutionary sequence of empidid mating behaviors. The eighth and final stage is represented by balloon-carrying species in which males swarm and the balloon alone has become the stimulus for courtship and mating. *Hilara* n. sp. thus is a representative of this stage.

Two of the other five North American balloon flies that have been studied are *Hilara* species. *Hilara wheeleri* is similar to *Hilara* n. sp. in that males swarm near broadleaf trees at heights less than 2 m, balloons are made of silk from tarsal glands. However, dipteran prey are always encased in the walls of the balloon (i.e. stage 5 of Kessel's sequence). *Hilara granditarsis* swarms at heights more than 3 m high in the branches of coniferous trees and males carry frothy balloons that contain no prey (stage 8). *H. sartor,* a European species, also swarm high in the branches of conifers and have frothy balloons without prey (stage 8).

Congregating on leaves before swarming may occur because both males and females respond to the same conspicuous landmark. One hypothesis on the evolution of swarming behavior is that going to such markers has been an efficient mechanism for unmated females to locate mates (Sullivan 1981). Selection then acts on both males and females to respond to these conspicuous landmarks. Though male *Hilara* appeared to search for females they did not try to court or mate with females on nearby leaves. Once males reach an area using long range visual cues they should try to locate specific swarm-

Table 1. Hind femur and wing length (mm) of *Hilara* females, coupled and uncoupled males.*

	n	femur length $\bar{x} \pm$ S.D.	wing length $\bar{x} \pm$ S.D.
females	8	$1.06 \pm .05^{A}$	$3.2 \pm .1^{A}$
coupled males	10	$1.15 \pm .06^{B}$	$3.4 \pm .1^{B}$
uncoupled males	22	$1.20 \pm .06^{B}$	$3.5 \pm .1^{C}$

*Means in a column with different letters are significantly different ($p < .05$).

ing sites that will be most profitable with respect to female-to-competitor ratio.

The time of swarming is restricted to a 20-minute period at dusk (Fig. 3). Crepuscular swarming is common in insects presumably because climatic factors, especially wind, are more favorable for swarming (Sullivan 1981). For balloon flies the change in light quality and quantity, particularly at sunset, may influence when the balloon would be most efficient in attracting females. Light does influence the timing of *Hilara* swarms since their activity begins and ends earlier in the evening on cloudy days (Fig. 3).

Males are expected to display when reproductive benefits are greater than alternative behaviors. That is males should swarm when females are most available and attractive to mates. When their availability is confined to brief periods females may "force" males to display synchronously. This benefits females since when large numbers of males display together females have a greater choice from potential mates. From this positive-feedback mechanism evolves the spree, a temporal analog of a lek (see Walker 1983).

Swarms are restricted in space as well as time and may therefore be compared to a lek where males display and females come to mate with males. Most often only a few males in the leks do all or most of the mating and females receive nothing more than sperm from their mates (Bradbury 1981). That *Hilara* females remain on vegetation during swarming and do not, until late in the swarming period, enter the swarm and couple with a male suggests that they may be evaluating males in swarms. The cue used in this evaluation remains in doubt. Perhaps the balloon is an effective means by which females can judge male vigor on the basis of flight patterns made more noticeable by the conspicuous balloon. Or once coupled a female might "analyze" the composition of the balloon as an indicator of a male's ability to accrue certain resources (Thornhill and Alcock 1983). This would be very important in species that presented prey as nuptial gifts.

That males are larger than females (Table 1), unusual in insects, points to selection for large males. Males that join swarms must compete for a limited number of females and, since males collide with others and mating takes place in the swarm, large males might have an advantage. However, it was found that coupled males had smaller wing lengths than those that were uncoupled (Table 1). That coupled males did not differ significantly in femur length indicates that coupled males have higher wing loading (wing area relative to body size) than uncoupled males. This wing loading difference may be important to a male's ability to maneuver in the swarm.

But why should mating pairs remain in the swarm? Males risk losing females in fights with other larger males in the swarm and females might be injured in such flights. An advantage a male might have would occur if mating durations are relatively short compared to the time remaining in the swarming period. Males then might profit by remaining in the swarm and continuing to advertise for other females. If a male has been selected by a female that evening he "knows" that he has outcompeted the other males in the same swarm. Provided females will mate with males that have already mated that evening, males will gain by remaining in the swarm. However, pairs were found hovering near the edge of the woods and durations of mating last until after swarming has ceased. Another alternative is males may remain in the swarm to exercise some choice over females that enter. If female size is an indication of her reproductive output then males may be waiting to see if a larger female enters the swarm. A male would gain reproductively by mating with a larger more fecund female. A female, on the other hand, might exercise her choice and fly back into the swarm if she is coupled to an unwanted male and force the male to prove his competitive ability.

SUMMARY

Mating swarms of *Hilara* sp. are made conspicuous by white, silken balloons carried by males. Groups of 1–25 males swarm beneath branches of broadleaf trees at a modal height of 1.4 m (range 0.5–4.5 m). Male activity periods begin about sunset and continue for 20 minutes with the beginning and ending of swarming correlated with light intensity. Females fly into swarms where coupling occurs. Unlike most other swarming Diptera, *Hilara* sp. pairs remain in the swarm while mating. Males are larger than females, though coupled males were significantly smaller (wing length) than other males in the swarm.

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HOST SPECIFICITY IN COLONY-FOUNDING BY *POLYERGUS LUCIDUS* QUEENS (HYMENOPTERA: FORMICIDAE)

By Linda Goodloe[1] and Raymond Sanwald[2]

Introduction

The pine barrens of eastern Long Island in Suffolk County, New York, provide a unique habitat for the obligatory slave-making species *Polyergus lucidus* Mayr. Here, four species of *Formica*, belonging to the *pallidefulva* species group, are used by *Polyergus* as slaves, although only one slave species is usually found in a single *Polyergus* nest. This is in contrast to related facultative slave-makers of the genus *Formica* belonging to the *sanguinea* species group, found in the same habitat, whose nests commonly contain two or more species serving as slaves. Choice of a host species can occur both through the colony-founding behavior of queens and through the choice of target nests for slave raids. The parasitic *Polyergus* queens found colonies either by adoption, where a queen invades the nest of a slave species, killing the resident queen and appropriating workers and brood present (Wheeler, 1910), or by "budding", in which a queen invades or is accepted into a host species nest accompanied by workers from her nest of origin (Marlin, 1968).

This experiment reports the results of a study designed to determine whether the choice of host species by a parasitic queen is influenced by her past experience. It was hypothesized that a newly-mated *Polyergus* queen would choose and/or be chosen by a colony of the same host species found in her nest of origin.

Method

The site for the experiment was a two acre lot in Suffolk County, N.Y., on which vegetation is kept closely cropped and where an unusually high density of colonies of potential slave species of

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Polyergus has been maintained. Also on this site are several artificially implanted in-ground *Polyergus* colonies that use two of the available slave species present. In addition, one portable colony of *Polyergus*, encased in a plywood box with a removable cover, was used. This colony was kept indoors except during afternoon hours, when it was occasionally placed in a fixed location on the site to allow raids to occur, and during mating flights, so the activity of the reproductives could be monitored. Only colonies using the slave species *F. schaufussi* or *F. pallidefulva nitidiventris* were used since these are the most common in the area.

In late August, when mating flights of *Polyergus* were expected to begin, female alates were retrieved and labelled as to their colony of origin. Those from in-ground colonies were recovered in the morning under sun-warmed rocks placed over the nest entrances. Those in the portable colony were either removed from inside the nest or recovered when they first emerged from the nest after it was placed outside. Each was briefly immobilized by cooling, labelled with a streak of enamel paint on her gaster, and immediately returned to her home nest. There were no observable behavioral effects of the labeling process once the subjects were returned to the ambient temperature.

On days when conditions were favorable for mating flights, the in-ground colonies were periodically inspected for activity, the portable colony was placed outside and constantly monitored, and the site was searched for labelled and mated *Polyergus* dealates on the prowl for appropriate host colonies. Recovered dealates were each placed in a 16 × 150mm test tube containing approximately 4cm of water held in place with a cotton plug, and were restrained with an additional cotton plug. They were then transferred to the laboratory and within 24 hours presented with a choice of two host species. In an 21.6cm × 29.2cm plastic box were two potential host "colonies", one of *F. schaufussi* and one of *F. pallidefulva nitidiventris*. Each colony consisted of 20 or 30 pupae, two or three callows, and two adult workers, in 16 × 150mm test tube with 4cm of water plugged with cotton. The test tubes were a preferred nesting place and once established inside, the small group always chose to remain there except for foraging, "exploratory" activity, and occasional aggressive encounters with workers of the alternate species or a *Polyergus* queen. Food of honey-water and *Tenebrio* larvae were provided.

Callows were included in the host groups because experience had shown that queens in laboratory "adoptions" experience a high death rate due to attacks by the adult slave-species workers, while callows appear to be more accepting and less hostile. The number of adults chosen was considered the absolute minimum required for an interaction, while the number of callows and pupae, equalized between the two species in each test box, was the result of the number available in laboratory colonies of the appropriate species during the course of the experiment.

Each queen, in her own test tube to avoid dehydration, was placed in a box between the parallel test tubes containing the two potential hosts, and the restraining plug was removed. Checks were made daily to see if an adoption had occurred. An adoption was considered complete when the queen was found living in a test tube with workers and brood, and being tended (groomed, fed, or provided with other frequent, non-hostile contact) by the workers, for at least 24 hours.

RESULTS AND DISCUSSION

Table I summarizes the labelling, recovery, and survival of *Polyergus* queens. Recovery of the mated queens was facilitated by the fact that all labelled dealates were found within one meter of the nest of origin and all appeared to be attempting to return to their nest, except for two queens who were recovered from under the rock covering the entrance to the home nest itself.

Overall mortality in the adoption test was 59%, but was disproportionately high for queens from Colony II. Of the 13 surviving queens from colonies containing *F. schaufussi* slaves and the one surviving queen from the nest containing *F. pallidefulva nitidiventris* slaves, *all* were adopted into "colonies" of the slave species found in their nest of origin (binomial test, $p < .001$, $n = 14$). Over 70% of the adoptions occurred within the first 72 hours. The most prolonged interval preceding a successful adoption was 17 days.

In this experiment, it is not possible to know whether the ultimate residence of the queens was determined by their "choice" or by the selective action of the slave species workers. Clearly queens and potential hosts must be accepting of each other for an adoption to occur. Observations of the interactions between the queens and their potential hosts suggested that the initial response to a queen by

Table 1. Summary of labelling, recovery, and adoption of *Polyergus* queens.

COLONY OF ORIGIN	II	IV	V	X	TOTAL
Host species*	FN	FS	FS	FS	
Labelled	21	12	26	61	120
Recovered	12	1	5	16	34
Laboratory adoptions	1	1	1	11	14

*FN – *Formica pallidelfulva nitidiventris*
FS – *Formica schaufussi*

adult workers of both slave species present is aggression or withdrawal. For a queen to succeed in becoming adopted, she must persist in her attempts to contact the workers and become acceptable over time. Laboratory interactions between individual conspecific slave species workers from different colonies usually result in the death of one or both workers, and the introduction of an alien conspecific into a slave species nest always results in the death of the newcomer. These findings suggest that a queen's association, in her home nest, with slave species workers of the same species as a potential host, probably does not give her any useful identifiable odor to diminish the initial aggression of this host.

The observation of large numbers of dealates returning to their home nest is consistent with findings of Marlin (1968). In the two recoveries of dealates found in the nest entrances of their original nest, queens were being attacked by resident slaves. We excavated a large colony of *Polyergus* in late August, 1984, and found five dealate and numerous alate queens. Since polygyny is not characteristic of *Polyergus*, and since mating flights had been occurring, we assumed that at least four of these had recently mated and returned to the nest. In the laboratory, the colony was divided into five parts. Each part contained one of the dealate queens and a mixture of slaves and raiders, and was placed in a plastic petri dish nest within a plastic arena with a sand floor. Four of the queens were usually found outside the nest dish, running along the sides of the arena, apparently attempting to escape. Only one queen was consistently found within the nest dish and tended by slaves. She was darker than the others and was assumed to be the founding queen. Other queens, both alate and dealate, were observed being attacked by slaves. All the dealates and most of the alates died within two months. However the corpse of the putative founding queen was retained in the nest dish for several days after death while the bodies of the other four were all found far removed from the nest. These observations suggest that it is unlikely that female reproductives are able to spend their first winter in their home colony.

Two matings of labelled alates from Colony X were observed. Both occurred within one meter of the nest entrance and took place with the queens clinging to blades of grass. The first occurred with a male from the same colony while the second occurred with a male, from a *Polyergus* colony using the same slave species, who had been introduced by the experimenters.

The adoption results indicate that at least one constraint exists on the interaction of *Polyergus lucidus* and potential slave species. The slave species found in a queen's nest of origin appears to determine the host species she will successfully invade, although the exact mechanism through which this occurs is unknown. Jaisson (1975) has demonstrated that callows imprint to brood, of their own or different species, present during a critical period following eclosion. Possibly the queens imprint to the host species they encounter upon eclosing. Other potential constraints to be explored include the possibility that the raiders' choice of species to raid, and a queen's choice of males, may be similarly determined by the slave species in their colony of origin.

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DOLICHODERUS TASCHENBERGI MAYR (HYMENOPTERA: FORMICIDAE) FROM AN EARLY HOLOCENE FOSSIL INSECT ASSEMBLAGE IN THE COLORADO FRONT RANGE

By André Francoeur* and Scott A. Elias†

A paleoenvironmental study of Holocene (Post-glacial) age sites in the Front Range of the Colorado Rocky Mountains was begun in 1981, with the excavation of organic detrital sediments from a deltaic deposit at the point where South St. Vrain Creek enters Lake Isabelle (Fig. 1). The study site lies in the ecotone between the subalpine forest and alpine tundra, and the insect faunal assemblages from the site consistently reflect past environments that fall within the same zone. Sediments ranging in age from 9000 to 7900 years before present (yr. BP) were analyzed for insect fossils, and yielded a total of 138 taxa, dominated by Coleoptera (Elias, 1985). A head capsule of a gynomorph of the ant *Dolichoderus taschenbergi* Mayr was recovered from an interval correlated with a radiocarbon age of 7900 yr. BP (Fig. 2). Other ant taxa from this time interval include *Camponotus* cf. *herculeanus* L., *Formica neorufibarbis* Emery and *Myrmica* sp., all of which may be found in the forest-tundra ecotonal regions of the Front Range today. In general, fossil insect assemblages from this and other high altitude sites in the Colorado Rockies suggest that the time interval associated with these ant fossils falls approximately in the middle of a two thousand year climatic optimum, in which altitudinal tree limit was at least as high as it is today (Elias, 1983, 1985).

The recovered fossil head capsule of *Dolichoderus* agrees obviously with recent specimens of *taschenbergi* Mayr (Fig. 3.). Such characters as the habitus of the capsule, the position, size and shape of the eyes, the diverging and widely separated frontal carinae, the flanges overhanging in part the antennal sockets, the sinuous anterior margin of clypeus, the absence of sculpture on the

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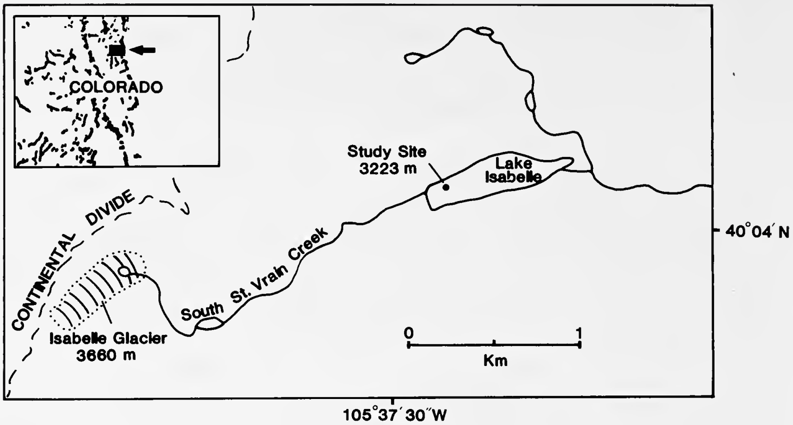

Figure 1. Map of fossil locality near Lake Isabelle, Colorado Front Range.

posterior half of head, and the blackish coloration are strongly congruent. Though partly obscured punctures, foveolae and faint striations are visible on genae and clypeus; the amount of sculptures varies on these parts in recent specimens. The presence of three ocelli identifies a gynomorph.

In the Nearctic region, the four representatives of the ant genus *Dolichoderus* belonging to the subgenus *Hypoclinea* are found only in the eastern half of the continent, from southern Canada to the Gulf States in U.S. (Smith, 1979). They are mainly associated with the deciduous forest biome and the transition zones with the boreal coniferous forest. The known range of *D. taschenbergi* covers the northern half of that territory with sporadic occurrences in the west from southern Manitoba to South Dakota. One might predict the rare occurrence of this insect in northern Colorado, but it is not reported there by Gregg (1963). He considers the genus as extinct in that state and concludes that it was an element of the Pre-glacial tertiary ant fauna. The discovery of the fossil head of Post-glacial age suggests a rather recent extinction from Colorado, if at all.

As noted in the discussion of fossil beetle taxa from the Lake Isabelle sites (Elias, 1985), it appears certain that a considerable percentage of the winged insects preserved in high altitude fossil-bearing deposits are derived from downslope regions, and were carried upslope by mind currents. The fossil specimen of the ant *D. taschenbergi* was probably deposited in the Lake Isabelle basin after

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Figure 2. Fossil head capsule of a gynomorph of *Dolichoderus taschenbergi*, recovered from a layer correlated with a radiocarbon age of 7900 yr. BP. The voucher specimen is deposited in the Institute of Arctic and Alpine Research Quaternary Entomology Collection, University of Colorado.

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Figure 3. Head capsule of a gynomorph of *Dolichoderus taschenbergi*, collected on a sandy ground after nuptial flight in Port Kent, Clinton, Co., New York, 1965-VII-02, AF-04783.

being carried upslope in a nuptial flight. The actual location of the mother colony was probably some tens of kilometers downslope, in the grassland-lower montane transition zone (*sensu* Marr, 1967), where deciduous trees are mixed with pines. The altitude of this zone ranges from 1700 to 1825 m as in the Front Range.

Colonies of *D. taschenbergi*, consisting of thousands of individuals, prefer to build their nests in sandy soil of partly open wooded areas or at the edge of woods. The entrance is usually covered with a low mound of thatch composed of either grass, twigs or needles (Creighton 1950, Smith 1979, Wheeler and Wheeler 1963). Such nests were observed in Quebec in mixed hardwoods with pines either on rocky grounds or on morainic and fluviatile sand deposits (Francoeur, unpublished data). Workers forage in typical files and actively collect sugary secretions of coccids and aphids on trees and bushes, or scavenge dead arthropods. Bradley and Hinks (1968) reported this ant attending aphids on jack pine in Manitoba.

These ecological and ethological traits were likely the same at the time when the reported fossil was living. At about 8000 yr. BP, altitudinal tree limit has apparently already reached the Lake Isabelle cirque basin, subsequent to deglaciation. The faunal evidence from insect fossil assemblages of this age from the Colorado Front Range suggests that climatic amelioration was well underway by this time, with mean July temperatures (an estimate of summer warmth) as warm or warmer than modern values (Elias, 1983, 1985).

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TOOL USE IN DIGGER WASPS (HYMENOPTERA: SPHECINAE)*

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"Tool-use" by a digger wasp was first described by Williston (1892) and Peckham and Peckham (1898). They observed this remarkable behavior in two species of ground-nesting wasps, *Ammophila urnaria* and *Ammophila aberti.* The female digs a burrow in the ground, provisions it with paralyzed caterpillars, lays an egg on top of the food cache and then fills the burrow with soil or stones. While closing the nest, the wasp picks up a pebble in her mandibles and pounds the substrate with it, thereby compacting and settling the soil that was used to fill the nest. The Peckhams said that in this behavior, the wasp had "...improvised a tool and made intelligent use of it." The behavior received much publicity (see Frisch, 1940; Lamburn, 1955; Evans, 1959) and several authors saw tool using as evidence that wasps have highly plastic, intellectual powers (Rau and Rau, 1918; McDougall, 1923; Bouvier, 1922). Others have interpreted the behavior differently. Rather than thinking of tool using as insightful, they described the behavior as a species-typical, instinctive act (Holmes, 1911; Frisch, 1940; Baerends, 1941; Evans, 1959) or possibly an example of trial-and-error learning (Thorpe, 1956). Although some have questioned whether the behavior should be considered true tool use (Frisch, 1940; Evans, 1959), the action clearly falls under the current definition (Alcock, 1972; Wilson, 1975). When *Ammophila* uses a pebble as a hammer, she is manipulating an object, not internally manufactured, with the effect of improving her efficiency in altering the position, form or condition of some other object in the environment (Beck, 1980; Alcock, 1972). How did such extraordinary behavior evolve?

The Sphecidae are a large family of solitary (usually), hunting wasps. In general, the female constructs a nest which she provisions with one to several paralyzed arthropod prey as food for the single

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egg she lays in each brood cell. Most species dig holes in the ground, but some nest in pre-existing cavities whereas others construct mud nests. Regardless of the type of nest, all species of sphecids show some sort of final nest closure. This nearly always includes behavior that apparently compacts or settles the material used. Most sphecids and pompilids (spider wasps) pack the soil by repeatedly tapping or pounding on the substrate with the last abdominal segment (Carpenter, 1930; Evans, 1966b), often while simultaneously vibrating the abdomen (Endo, 1981). However, one subfamily of sphecids, the Sphecinae, differs in that they tamp or press the soil with the front of the head. It is in this group that tool-using behavior has evolved. In this paper I examine the frequency, origin and adaptive value of tool using in the Sphecinae.

Throughout the following discussion of nest closure in the Sphecinae, I include observations I have made on various species. Descriptions of *Sphex ichneumoneus* come from notes, slides and films taken during a five-summer study (July–August) at sites in Dearborn, MI (1972–75, an aggregation of 73 individually marked wasps was observed completing 200 final closures over the four years), Exeter, NH (1975, 33 wasps and 60 permanent closures) and Northfield, MN (1976, 136 wasps and 150 closures) (see Brockmann 1979 and Brockmann and Dawkins 1979 for further details). The great black wasp, *Sphex pensylvanicus,* was observed in 1974 (25 Aug–16 Sep) at a gravel pit near Rensselaerville, NY (25 individually marked wasps and 12 final closures were observed). Brief observations of *Ammophila urnaria* were made at the same site (3 wasps, 2 nest closures). One observation of nest closing was made on *Podalonia pubescens, Ammophila wrightii* and *A. breviceps* near the Southwestern Research Station, Portal, AZ (30 May–22 June 1975). *Ammophila aberti* was observed briefly at Chaco Canyon National Monument (10 wasps seen, one nest closure, 30 June 1975). Brief observations on *A. aureonotata* and *A. pictipennis* were made at the Archbold Biological Station, Lake Placid, FL (14–17 April 1974).

Nest Closure

The ground-nesting Sphecinae generally construct a simple nest: a long, straight, main-tunnel with a perpendicular side-tunnel and terminal brood chamber. They dig the nest by biting at the substrate and scraping away the loosened soil with rakes on their front tarsi

(Brockmann, 1980). Unlike other members of the family, all Sphecinae gather up the loosened soil into a ball and carry it out of their burrow, holding the bolus up under the head with their front legs, while walking on the middle and hind legs (Olberg, 1959; Evans and West Eberhard, 1970; Brockmann, 1980). In most species the wasp drops her load immediately outside the nest entrance, which results in a mound or tumulus. This accumulated soil is later used for filling the burrow after the provisioning is complete. In contrast with this, *Ammophila* usually flies up with the armload of soil and drops it some distance from the nest entrance (Table 1A; Evans, 1959). Some *Ammophila* walk out of the nest carrying armloads of soil, but then drop them away from the nest entrance, usually in different directions (Table 1A). The effect of this is that the *Ammophila* do not usually have a distinct mound from which they can fill their nest during the final closure, as do other ground-nesting Sphecinae.

There are four stages to nest-closure and each involves different kinds of behavior (Table 1A; Evans, 1959). (1) The wasp closes off the chamber or blocks the bottom of her burrow, and then (2) fills in the main tunnel. (3) When the tunnel is nearly filled, she blocks off or levels the soil in the entrance and then (4) disguises the location of her nest. Most species of Sphecinae do not show a distinct closure at the bottom of the burrow, but rather begin immediately by filling the side and main tunnels with soil (Table 1A). *Ammophila,* on the other hand, does not usually fill the short side-tunnel but blocks the bottom of the main tunnel by adding a single large or several small stones, clods of soil, sticks or other debris. Sphecinae fill the main shaft of the burrow by adding soil, by alternating soil and stones or by adding just stones (a few species use mud) (Table 1B). In nearly all species these materials are alternately added and packed. Most wasps remove some objects such as large stones, sticks and leaves, as they scrape and pack. They do this by pushing the object aside with their mandibles, by picking it up with the mandibles and depositing it to one side of the nest entrance or flying up and releasing it at some distance (Frisch, 1937, 1940; Evans, 1959; personal observation).

There are four different kinds of filling behavior used by the Sphecinae (most species use some combination of these four methods). (1) Standing at the nest entrance, the wasp scrapes soil underneath her and into the burrow with her front legs "dog-

Table 1A. The behavior used in permanent nest-closure by the ground-nesting Sphecinae (X = observed, S = sometimes observed, ? = not known due to incomplete observations, – = not observed).

	Digging Behavior						
	Method of Digging			Method of Filling the Nest			
Species	Piles up soil outside	Carries soil some distance	Flies up and discards	Scrapes soil in	Pushes soil in	Carries soil or stones in	Bites off soil (or mud)
Sceliphrini							
Stangeella cyaniventris	X	–	–	X	–	X	–
Penepodium Luteipenne	X	–	–	–	–	X	X
Sphecini							
Sphex argentatus	X	–	–	X	X	–	–
Sphex ichneumoneus	X	–	–	X	X	–	X
Sphex muticus	X	–	–	X	–	–	–
Sphex pensylvanicus	X	–	–	X	X	–	X
Sphex subtruncatus	X	–	–	X	–	–	X
Sphex Fernaldina lucae	X	–	–	X	X	–	–
Palmodes dimidiatus	X	–	–	X	–	–	X
Palmodes laeviventris	X	–	–	X	–	X	–
Prionyx atratus	X	–	–	X	–	–	X
Prionyx kirbii	X	–	–	X	–	X	–
Prionyx subfuscatus	X	–	–	X	–	–	–
Prionyx thomae	X	–	–	X	–	X	X
Prionyx viduatus	X	–	–	X	–	–	–
Ammophilini							
Podalonia spp.	X	–	–	X	–	–	–
Podalonia hirsuta	X	–	–	X	–	X	–
Podalonia luctuosa	X	–	–	X	–	X	–
Podalonia pubescens	X	–	–	X	–	–	–
Podalonia violaceipennis	X	–	–	X	–	–	X
Eremochares dives	X	–	–	X	–	–	X
Eremnophila aureonotata	–	–	X	X	–	–	–
Ammophila aberti	–	–	X	X	–	X	–
Ammophila azteca	–	–	X	X	–	X	X
Ammophila clavus	–	–	X	X	–	X	–
Ammophila harti	–	–	X	X	–	X	–
Ammophila heydeni	–	–	X	X	–	X	X
Ammophila juncea	–	–	X	X	–	X	–
Ammophila kennedyi	–	?	?	X	–	X	–
Ammophila macra	–	X	X	X	–	–	X
Ammophila pictipennis	–	X	S	X	–	X	X
Ammophila placida	–	S	X	X	–	X	X
Ammophila procera	–	S	X	X	–	X	X
Ammophila pruinosa	–	S	X	X	–	X	–
Ammophila pubescens	–	S	X	X	–	X	X
Ammophila sabulosa	–	S	X	X	–	X	–
Ammophila urnaria	–	X	S	X	–	X	X
Ammophila wrightii	–	X	–	X	–	X	X
Ammophila zanthoptera	–	X	–	X	–	X	X

*Stone, stick, seed or other hard object

Nest-closure Behavior									
Method for Packing the Fill								Method for Concealing the Entrance	
Presses down with head	Presses down with stone*	Removes stone after pressing*	Uses same stone repeatedly*	Pounds with head or mandibles	Pounds with stone	Removes stone after pounding	Selects stone for pressing for pounding*	Scrapes soil	Moves stones and debris
?	?	–	–	–	–	–	–	X	–
		(uses mud to fill nest)						?	?
X	–	–	–	–	–	–	–	X	X
X	X	S	–	–	–	–	–	X	X
X	–	–	–	–	–	–	–	X	X
X	X	–	–	–	–	–	–	X	X
X	X	–	–	–	–	–	–	X	X
X	–	–	–	–	–	–	–	X	–
X	–	–	–	–	–	–	–	X	X
X	X	S	–	–	–	–	S	X	X
X	X	–	–	–	–	–	–	X	X
X	X	–	–	–	–	–	X	X	X
X	X	–	–	–	–	–	–	X	X
X	X	–	–	–	–	–	–	X	X
X	–	–	–	–	–	–	–	X	X
X	X	–	–	–	–	–	–	X	–
X	X	–	–	–	–	–	X	?	?
X	X	–	–	–	–	–	–	X	–
X	X	–	–	–	–	–	X	X	–
X	X	–	–	–	–	–	–	X	–
X	X	–	–	–	–	–	–	–	–
X	X	–	–	–	–	–	–	X	–
X	X	X	X	–	X	S	X	X	X
X	X	S	–	–	S	S	X	X	X
X	X	X	X	–	X	X	X	X	X
X	X	–	–	–	–	–	X	X	–
X	X	X	X	–	S	S	X	X	X
X	X	–	–	–	S	S	–	X	–
X	–	–	–	–	–	–	–	X	X
X	X	–	X	–	X	–	X	X	X
X	X	X	X	–	X	X	X	X	X
X	X	S	X	–	S	S	X	X	X
X	X	S	S	–	S	S	X	X	X
X	–	–	–	–	–	–	–	X	–
X	X	–	S	–	–	–	X	X	X
X	X	X	X	–	S	S	X	X	X
X	X	S	X	X	S	S	X	X	X
X	S	S	S	–	–	–	X	X	X
X	X	S	S	–	X	S	X	X	X

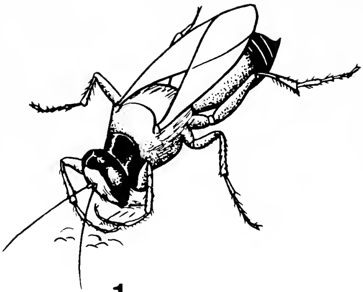
fashion" (Fig. 1; Olberg, 1959). (2) She bites at the soil around the nest entrance, and scrapes the loosened material into her nest. These are the same scraping and biting movements that are used during digging, only the body is now oriented away from the nest rather than toward it. (3) The wasp may also nudge or push soil ahead of her into the burrow with the front of her head (Fig. 2; Tsuneki, 1963; Cazier and Mortenson, 1965). (4) Some wasps pick up clods of soil, clumps of sand or stones in the mandibles and drop or place them in the nest (Carpenter, 1930; Adriaanse, 1943), often pressing them into the substrate (Fig. 3). In most species the wasp fills her nest with soil from the mound that accumulated at the nest entrance during digging (*Sphex, Prionyx, Palmodes, Podalonia;* Parker, 1915). However, in *Ammophila* where there is no mound, much of the burrow is filled with stones and debris found around the nest which are picked up and placed in the burrow. Soil is also chewed from the surrounding substrate and scraped in. Biting and scraping at the soil around the nest also occurs in *Sphex* when the mound is insufficient to completely fill the main tunnel. This is particularly common in *S. pensylvanicus* which digs exceptionally long, multichambered nests which it occupies for many days. When females of this species finally come to filling the main tunnel, the mound has often disappeared. She chews soil from around the nest entrance, often breaking down the sides of the tunnel and leaving a wide depression where the entrance once was. When there is more than one brood chamber in a nest (Sphecini), soil from digging the next side tunnel may be used to close off the previous one. (Ammophilini have only one brood cell in a nest.) A few species (*A. placida, A. zanthoptera* and *A. pubescens*) have been observed to dig "false burrows" or "mines" during nest closure, using the dug material to fill their nest (Adriaanse, 1943; Evans, 1959, 1966c). Adriaanse (1943) suggested that in *A. pubescens* the building of a mine was associated with a lack of suitable material for closing at the surface. I have observed similar behavior in *Sphex ichneumoneus* when they do not have enough soil on the mound with which to close the nest. This can occur after a rain or when another female has filled her nest with soil from her neightbor's mound (similar behavior has been described for other *Sphex* by Iwata, 1976).

Wasps complete the burrow filling by either continuing to add and pack soil, by piling up stones, by packing stones into a kind of pavement, or by pushing stones, sticks, leaves or other debris into the nest entrance (Table 1B). Finally, the wasps disguise the location of the nest by scraping soil in the vicinity and by moving leaves, sticks and other debris in the area over or near the nest entrance (Fig. 4; Table 1A). Some wasps do not perform this disguising behavior at all, whereas others move a few objects around in a perfunctory manner and still others spend long periods of time carefully concealing the nest entrance (Evans, 1959; Peckham and Peckham, 1898). Like other aspects of nesting behavior, nest-closure is highly variable, with individuals sometimes spending long periods of time filling, whereas at other times they only partially fill the burrow or do little packing (Adriaanse 1943; Tsuneki, 1968; Ristich, 1953; Hartman, 1905; personal observation).

The Sphecinae that dig the nest before hunting usually have some sort of temporary nest closure while they are away from the nest. *Ammophila* usually cover the nest at the surface with a pebble or piece of debris selected to fit the burrow entrance precisely (Evans, 1959, 1965). *Sphex* scrapes and nudges a little soil across the entrance to the side-tunnel, but leaves the main-tunnel open while they are out hunting. At the end of the day, most *Sphex* close off the nest overnight, digging it out again in the morning. This temporary overnight closure differs from the final closure in that the wasp quickly scrapes loose soil into the burrow, turning around to pack only occasionally and for shorter periods of time. In contrast with this, during the final nest closure, the wasp alternates a few scrapes of soil into the nest followed by long bouts of intensive packing (Fig. 3). The result is that the soil in the temporary closure is loose whereas in the permanent closing the soil is tightly compacted. When excavating even a recently closed nest, it is very difficult to distinguish the soil of the closure from the surrounding soil.

Packing Behavior

There are three general methods of packing soil into the burrow which grade into one another. (1) The wasp applies the clypeus and open mandibles to the substrate and pushes or presses down on the soil, usually while making low amplitude, high frequency vibrations of the head and body (Fig. 3). The body is normally angled well below the vertical; the wasp may raise her head and then press down again repeatedly within a short period of time at the same or slightly different spot. This action seems to grade into pounding. (2) The



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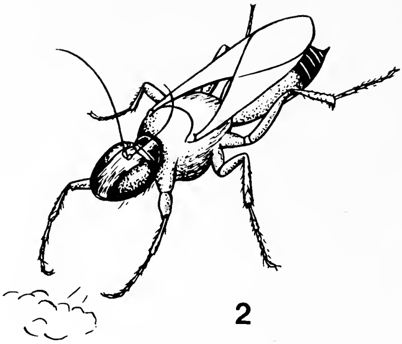

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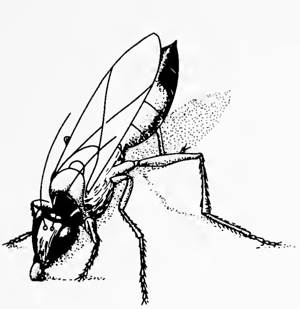
Fig. 1. *Sphex ichneumoneus* filling her nest. The wasp stands at the nest entrance (facing away) and scrapes soil between her legs, using the tarsal rakes on her prothoracic legs. She starts close to the nest entrance and gradually works her way up the mound. This means that early in a bout of scraping, the soil is flung into the burrow, whereas later the soil lands close to the nest entrance, and is thrown into the burrow during the next bout of scraping. Scraping is accompanied by frequent biting at the substrate with the mandibles to loosen the soil. The same behavior was observed in *Sphex pensylvanicus*.

Fig. 2. *Sphex ichneumoneus* nudges soil into her burrow. After scraping, the wasp turns around and walks down the mound toward her burrow. She often pauses at the nest entrance and nudges at the soil around the lip of the burrow. She pushes the soil ahead of her using the front of the mandibles and clypeus in quick, short, posterior to anterior motions of the head. Similar nudges were observed in *S. pensylvanicus*.



3

4

Fig. 3. *S. ichneumoneus* packing soil. After a bout of 5–15 seconds of scraping, the wasp enters her nest and packs the soil. She applies the open mandibles and oral surface of the head to the substrate and presses down for one half to two seconds, vibrating her head and body intensely. She occasionally raises one or both hind legs above the substrate. After 5–20 sec of packing she then reemerges at the surface for another bout of scraping. Late in the filling process, when the nest fill is within 1 cm of the surface, the wasp engages in particularly intense and prolonged packing. In addition to pressing on the fill, she also picks up stones, sticks, clods of dirt, or other pieces of debris, carries it to the nest in her mandibles and presses it down into the soil (seen here). Clods of dirt usually disintegrate, whereas stones and debris are either left in place or occasionally picked up and discarded. On rare occasions wasps have been observed to use the same object several times as a compacting tool. *S. pensylvanicus* shows similar packing behavior.

Fig. 4. *S. ichneumoneus* disguising the nest entrance. The wasp scrapes the region around the nest many times. Leaves, sticks and other debris are grasped with the mandibles and either pulled (seen here) over or pushed to the nest entrance or just picked up and moved to another location around the nest. The effect of this is that the exact location of the entrance is impossible to detect either by the degree of compaction of the soil or by the appearance of the area around the nest. *Sphex pensylvanicus* often chews around the nest entrance, breaking down the sides of the burrow and leaves a wide depression at the site of the nest entrance.

wasp pounds the substrate by rapidly raising and lowering the head and body. The pressing and pounding behavior differ in the amount of time that the mandibles spend in contact with the substrate and in the height to which the wasp raises her head between substrate contacts. (3) The wasp assumes a nearly vertical position, applies the front of the head to the substrate and vibrates (high amplitude, high frequency) the entire head and body like a sort of pile driver. This behavior has been described explicitly only for *A. procera* (Wheeler and Wheeler, 1924; Evans, 1959). This behavior seems to differ from pressing by the angle of the body (although pressing with the body in a nearly vertical position can occur in any species depending on substrate conditions and whether she is in the burrow or not), the amplitude of the vibrations and the long, continuous time that the head is in contact with the substrate. Any of these packing movements may be accomplished with the mandibles alone or while holding a stone, clump of soil, stick or piece of debris (i.e. tool use). (Some species combine these packing methods.) Most Sphecinae pick up a stone, clod of dirt, leaf, twig or other object, apply it to the substrate and push down while vibrating. This action serves either to embed the object or to pack the underlying soil or both. If the object is friable, the pressure and vibration serve to disintegrate it. Sometimes, and with some species more commonly than with others, wasps remove the object after having pressed it into the substrate and use it again or discard it to one side of the nest entrance (Table 1A; Peckham and Peckham, 1898; Rau and Rau, 1918; Evans, 1959; Evans and West Eberhard, 1970).

Tapping or pounding is a far less common form of packing behavior than pressing (Table 1A). Repeated tapping of the substrate with the oral surface of the head has been observed in several species of trap-nesting and mud-daubing Sphecinae (Rau, 1937; Iwata, 1938; Tsuneki 1963b, 1968; Krombein, 1970; personal observation). While pounding some species of *Ammophila* hold a stone in the mandibles, thereby giving the appearance of using a hammer (Williston, 1892; Peckham and Peckham, 1898; Rau and Rau, 1918; Wheeler and Wheeler, 1924; Evans, 1959, 1963, 1965; Powell, 1964; Evans and West Eberhard, 1970). The same stone is often used repeatedly and some authors describe the wasp as carefully selecting her hammer, picking up and discarding many stones before settling on one.

Origin and Adaptive Significance of Tool Use

The preceding review of nest-closing behavior reveals that "tool use" is widespread among the Sphecinae, and is not limited to the *Ammophila* (Table 1A). Many species pick up stones and press and vibrate them down into the substrate during nest closure, an action that almost certainly serves to compact the underlying soil at the nest entrance (Newcomer, 1930; Frisch, 1940; Spangler, 1973; personal observation). Whether the object is removed or not, whether it is used repeatedly or only once, whether the wasp pounds or pushes with it, the result is almost certainly the same. If the stone is not removed, then in addition to being used as a compacting tool, it serves to block the nest entrance at the surface. The origin of this tool-using behavior among digging wasps coincides with the evolution of packing by means of the head and mandibles rather than the abdomen. Most species of Sphecinae which have been observed to pack soil with their mandibles have been observed to manipulate and press stones or other objects into the substrate (Table 1A). Evans (1959) describes a gradual progression from packing movements involving only the mandibles, to packing by pressing down with a stone, to the more complex pattern of pounding with a pebble which is later discarded. Table 1A demonstrates that pounding with a stone is confined to some species of *Ammophila,* whereas pressing and pressing while holding an object are found among most of the ground-nesting Sphecinae. The intriguing question now becomes, what is the adaptive significance of these different sorts of packing techniques?

Several hypotheses have been proposed to explain the origin of the pounding-with-a-stone behavior found in *Ammophila.* Rau and Rau (1918) and Hicks (1932b) suggest that the availability of stones affects the frequency of pounding behavior in *Ammophila.* However, Table 1A and 1B reveal no association between the material used in nest closure and the kind of packing behavior. Eleven species of *Ammophila* use stones during nest closure, nine pound, two do not; six species do not use stones (or use only small pebbles) and three pound while three do not ($\chi 2 = 0.67$, $p = 0.4$, $df = 1$). Evans (1959) suggests that species such as *A. aberti* and *A. zanthoptera* which nest in compactable soil, show frequent pounding behavior whereas those living in sandy soils that resist compaction (such as *A. harti*) do not. He argues that *A. urnaria* and *A. juncea* which nest in

Table 1B. The materials used in nest-closure by ground-nesting Sphecinae.

	Blocking bottom of burrow			Filling main burrow				Final blocking at top of burrow			
Species	soil	small stones, clods of dirt or debris	large stone or clod of dirt	soil	alternates soil and stones	all stones	mud	soil	debris and stones	pile of stones or one large stone	pavement of stones
Sceliphrini											
Stangeella cyaniventris	X	–	X	X	–	–	?	–	–	–	–
Penepodium luteipenne	X	–	–	–	–	–	X	?	–	–	–
Sphecini											
Sphex argentatus	X	–	–	X	–	–	–	X	–	–	–
Sphex ichneumoneus	X	–	–	X	–	–	–	X	X	–	–
Sphex muticus	X	–	–	–	–	–	–	X	–	–	–
Sphex pensylvanicus	X	–	–	X	–	–	–	X	–	–	–
Sphex subtruncatus	X	–	–	X	–	–	–	X	X	–	–
Sphex Fernaldina lucae	X	–	–	X	–	–	–	X	–	–	–
Palmodes dimidiatus	X	–	–	X	–	–	–	X	–	–	–
Palmodes laeviventris	–	–	X	–	X	–	–	–	X	X	X
Prionyx atratus	X	–	–	X	–	–	–	X	–	–	–
Prionyx kirbii	–	X	–	X	X	–	–	X	X	X	–
Prionyx subfuscatus	X	–	–	X	–	–	–	X	–	–	–
Prionyx thomae	X	–	–	X	–	–	–	X	X	X	–
Prionyx viduatus	X	–	–	X	–	–	–	X	–	–	–
Ammophilini											
Podalonia spp.	X	X	–	–	X	–	–	–	X	–	–
Podalonia hirsuta	X	–	–	X	X	–	–	–	–	X	–
Podalonia luctuosa	X	–	–	–	X	–	–	X	X	–	–
Podalonia pubescens	X	–	–	X	–	–	–	X	–	–	–
Podalonia violaceipennis	X	–	–	X	–	–	–	X			

Table 1B. (Continued)

Species	Blocking bottom of burrow			Filling main burrow				Final blocking at top of burrow			
	soil	small stones, clods of dirt or debris	large stone or clod of dirt	soil	alternates soil and stones	all stones	mud	soil	debris and stones	pile of stones or one large stone	pavement of stones
Eremochares dives	–	–	X	X	–	–	–	X	–	–	–
Eremnophila aureonotata	–	X	X	X	–	–	–	X	–	–	–
Ammophila aberti	–	X	X	–	X	X	–	X	X	–	–
Ammophila azteca	–	–	X	X	X	–	–	X	X	–	–
Ammophila clavus	–	X	–	–	X	–	–	–	X	–	–
Ammophila harti	–	X	–	X	X	–	–	X	–	–	–
Ammophila heydeni	X	–	X	X	–	–	–	–	X	X	–
Ammophila juncea	–	X	X	X	–	–	–	–	X	–	–
Ammophila kennedyi	X	–	–	X	–	–	–	X	–	–	–
Ammophila macra	–	–	X	–	X	–	–	–	X	–	–
Ammophila pictipennis	–	X	–	X	–	–	–	X	–	–	–
Ammophila placida	–	X	X	X	X	–	–	X	X	–	–
Ammophila procera	–	X	X	X	X	X	–	X	X	X	X
Ammophila pruinosa	–	X	–	–	X	–	–	–	X	–	–
Ammophila pubescens	–	X	X	X	X	–	–	X	X	–	–
Ammophila sabulosa	X	X	X	–	X	–	–	–	X	–	–
Ammophila urnaria	X	–	X	X	–	–	–	–	X	X	–
Ammophila wrightii	–	X	X	X	X	–	–	–	X	X	–
Ammophila zanthoptera	X	–	–	X	–	–	–	X	–	–	–

a wide range of soils show highly variable tool-using behavior, pounding when nesting in compactable soil and not when nesting in sand (Peckham and Peckham, 1898; Thorpe, 1956). Unfortunately, the data were too sparse to include substrate in Table 1 and hence no test of this hypothesis is possible at present. However, it is possible to say that while this association may hold within the *Ammophila,* it does not explain the diversity of packing behavior found among the ground-nesting Sphecinae. I have observed two species of *Sphex* (*S. ichneumoneus, S. pensylvanicus*) and one species of *Ammophila* (*A. urnaria*) nesting side-by-side and only the *Ammophila* showed the pounding behavior. Table 1A reveals that this behavior is unique to *Ammophila*—but this is not the only unique behavior found in the genus. They also dig their burrows in quite a different manner from the other Sphecinae, depositing soil at some distance from the nest entrance. Therefore, *Ammophila* have no mound of soil from which to scrape nest fill and they must use whatever they can find around the nest. Some of these objects are not particularly appropriate for the purpose and may require more persistent and strenuous packing to achieve the same level of compaction; certainly hunting around for objects takes more time than simply filling from the mound (Adriaanse, 1943). *Sphex,* on the other hand, (and other species with a mound) have a ready supply of suitable material with which they can rapidly fill their nest. It might also be noted that *Ammophila* are particularly slender, light-bodied wasps (as compared with other Sphecinae) and it may be difficult for these animals to apply any significant force to the substrate without the added weight of a stone (which can be as much as ten times the weight of the wasp, Iwata, 1976).

No one has ever demonstrated the survival value of packing for digger wasps, although there is no doubt that they expend considerable time and effort in carefully compacting the fill and disguising the location of the nest entrance. There are no observations of parasites or predators digging into closed nests, although the very common parasitic flies (Sarcophagidae) and velvet ants (Mutillidae) must be able to dig their way out. I have observed several species working their way in through temporary closures of *Sphex ichneumoneus,* including various species of ants (which rob the nest of its provisions), a cleptoparasitic sphecid, *Nysson plagiatus,* and possibly sarcophagid flies (*Senotainia trilineata*) and cuckoo wasps

(*Chrysis*) (they certainly enter *Sphex* nests frequently) (see also Evans, 1966a). The most common marauders, however, are conspecifics which regularly dig up the temporarily filled nests of neighbors. They sometimes discard the contents of the brood chamber when they encounter it or they may take over the nest and use the provisions for their own offspring (Brockmann and Dawkins, 1979). Occasionally a wasp will dig her burrow into the completed nest of another female, and when she does she pulls out the contents (be they provisions or pupa), flies up and discards them away from the nest. In a study of nest-site selection in *Sphex ichneumoneus* (Brockmann, 1979), I observed wasps biting repeatedly at different spots on the substrate. They would finally begin to dig when they encountered a spot that gave way to their chewing, i.e. a spot that was slightly less compacted. Therefore, it seems likely that one important selective pressure acting on the final-closure behavior is reducing the chance that another female will dig in the exact same location. This may be particularly crucial in species that regularly nest in aggregations.

Once the survival value of packing is known, then it may be possible to assess the value of different packing methods to different species of wasps. Far more information is needed on the nature of the nesting substrate, the details of the packing behavior, the consequences of the various packing methods on different soils and the behavior of parasites, predators and conspecifics when digging under different conditions of compaction.

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Species and References
(Tables 1A, 1B)
(Taxonomy after Bohart and Menke 1963, 1976 and Menke and Bohart 1979)

Sceliphrini

Stangeella cyaniventris (Guérin-Méneville)—Bohart and Menke 1976
Penepodium luteipenne (Fabricius)—Williams 1928

Sphecini

Sphex argentatus Fabricius—Tsuneki 1963a, Iwata 1964
Sphex ichneumoneus (L.)—Carpenter 1930, Frisch 1937, Ristich 1953, Brockmann 1976, 1980
Sphex muticus Kohl—Williams 1919
Sphex pensylvanicus L.—pers. obs.
Sphex subtruncatus Dahlbom—Tsuneki 1963a
Sphex Fernaldina lucae Saussure—Cazier and Mortenson 1965
Palmodes dimidiatus (De Geer)—Krombein 1952, 1955 (referred to as *Palmodes daggyi*)
Palmodes laeviventris (Cresson)—La Rivers 1945
Prionyx atratus (Lepeletier)—Peckham and Peckham 1898, Rau and Rau 1918, Carpenter 1930, Strandtmann 1945, Evans 1958
Prionyx kirbii (Vander Linden)—Benz 1959, Tsuneki 1963a (as *P. albisectus)*

Prionyx subfuscatus (Dahlbom)—Evans 1958, Tsuneki 1963a
Prionyx thomae (Fabricius)—Rau and Rau 1918, Hartman 1905, Evans 1958 (as *P. pubidorsum*), Grissell 1981
Prionyx viduatus (Christ)—Kazenas 1968

Ammophilini
Podalonia spp.—Murray 1940
Podalonia hirsuta (Scopoli)—Carpenter 1930
Podalonia luctuosa (F. Smith)—Newcomer 1930
Podalonia pubescens Murray—pers. obs.
Podalonia violaceipennis (Lepeletier)—Parker 1915, Krombein 1936
Eremochares dives (Brullé)—Kazenas 1970, Bohart and Menke 1976
Eremnophila aureonotata (Cameron)—Peckham and Peckham 1898, Krombein 1958, Evans 1959
Ammophila aberti Haldemann—Williston 1892, Hicks 1932b, Evans 1959, 1963, Powell 1964, Menke 1965, pers. obs.
Ammophila azteca Cameron—Powell 1964 (as *A. pilosa*), Evans 1965, Evans and West Eberhard 1970
Ammophila clavus (Fabricius)—Iwata 1939, 1964, 1976, Tsuneki 1968
Ammophila harti (Fernald)—Evans 1959, Powell 1964, B. Hager (pers. comm.)
Ammophila heydeni Dahlbom—Thorpe 1956 (and references therein)
Ammophila juncea Cresson—Evans 1959, 1963, Powell 1964
Ammophila kennedyi (Murray)—Ainslie 1924 (as *S. vulgaris*)
Ammophila macra Cresson—Evans 1965
Ammophila pictipennis Walsh—Rau and Rau 1918, Carpenter 1930
Ammophila placida F. Smith—Hicks 1932a (as *S. xanthopterus*), Strandtmann 1945, Evans 1959, Powell 1964, Menke 1965
Ammophila procera Dahlbom—Pergande 1890 (as *A. gryphus*), Hartman 1905, Rau and Rau 1918, Wheeler and Wheeler 1924 (as *A. gryphus*), Carpenter 1930, Krombein 1952, Stucker 1953, Tilden 1953 (as *A. saeva*), Evans 1959, Powell 1964
Ammophila pruinosa Cresson—Hicks 1933, Evans 1959, Powell 1964
Ammophila pubescens Curtis—Baerends 1941 (as *A. campestris*), Adriaanse 1943 (as *A. campestris*), 1947, Olberg 1959
Ammophila sabulosa (L.)—Fabre 1920, Iwata 1939, Olberg 1959, Tsuneki 1968, Iwata 1976 (as *A. infesta*)
Ammophila urnaria Dahlbom—Peckham and Peckham 1898, Parker 1915, Frisch 1940, Evans 1959, Powell 1964, pers. obs.
Ammophila wrightii (Cresson)—Hicks 1934, Adriaanse 1947, Evans 1959, Olberg 1959, Powell 1964, Evans and West Eberhard 1970
Ammophila zanthoptera Cameron—Evans 1959, Powell 1964

BIOECOLOGICAL OBSERVATIONS ON A PIGMY LOCUST, *POTUA SABULOSA* HANCOCK (TETRIGIDAE: ORTHOPTERA)*

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Introduction

Faunistic studies of the tetrigids of Indian subcontinent have been made by Kirby (1914) and Hancock (1915). These are of great fundamental value but dealing necessarily with the taxonomic description. The biology and ethoecology of many species of tetrigids are largely unknown. Moreover, there is practically no published research on the bioecology of Indian tetrigids.

The present paper deals with bioecological observations on a tetrigid, *Potua sabulosa* Hancock. This work is based on the field observations of well over six years, in certain localities in Maharashtra State (M.S.) a south-western region of India. It forms a part of 'Survey, Taxonomy and Etho-ecological studies on Tetrigids,' an on-going research project (F.1-20/79-PP) supported by Indian Council of Agricultural Research, New Delhi.

Potua sabulosa belongs to sub-family Cladonotinae. The species was first taxonomically described by Hancock (1915) and the habitat was recorded as Venna valley, Mahabaleshwar (M'shwar), Dist. Satara. In our extensive survey, we collected *P. sabulosa* not only from Venna valley but also from other valleys in M'shwar, namely Blue valley, Krishna valley and Koyana valley. In the region under survey, we also collected these insects from certain other localities of Western Ghats of Maharashtra, such as, Pratapgad, Panchgani in Dist. Satara and Sinhagad, in Dist. Pune. Our collection of *P. sabulosa* from these new localities constitutes a first record.

Materials and Methods

Samples of living *Potua* were collected from the above mentioned localities. The insects are somewhat difficult to locate on account of

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the small size and the ability to blend with the surrounding. However, being sluggish these are easy to catch, once detected. After collection, the specimens were transferred to insect cages containing their natural food. These cages were then brought to the research centre for further investigations. The insects were maintained in the cages by simulating the natural conditions to the extent possible.

Field observations were periodically made to gather the data in relation to habitat, seasonal variations in the population size and of bioecological behaviour.

Measurements of body parts of male and female *Potua* were made with calibrated eye-piece gratings, of a zoom type trinocular dissecting microscope.

OBSERVATIONS AND DISCUSSION

P. sabulosa Hancock is smallest of the tetrigids studied in our laboratory. It can be aptly called the 'Pigmy locust' (Fig. 1). Table 1 summaries the information about the localities where it has been observed, so far. These localities generally have lush forests in common, as well as year around humid and relatively cool climate.

Furthermore, it may be noted here that in the surveys undertaken of certain altitudinally near-similar localities in Western Ghats such as Lonavala-Khandala (Dist. Pune, Alt. 733 & 630 mts respectively) Matheran (Dist. Raigad, Alt. 833 mts) and Trimbak (Dist. Nasik, Alt. 950 mts) the authors could not, so far, come across *P. sabulosa.* This presumably means that besides altitude certain other ecological conditions could be playing some role in the distribution of this insect.

Typically, the insect is found on the walls of buildings, large stems of plants, in the crevices of rocks, fencings and similar other places which are covered with bryophytes, especially the moss. Its sitting posture is typically like that of other locusts. The body colour is usually dull brown to gray, very similar to the soil and rocks of the Deccan plateau of Western Ghats. Insects are usually very well camouflaged with their habitat. The pronotum is high, arched, slightly roof-like, wrinkled and with tubercles. It is as long as the abdomen in both the sexes (Fig. 2). Hind femora are large, stout, marginally serrated and tuberculate on the outer side. Table 2 gives the measurements of various body parts of the male and female

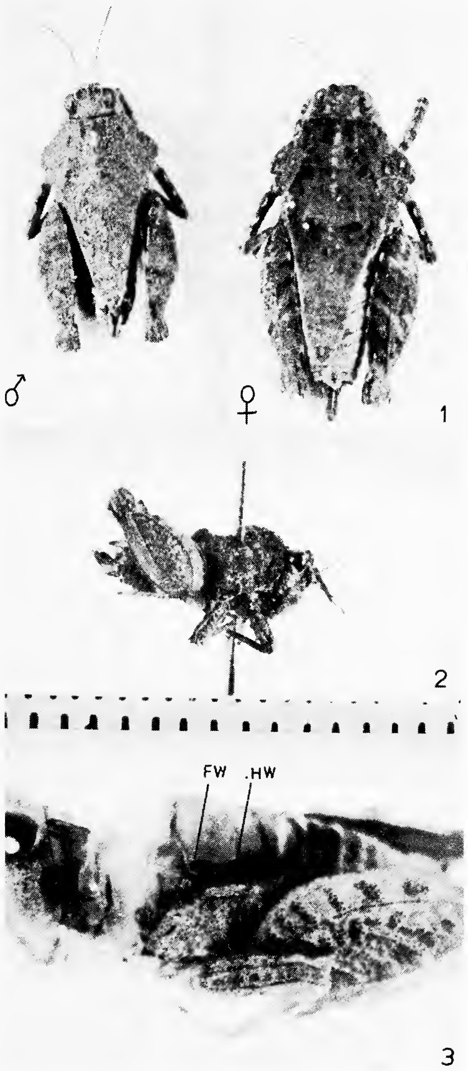

Fig. 1–3, *Potua sabulosa* Hancock. 1. Dorsal view of male (× 6) and female (× 6). 2. Lateral view of male. 3. Lateral view, with pronotum removed to show left vestigial fore wing (FW) and hind wing (HW).

Table 1. Climatological information of certain localities in which *Potua sabulosa* Hancock has been reported by us.

Locality	Lat./Long.	Altitude (Height from M.S.L. in mts)	Average Rainfall mm/anum.	Average Max. and Min. Temp.	Average Humidity
M'shwar	Lat. 17°56′N Long. 73°40′E	1573	6226	Max. 24.1°C Min. 13.6°C	70%
Pratapgad	Lat. 18°0′N Long. 74°22′E	1185	7250	Max. 25°C Min. 16°C	68%
Panchgani	Lat. 17°55′N Long. 73°49′E	1464	1865	Max. 35.6°C Min. 16.1°C	70%
Sinhagad	Lat. 18°22′N Long. 73°45′E	1436	1100	Max. 33°C Min. 17°C	70%

Potua. Underneath the pronotum there is a pair of triangular, thick and scaly elytra while hind wings are very reduced. Hancock (1915) has mentioned that elytra are minute and elongate and hind wings are wanting. However, after careful observations we have found that the wings, even though thickened like elytra and vestigial, are unfailingly present (Fig. 3). The measurements of elytra and these wings in male and female *Potua* are given in Table 2. Therefore, this insect comes under the category of 'brachypterous form', although certain other genera belonging to the subfamily Cladonotinae are apterous in nature. Meopterism of this pigmy locust favourably indicates its distribution to relatively high altitudes. *Potua* usually crawls when disturbed and rarely jumps. It can jump to a distance of about 25 to 35 cm.

The insects feed on humus along with bryophytes like moss (*Funaria* sps.), algae, fungi and lichens present in the vicinity of the habitat. From laboratory observations there appears to be a strong preference for humus as well as for smaller and tender plants such as moss. *P. sabulosa* appears to be unusually hardy and can survive periods of long starvation both in natural habitat as well as under laboratory conditions. For example, our laboratory observations indicate that the adults can survive total starvation for a period of more than two months. However, the nymphs lose their vitality very rapidly, when kept starved in the cages.

Potua, like other tetrigids, shows well defined sexual dimorphism. Copulating pairs can be observed immediately after the initial mon-

Table 2. Average measurements in mm of various body parts in 10 specimens of *Potua sabulosa* Hancock

	Length					Breadth	
Sex	Body	Pronotum	Hind femur	Fore wings (Elytra)	Hind wings	Fore wings (Elytra)	Hind wings
Male	6.0	5.5	4.2	1.04	1.13	0.42	0.34
Female	8.0	6.5	5.0	1.13	1.25	0.46	0.38

soon showers. The female *Potua* excavates small burrow at a depth of about 2 mm in the loose superficial soil or between the dense tufts or patches of moss and other bryophytes with the help of its ovipositor, and lays 23–25 eggs in a loose cluster. The eggs are smaller in size with very short and stubby chorionic filaments or 'horns'. These are laid in a more or less single layer. In this connection, it is interesting to note that in other tetrigids, such as *Euscelimena harpago* Serv. belonging to the semiaquatic subfamily Scelimeninae, the eggs have elongate filaments. Moreover, they are laid relatively deeper and the cluster is arranged in 3 to 4 tiers (Bhalerao & Paranjape, 1984). *Potua,* brought to the laboratory and kept in cages provided with moist soil and moss, laid eggs in July–August as well as in April and May. However, in their natural habitat, we could find pigmy locusts laying eggs in July–August only. The hatching takes place in about 10–12 days at room temperature of 23° to 25° C. The early instars are minute, stumpy replicas of the adults.

The insect population is considerable immediately after monsoon and one can see 5–10 individuals per square meter. The population level gradually declines with the onset of summer until about late April, when practically no adult *Potua* can be observed in the exposed, dried out niches. However, when searched critically, very few adults can be located, hidden about 3 to 5 cm beneath the soil of the fence-walls. The pigmy locusts actually burrow to reach this relatively cool soil and remain in this condition, to tide over the hazardous summer season. This peculiar behaviour of the pigmy locusts has been observed by us for the first time. After two or three showers of monsoon, these insects once again come out into the open, copulate and lay eggs. The adults of the previous season then die, while the eggs hatch, and the life cycle of *Potua* continues.

During our extensive survey and collection of this tetrigid in various parts of Western Ghats, we came across some variations in the colour pattern, body size and in the nature of pronotum. This suggests that *P. sabulosa* shows some 'ecotypes' due to climatological or other ecological variations in these localities. Further studies on various interesting aspects of this insect are in progress.

ACKNOWLEDGMENT

The authors are grateful to ICAR New Delhi, for financial support and to Dr. N. C. Pant, Director, Commonwealth Institute of Entomology, London, for arranging for the determination of the insect by Mr. W. J. Reynolds, taxonomist, British Museum, London. The genus and species name was later confirmed by Dr. M. S. Shishodia, taxonomist, Zoological Survey of India, Calcutta. Thanks are due to the taxonomists. Thanks are also due to Shri Kamble for valuable help during survey; to Dr. H. V. Ghate in discussions, and photography; to A. D. G. Meteorology Department Pune, for giving the necessary data and to Prin. S. Y. Gambhir for providing facilities and giving encouragement.

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CRYPTIC PHRAGMOSIS: THE STRUCTURAL MODIFICATIONS

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Introduction

Cephalotini is an exclusively arboreal tribe of Neotropical ants that has specialized in passive defense. In the largest genus, *Zacryptocerus,* the entire body is heavily armoured and the expanded head surface of the soldier is particularly suited for blocking the nest entrance. Soldiers act as living doors, closing off nest entrances with their heads. Wheeler (1927) termed this phenomenon *phragmosis.* The most extremely modified heads within *Zacryptocerus* are found in the subgenus *Cyathomyrmex,* which is characterized by a completely rimmed, saucer-shaped, cephalic disc on the heads of soldiers and queens (Kempf, 1958).

Wheeler (1942) was the first to notice that in two species in this group queens and older soldiers tend to accumulate dirt on their heads. He also commented that the accumulation of this material made the heads resemble the bark of a plant and implied that the debris camouflaged this living gate to the nest.

Recent discoveries of soil-binding pilosity in basicerotine and stegomyrmicine ants (Hölldobler and Wilson, 1986) stimulated us to look for similar dirt collecting structures on these bizarre cephalotines. This led us to the discovery of remarkable features on the

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heads of soldiers and queens, unlike those described for any other ants.

Methods

Zacryptocerus pallens porrasi was collected on Barro Colorado Island (BCI) in Panama, and *Z. varians* was collected on Upper Matecumbe Key, Florida. Specimens of *Z. pallens* from British Guiana, from the Florida keys, and *Z. setulifer* from Ancon, Panama, were obtained from the MCZ collections. The micrographs were taken with an AMR 1000 A scanning electron microscope.

Results

Z. varians (Figs. 1–3). The heads of soldiers were covered with large, blade-like setae arched over large shallow pits. The sparse distribution of the pits gives the head a pock-marked appearance. The most remarkable feature of clean specimens was the high density of pores 1–3 μ in diameter. These are almost certainly glandular openings (Fig. 1). The density of pores was about 1 pore/350 μ^2, and the total number of pores on the disc was estimated to be over 8000. One specimen, which appeared only slightly grimy to the eye, was in fact covered with a dense tangle of material (Figs. 2, 3a) which resembled a mass of fungal filaments (mycelia). Patches of material on the head of a second specimen consisted of an encrusting layer as well as some filaments (Fig. 3b). Examination of the mat material under a light microscope revealed, however, none of the branching or internal structure indicative of a fungal origin. We suggest that the filaments are material extruded through what are apparently glandular openings.

Z. pallens (Figs. 4–6). To the eye, the head of the soldier shown in Fig. 4a appeared to be covered with a thin layer of dirt. Closer examination revealed that the surface was covered with irregular ribbons of material (Figs. 4b, 5a). Pores were visible along part of the central ridge (see Fig. 5b). Material seemed to be extruded in lumpy strands from a number of the pores (Figs. 5b, 6), supporting the suggestion that it is secretory in origin.

Z. pallens porrasi (Figs. 7–9). The two soldiers shown in Figs. 7–9 were collected from the same colony. They represent the recognizable form of *Z. pallens* that Wheeler (1942) described as the variety *porrasi* (referred to in the remainder of this paper as *Z. pallens porrasi*). The soldier is characterized by large brush setae on the cephalic disc (Fig. 7). Similar views of the two soldiers, one clean and one dirty, are shown in Fig. 8. In the soldier that appeared clean, the brush setae were free of accumulated material, but the surface seemed to be obscured by a thick encrusting material (Figs. 7, 8a). The second soldier had such a thick accumulation that the large brush setae were almost completely buried (Figs. 8b, 9a). The material on the head of the dirty soldier appeared fibrous (Fig. 9b), much like the material seen on the head of *Z. varians* (Fig. 3a).

Z. setulifer (Figs. 10–11). The MCZ collection includes 3 queens and 1 soldier of this little-known species. The heads of all 4 specimens are caked with debris. We examined one queen and found that the material encrusting the head appeared more solid than that seen in the other species. Brush setae on the head, as far as they can be seen (Fig. 10b), were not as complex as those on *Z. pallens porrasi.* On the thorax, where the hairs were visible, were two layers of setae: erect brush hairs and a lower layer of flattened appressed setae (Fig. 11). The same pattern was found on the thorax of the soldier.

Discussion

Wheeler (1942) was the first to suggest that the encrusting material found on the heads of soldiers and queen in two different cephalotines functioned as camouflage for the nest entrance. His description of *Z. pallens* var. *porrasi* was based primarily on the large, sparse hairs on the heads of soldiers and queens. He commented that the cephalic disk of older soldiers and the queen were often coated with "dirt and extraneous particles so that it closely resembled the bark of the plant." In addition, he gave the first description of the soldier caste for *Z. setulifer* and noted that the cephalic discs were encrusted with "foreign matter from exposure to the elements during guard duty at the oval nest entrance."

The soldiers, and perhaps the queen during early stages of colony development, act as living gates at colony entrances. Clean, shiny head surfaces might be more easily spotted by visual predators, such as birds and lizards, which could break open twigs for the rich reward of ant brood. The resemblance of heads to bark would effectively conceal the location of the nest and nest entrance.

The use of accumulated debris as camouflage has been found in basicerotine and stegomyrmicine ants. These are unusually slow, dirty ants that freeze when disturbed. The entire dorsal surface is covered with soil-binding pilosity that enhances accumulation of dirt particles (Hölldobler and Wilson, 1986). In *Z. varians* and *Z. setulifer,* the complex setae and the accumulation of dirt is also restricted to the exposed surface, in this case the cephalic disk. Here too, camouflage is enhanced by lack of motion, since guards remain stationary at the entrance.

Pilosity

The structure of setae on the cephalic disc differed among the four forms of *Zacryptocerus* we examined (*varians, pallens, pallens porrasi,* and *setulifer*). *Z. varians* and the typical form of *Z. pallens* bore setae typical of the genus: a flattened blade arched over a shallow pit. Setae of this form probably do not encourage accumulation of extraneous material on the disc surface.

Both *Z. pallens porrasi* and *Z. setulifer,* however, had upright brush setae that probably do enhance collection of material. The setae on *Z. pallens porrasi* were thick and split to the base, much like a shaving-brush. They appeared identical to hairs found in the genus *Eurhopalothrix.* More slender brush hairs split only near the tip are common throughout the Basicerotini (Hölldobler and Wilson, 1986). Both forms of brush hairs are correlated with soil-binding in these cryptic terrestrial ants.

In *Z. varians, Z. pallens* and *Z. pallens porrasi,* all hairs on the cephalic disc were of a single type. In *Z. setulifer,* there may be more than one hair type on the head, if the hair pattern is similar to that found on the thorax. One type was the erect brush hair and the other was an appressed blade-like holding seta. This double-layered arrangement is common in ants that bind soil particles to their cuticle (Hölldobler and Wilson, 1986).

Kempf (1958), in his revision of the Cephalotini, struggled with variability of pilosity and disc sculpture within the *pallens* complex. In the end, he lumped all forms into one species. In view of our findings, some of the confusing variation in sculpture and pilosity may be only apparent and due to varying degrees of coverage, rather than actual structural differences. The value of pilosity as a taxonomic tool may deserve re-evaluation and could be used to distinguish closely related species in what appears to be a *pallens* complex.

Encrusting material

The accumulation of material on heads of soldiers and queens was common to all the species we examined. In some cases the accumulation was extreme (Fig. 8b, 10a) and in some it was slight (Figs. 1a, 3b). Remarkably, the material seemed to be internal in origin, rather than an accretion of environmental debris. The glandular origin of the material was suggested by the following aspects of external morphology, but confirmation awaits histological study. First, thousands of pores resembling glandular openings covered the head of the *Z. varians* soldier, as shown in Figs. 1b, 3b. Second, material caught in the process of extrusion was found in *Z. pallens* (Fig. 6). The diameter of the fibers in both *Z. varians* and *Z. pallens* was appropriate for the size of the pores. Finally, examination with a light microscope of the material on *Z. varians* did not suggest a fungal origin. The possibility that some of the material found in the dense mats of fibers were fungal mycelia (Fig. 8a) has not been completely eliminated, however.

The fibrous material may not be the only type of material extruded onto the disc surface. A sheet of material covering the floor of the disk was seen on some specimens of *Z. varians* (Fig. 3b). In addition, what appeared to be a blanket of thicker material coated the floor of the apparently clean specimen of *Z. pallens porrasi* (Fig. 7b). The even coating may not be confined to the queen and soldier castes. Minor workers of *Z. varians* appeared to be coated with a homogenous layer of coagulated film over the surface of the head.

The function of the fibrous material on the cephalic discs of soldiers and queens is not entirely clear. When the whole bowl of the cephalic disc is filled with material, as in *Z. pallens porrasi* and *Z. setulifer,* a camouflage role seems likely. In less extreme cases, the possibility of crypsis is less obvious. However, a thin, grimy layer may be sufficient visual or tactile camouflage in some environments.

The internal origin of the material on the cephalic discs contrasts with the extraneous origin found in the Basicerotini and Stegomyrmicini (Hölldobler and Wilson, 1986). It may be that in the arboreal environment in which all cephalotines live, suitable dirt particles are relatively scarce, and a more reliable source of camouflage material is from within. In *Z. pallens porrasi, Z. setulifer,* and the Basicerotini, complex setae enhance the accumulation of material, regardless of its source.

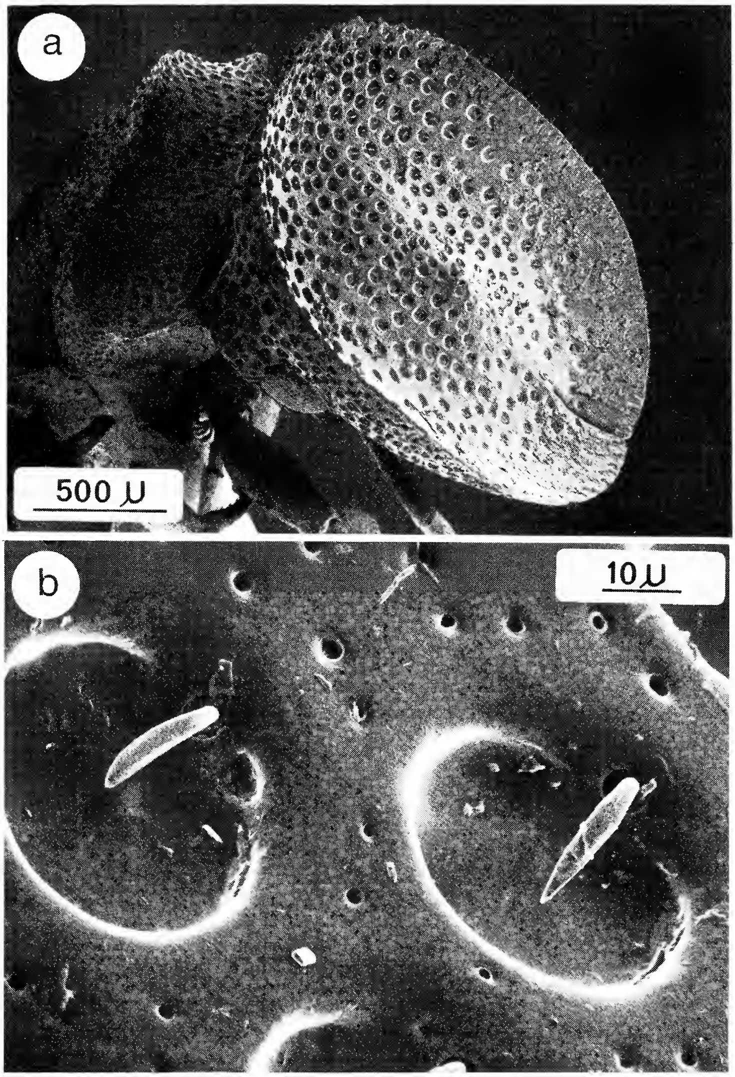

Fig. 1. *Zacryptocerus varians* (Upper Matecumbe Key, FL). Soldier. a. SEM view of relatively clean cephalic shield. b. Surface of clean shield. Note the numerous pores (glandular openings).

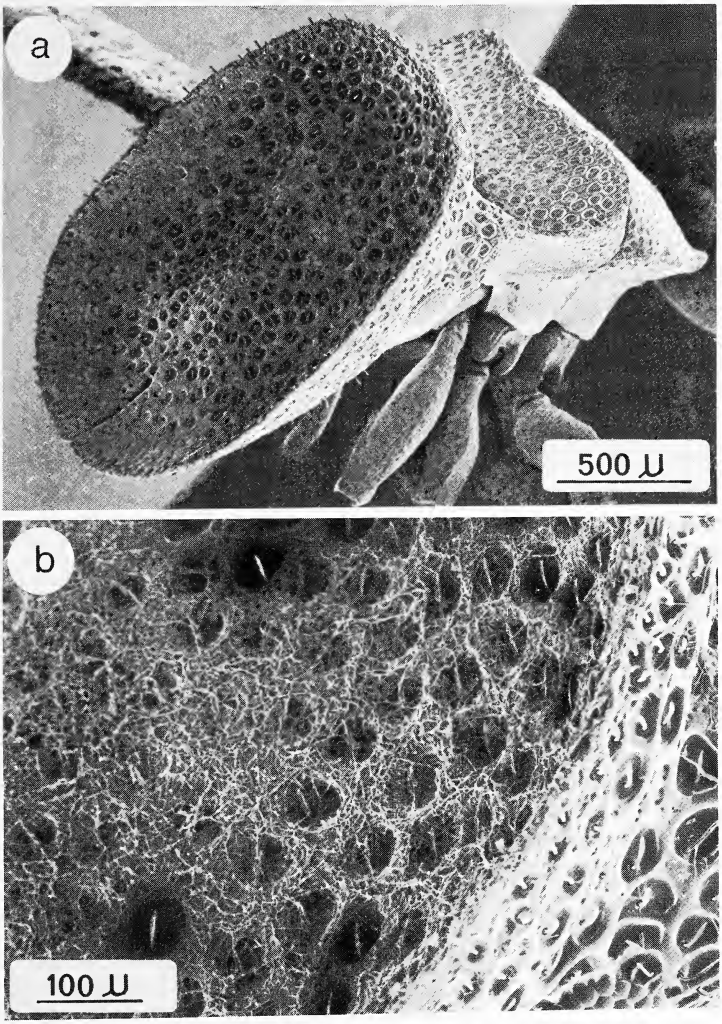

Fig. 2. *Z. varians* (Lignumvitae Key, FL). a. Soldier head covered with tangled mat of fibers. b. Mat of fibers is confined to the cephalic shield.

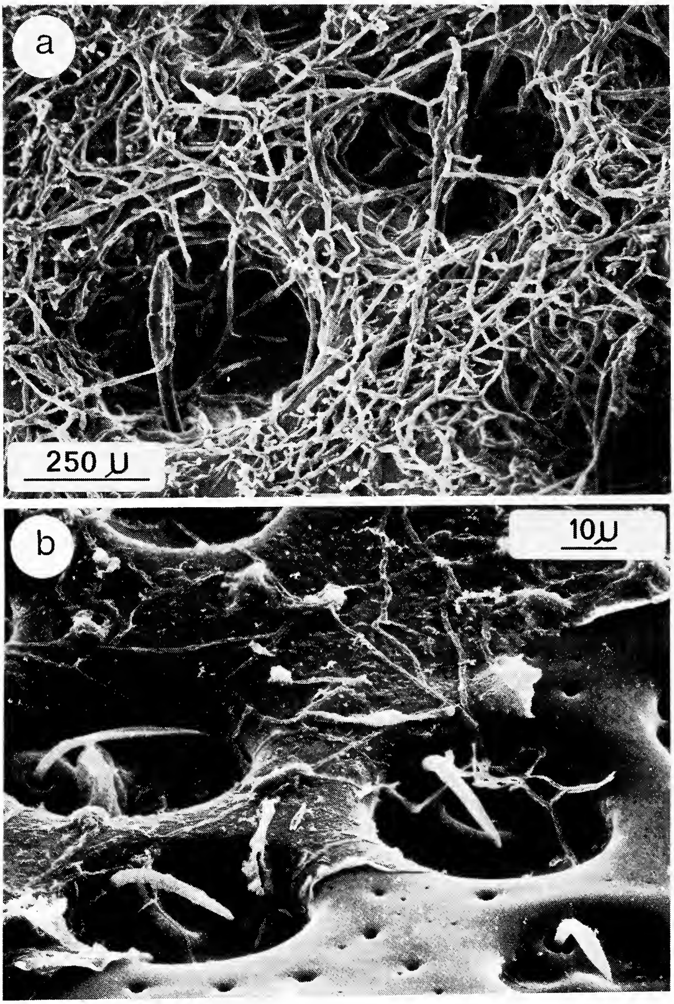

Fig. 3. a. *Z. varians* (Lignumvitae Key, FL) (same individual as Fig. 2). Close-up of mat covering the large, blade-like setae. b. *Z. varians* (Card's Point, FL). Soldier. Clean and coated areas of cephalic shield. Note the pores in the clean section and the uniform coating in addition to some fibers in the encrusted area.

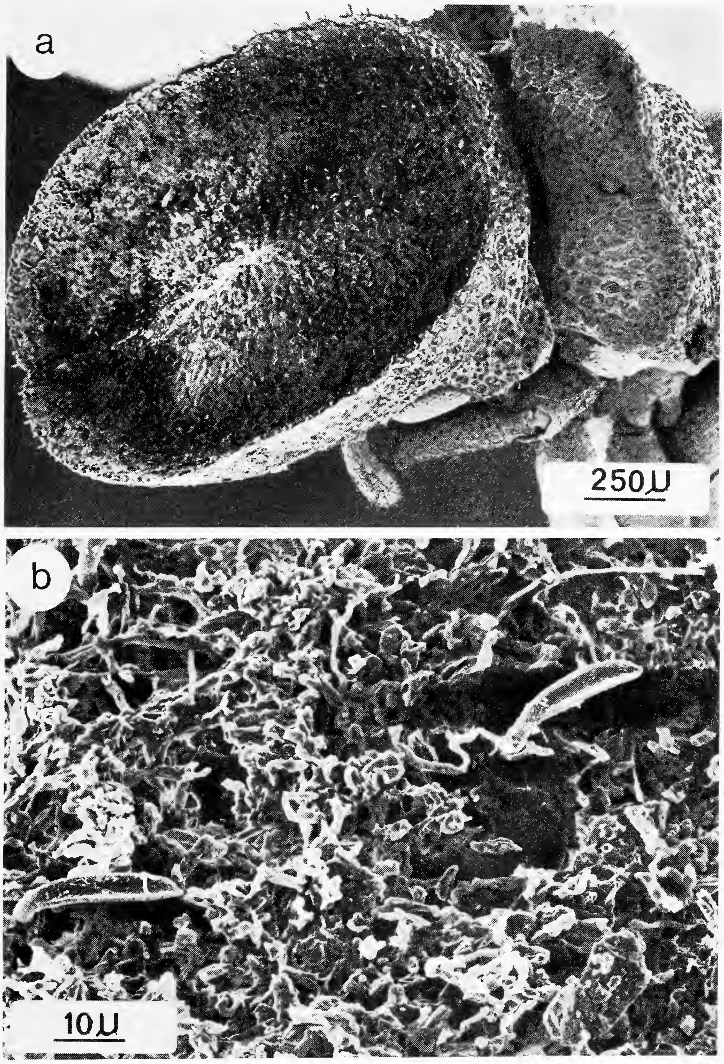

Fig. 4. *Zacryptocerus pallens* (Kartabo, British Guiana). a. Cephalic shield of soldier. Note central ridge. b. Close up of setae and encrusting materials.

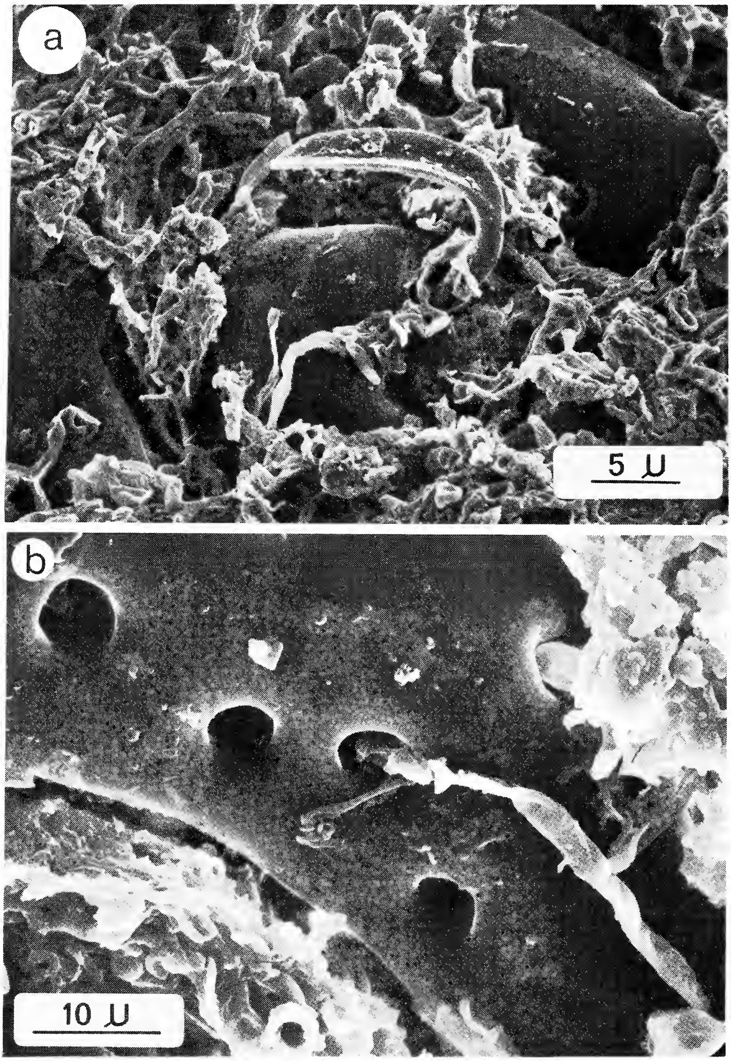

Fig. 5. *Z. pallens* (same individual as Fig. 4). a. Close up of shoe-horn shaped setae and encrusting ribbons. b. Region on central ridge on which pores are visible.

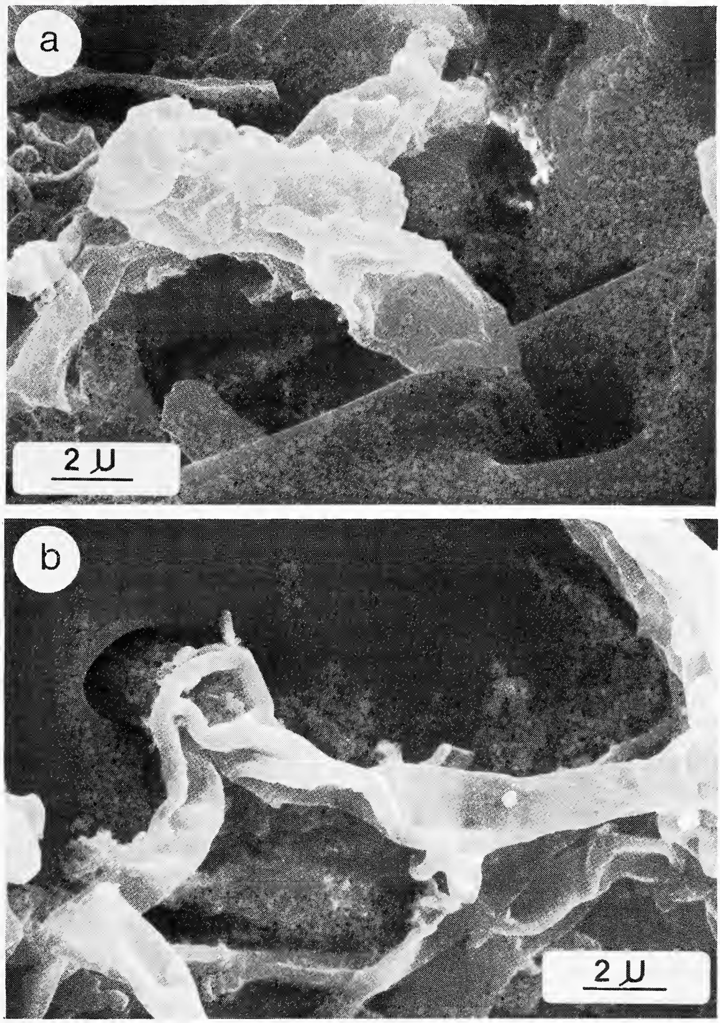

Fig. 6. *Z. pallens* (same individual as Figs. 4, 5). Pores from which surface coating seems to flow.

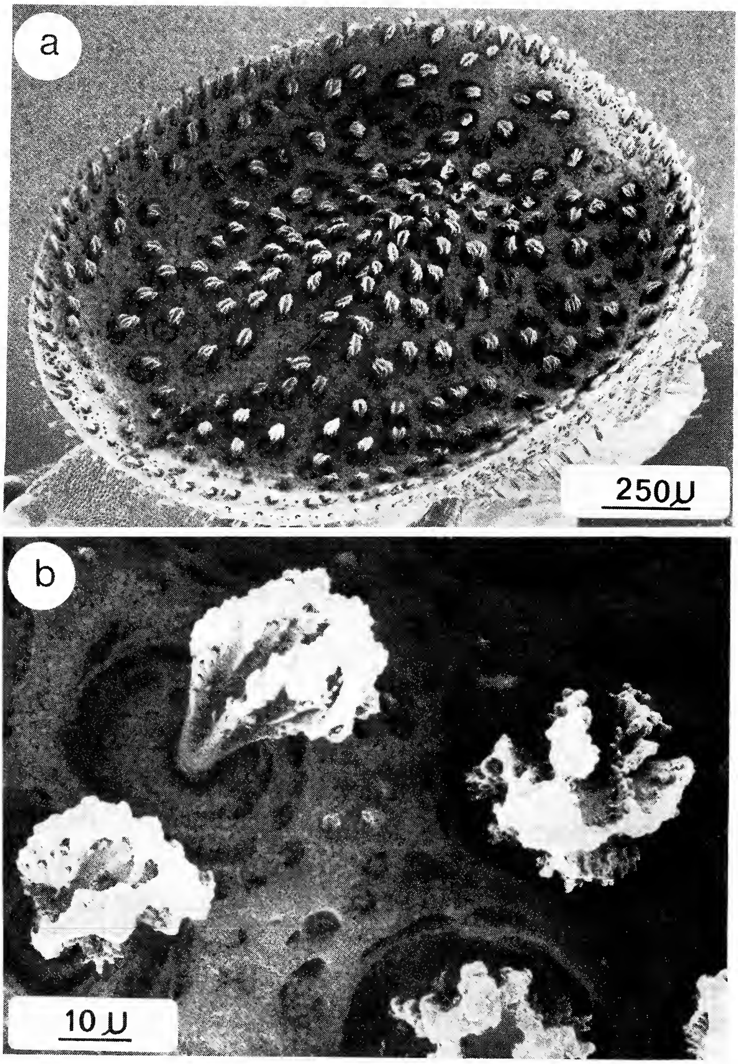

Fig. 7. *Z. pallens porrasi* (BCI, Panama). Clean soldier. a. Cephalic disc covered with brush setae. b. Close-up of large brush setae.

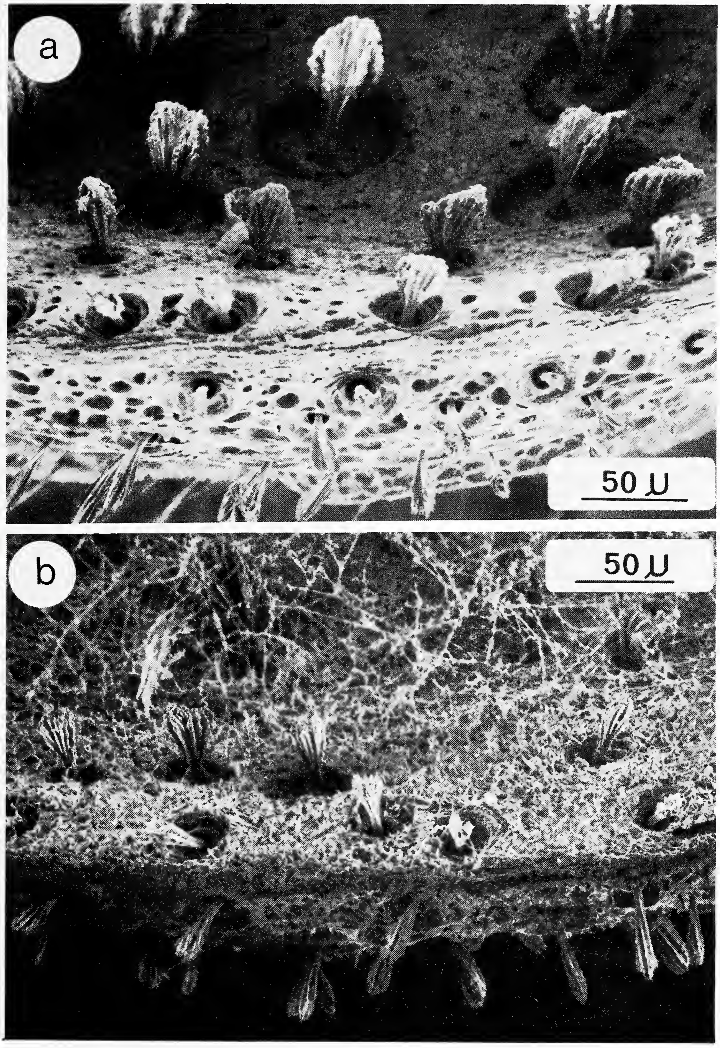

Fig. 8. *Z. pallens porrasi.* Views from rim of cephalic shield. a. (same individual as Fig. 7). Clean surface. b. *Z. pallens porrasi,* second soldier, nestmate of individual in Fig. 8a. Shield is so matted that setae beyond the second row are completely obscured.

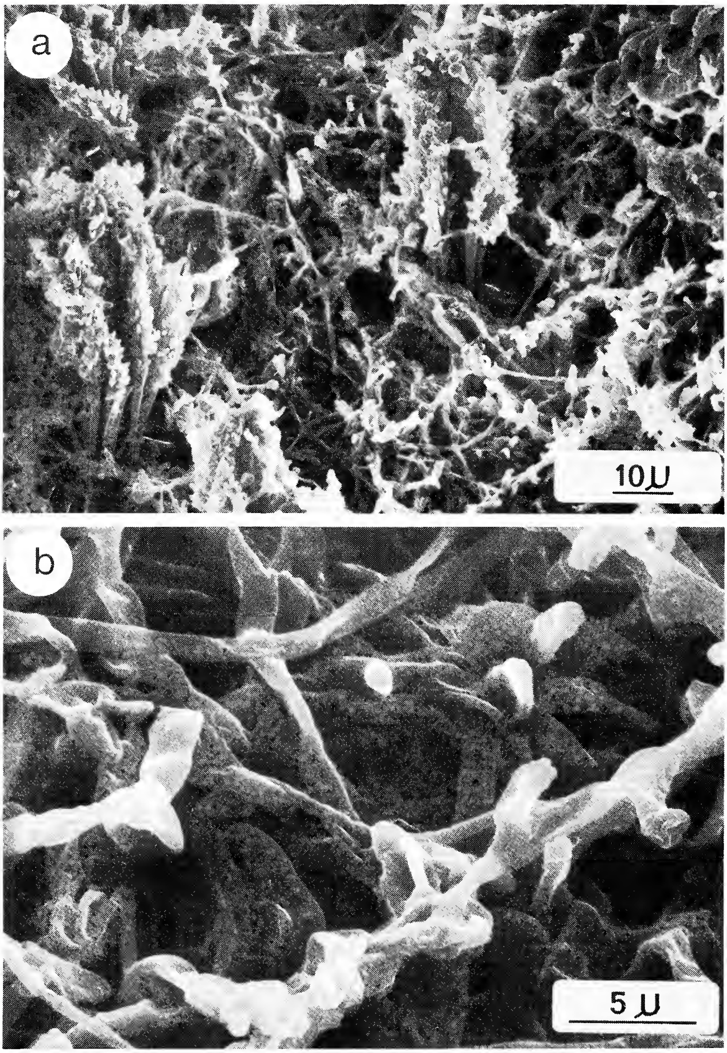

Fig. 9. *Z. pallens porrasi* (same individual as Fig. 8b). a. Heavily matted cephalic shield, showing tips of brush setae. b. Close-up of fibrous material.

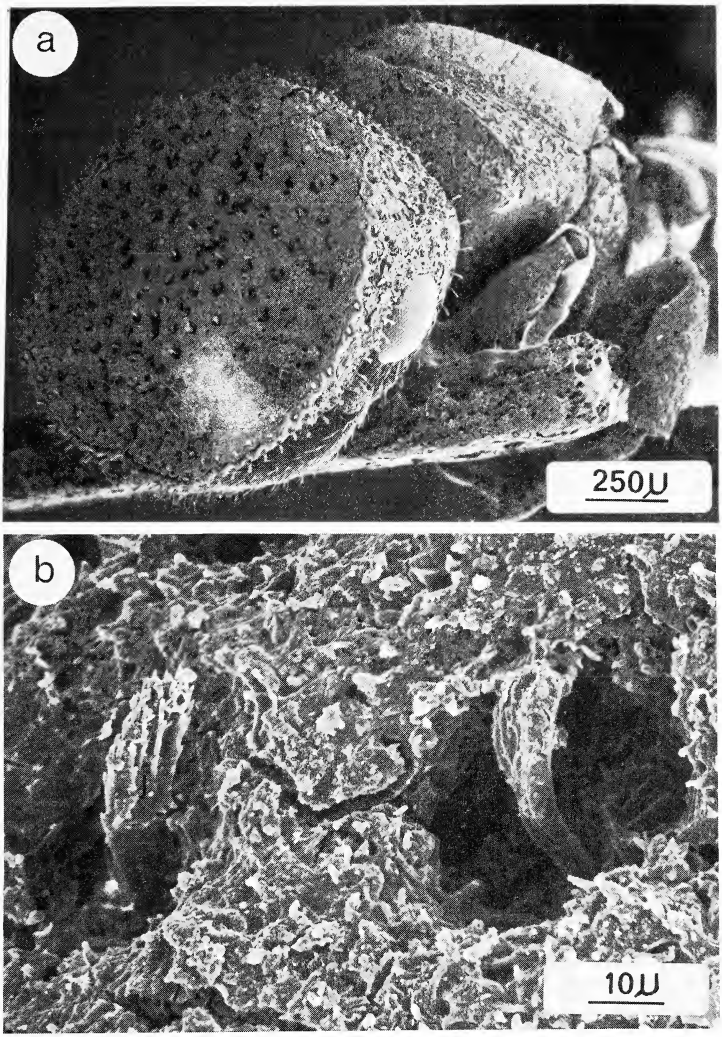

Fig. 10. *Z. setulifer* (Ancon, Panama). Queen. a. Head is heavily encrusted with material. b. Setae on head, with encrusting material.

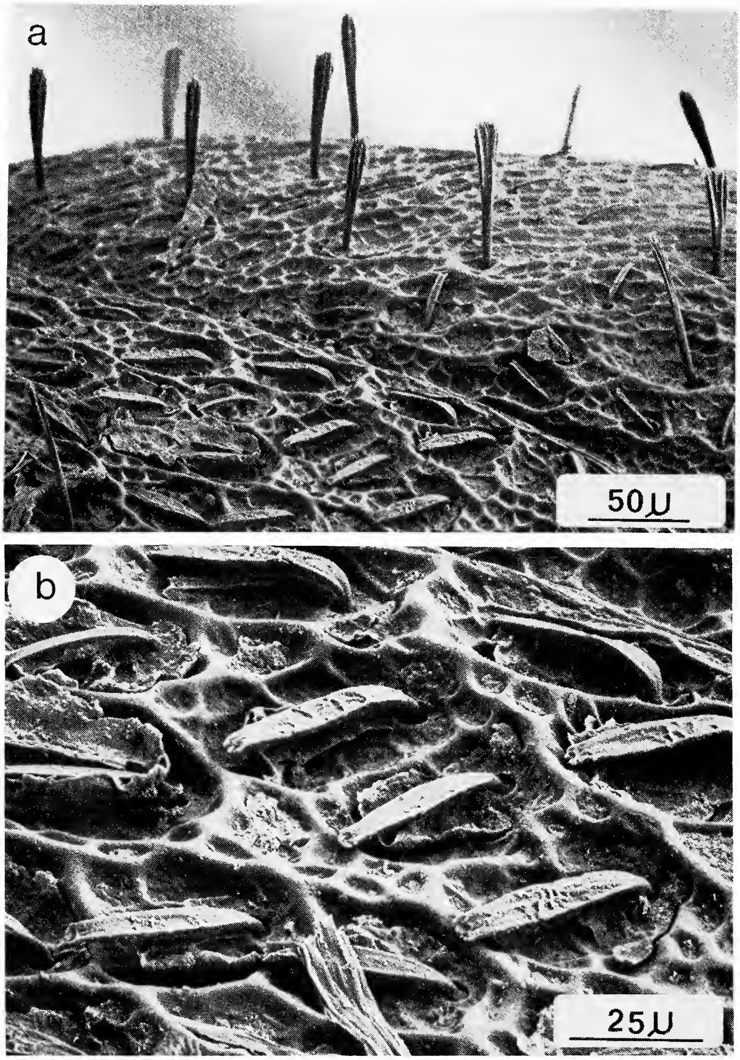

Fig. 11. *Z. setulifer* (same individual as Fig. 10). Thorax. a. Erect brush setae and second layer of holding setae appressed on surface. b. Holding setae.

ACKNOWLEDGMENTS

We thank W. M. Maddison for collecting the clean *Z. varians* specimens, and Ed Seling for valuable SEM work. Funds were provided by NSF Grants PCM 83-01763 and BNS 82-19060.

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ECOLOGICAL LIFE HISTORY OF *BAETISCA CAROLINA* TRAVER IN PANTHER CREEK, NICHOLAS COUNTY, WEST VIRGINIA (EPHEMEROPTERA: BAETISCIDAE)

By Daniel K. Pettry and Donald C. Tarter[1]

The main objective of this study was to elucidate the ecological life history of the mayfly *Baetisca carolina* Traver in Panther Creek, Nicholas Co., West Virginia. Additionally, multivariate discriminate analysis was used to separate *B. carolina* from the closely related *B. berneri.* Other authors, including Berner (1955, 1959), Pescador and Peters (1971, 1974), Lehmkuhl (1972), Chaffee and Tarter (1979), Morris et al. (1980) and Berner and Pescador (1980), have reported ecological studies on *Baetisca* species. Only a few investigators, including Smith (1935) and Traver (1931, 1937), have noted ecological information on *B. carolina.* Pettry and Tarter (1983) reported a relationship between body size and body coloration in *B. carolina* nymphs.

Taxonomy and Distribution

The endemic family Baetiscidae is monotypic, containing only the genus *Baetisca* (Walsh 1862). Traver (1931) described the nymph, subimago and imago of *B. carolina.* Traver (1937) described *B. thomsenae* which Berner later synonymized with *B. carolina.* Pescador and Berner (1981) proposed that *B. carolina* is part of a group that was pushed into or trapped in the ice-free streams of the Appalachians (Georgia, South Carolina, North Carolina, Tennessee and Virginia) during the Pleistocene glaciation and has remained in the cool mountain streams until the present time. Needham et al. (1935) reported *B. carolina* nymphs from the Morgantown, West Virginia vicinity.

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MATERIALS AND METHODS

The study area is Panther Creek of the Gauley River in Nicholas County, West Virginia. The total length is 16 km and the area of the drainage basin is 42.2 km ^{2} (Reger, 1921). The study site is located along Route 39 at the community of Nettie, 22.7 m from the junction of Route 19 at Summersville, West Virginia. The stream width averages 9 m and the water depth averages 46 cm. Substrate consists of sand, gravel, and small rocks. The most dominant species of the riparian forest are Hemlock, *Tsuga canadensis* (L.) Carr, and Rhododendron, *Rhododendron maximum* L.

Monthly samples of nymphs were collected from October 1981 to September 1982. The substrate was disturbed by kicking the rocks and a hand dredge (mesh size, 0.75 mm^2) was held downstream to collect the nymphs. The nymphs were preserved in 70 percent ethanol.

The water chemistry parameters were measured monthly with a Hach kit, Model AL-36-WR. Dissolved oxygen (mg/1), carbon dioxide (mg/1), alkalinity (mg/1 $CaCO_3$), total hardness (mg/1 $CaCO_3$), and pH were recorded throughout the study period. Water temperature was recorded monthly with a Taylor thermometer placed about 5 cm below the surface of the water.

Nymphal size classes were determined by length-frequency histograms arranged in 1 mm length groups. Body length from the tip of head (excluding genal spines) to the base of the caudal filament was measured to the nearest 0.1 mm using an ocular micrometer. Males, females, and immatures were combined for the histogram analysis. Head capsule width, measured to the nearest 0.01 mm with an ocular micrometer, was used as an index of growth. Monthly differences in nymphal head capsule widths were used to calculate the mean, range and two standard errors of the mean.

Five nymphs were randomly selected for each month for foregut analysis. The head was severed with microdissecting scissors and the thoracic shield was removed, thus exposing the foregut. The foregut was removed and its contents emptied onto a glass slide with an iodine solution as the mounting medium. The contents were examined under a Bausch and Lomb (430×) dissecting microscope containing a Whipple ocular grid. Five grids were randomly selected for examination from each nymph. The percentage composition for each food category (filamentous algae, plant detritus, mineral detritus, diatoms) was determined by figuring the percentage of small grid squares within each field that contained each of the different food categories.

Multivariate discriminant analysis, using the computer program BMDP7M (Dixon, 1981), was used to separate *B. carolina* from the closely related *B. berneri.* Thirteen morphological characters (shield length and width, head width, length of caudal filament, body length, prothoracic leg and claw length, mesothoracic leg tibia and femur length, mesothoracic leg tarsus and claw length, width of abdominal segment 10, labrum width) were measured on all nymphs (15) of *B. berneri* (holotype locality, Laurel Fork, West Virginia) and from five different geographical populations (Georgia, North Carolina, Tennessee, Virginia, and West Virginia - Panther Creek) of *B. carolina* nymphs (85). Two colormorphs from Panther Creek were included in the analysis. Males and females were grouped together in the analysis. Because of size variation within and among populations, regression analyses were applied to all measurements to remove the linearly related effects of size. Head width was used as the independent variable for regression of the other variables. The SAS General Linear Models procedure (Barr et al., 1976) produced residual values for each character; these values were then used as "size-free" variables. In the final analysis, the computer program (BMDP7M) generates canonical variates with maximum between group variance relative to their within group variance. The canonical variate means are plotted on the first two canonical axes, and analysis of variance describes significant differences between groups ($P < 0.01$). Using canonical functions, the posterior probability of each nymph belonging to its respective population is computed and classified accordingly.

In order to determine the fecundity of *B. carolina,* direct egg counts were made on adults. The dorsal body cavity of ten females (four imagos and six subimagos) was opened longitudinally with microdissecting scissors. The eggs were carefully removed, placed in a Petri dish, and counted under a Bausch and Lomb dissecting microscope. The regression of fecundity on body length was calculated and a coefficient of correlation was determined. The diameter of 50 eggs per female was measured with an ocular micrometer in a dissecting microscope to the nearest 0.01 mm.

RESULTS AND DISCUSSION

Water Quality. Dissolved oxygen concentration ranged from 8 (May and July) to 13 mg/l (December); the mean was 11.0 mg/l. The mean hydrogen ion concentration (pH) was 8.5; a range of 7.0 (June) to 10.0 (August). The carbon dioxide level was 0.0 mg/l during all months except August (15.0). Total hardness ranged from 34.2 (December–April) to 102.6 mg/l (August); the mean was 48.5 mg/l. The mean annual water temperature during the study period was 9.8 C; the range was −1 (December) to 19.0 C (May, June, September).

NYMPHAL STAGE

Foregut Analysis. The nymphs are detritivorous with 68.5 percent of the diet composed of plant detritus. Plant detritus was greatest during the months of December through May. Mineral detritus, probably ingested accidentally, was regularly observed in the foregut every month ($\bar{X} = 21.7\%$). Diatoms, usually *Cymbella* and *Navicula,* comprised 8.9% of the diet. They increased during the months of July through October. Filamentous algae, mainly *Oedogonium* and *Oscillatoria,* made up about one percent of the diet.

Chaffee and Tarter (1979) noted that the nymphs of *B. bajkovi* (= *lacustris*) are detritivorous with 65.3 percent of the diet composed of plant and leaf detritus. The nymphs of *B. berneri* are detritivorous with 74.5 percent of the diet made up of organic and mineral detritus (Morris et al., 1980).

Development. Monthly length-frequency histograms indicated a one year (univoltine) life cycle (Figure 1). The smallest nymph (1.3 mm) was collected in September and the largest nymph (10.9 mm) was collected in late April.

Univoltine life cycles were reported for *B. rogersi* (Pescador and Peters, 1974), *B. berneri* (Morris et al., 1980) and *B. bajkovi* (= *lacustris*) (Chaffee and Tarter, 1980).

The monthly progression of mean head widths for male and female nymphs is illustrated in Figure 2. Male nymphs showed the greatest growth in April (28%) and July (27%). Female nymphs showed the greatest growth in April (16%) and July (34%). Little or

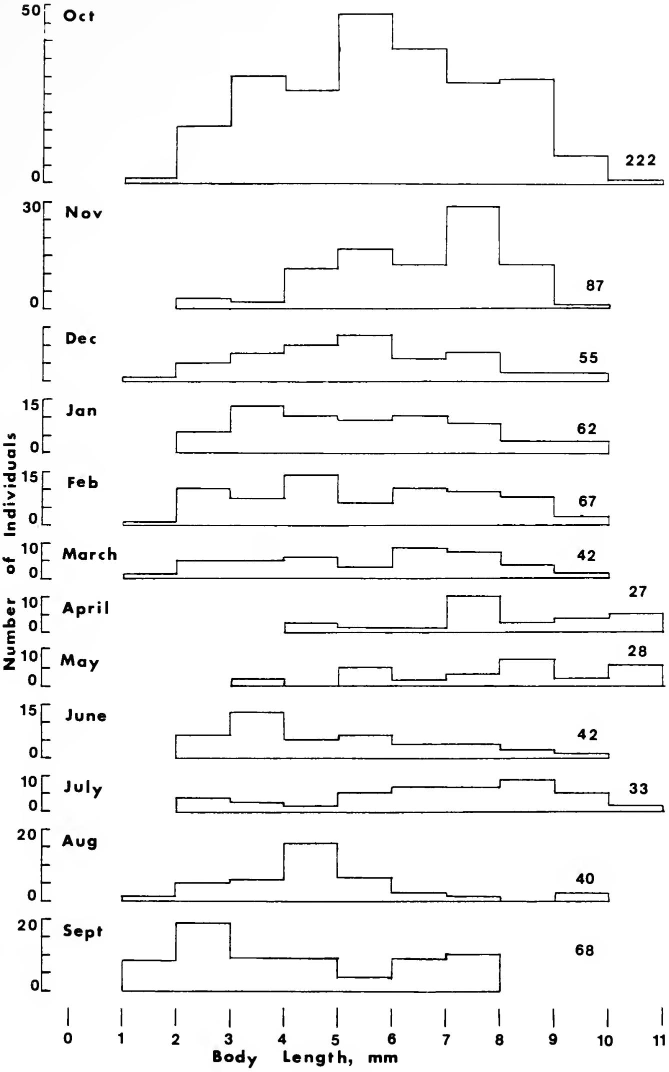

Figure 1. Length-frequency histograms showing the monthly distributions of *Baetisca carolina* nymphs from Panther Creek, Nicholas County, West Virginia. The number of individuals collected is indicated at the right.

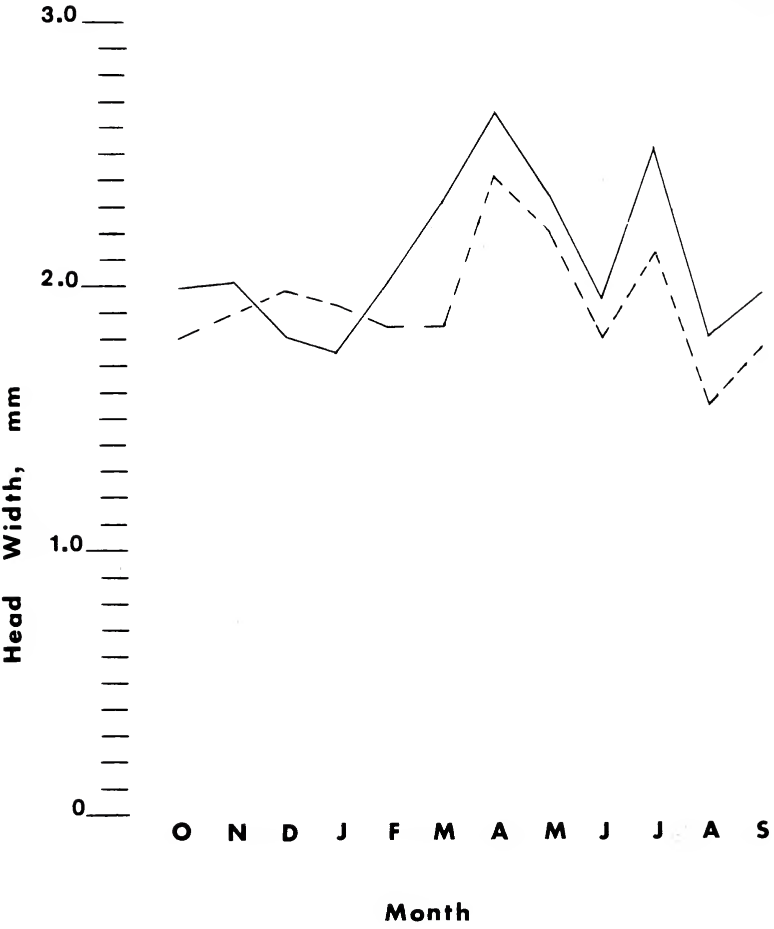

Figure 2. Growth of *Baetisca carolina* nymphs based on mean monthly head widths. Solid line represents female growth; broken line represents male growth.

no growth occurred in the winter months, but as the water temperature began to rise, growth began to occur. Nymphs showed the greatest head width in April, while they exhibited a decline in mean head width in May and June. This decline is due to the emergence of the larger nymphs. The large growth rate in July is probably due to nymphs growing in preparation for a second emergence in August. These data, along with data from nymphal exuviae and length-frequency histograms, support the viewpoint of bimodal emergence and a univoltine life cycle.

The population range diagram shows the wide range of head widths that occurred each month (Figure 3). Immature nymphs that were too small to be sexed are not represented in the diagrams. The largest head width for males was 2.9 mm, and for females 3.4 mm; both occurred in April. Size superiority exhibited by females is shown in Figures 2 and 3.

Morphological Analysis. Results from the discriminant analysis of all *B. carolina* popultions are presented in Figure 4. The first two canonical axes were responsible for 83.2 and 8.5 percent of the total dispersion, respectively. One hundred percent dispersion was obtained when four axes were utilized. The most influential characters providing separation on the first axis, in order of increasing weight, were: mesothoracic leg femur length; body length; shield width; and mesothoracic leg tarsus length. Overlap of canonical coordinates for individuals of different geographical populations indicates that substantial morphological variation exists within populations. Canonical coordinates for populations on the first (horizontal) axis generally followed a north-south geographical cline.

The light and dark colormorphs from Panther Creek showed extensive overlap, and a relatively high percentage of individuals were classified incorrectly between these two groups relative to the other groups in this analysis. This further indicated that one species of *Baetisca* nymphs exists in Panther Creek, rather than two species as was assumed at the onset of this study.

Baetisca berneri nymphs from the holotype locality showed considerable morphological similarity to the Virginia and Tennessee populations of *B. carolina.*

Pescador and Berner (1981) noted morphological variation among geographical populations of *B. carolina* nymphs. They reported that nymphs from the northern extension of their range have a broader mesonotal shield and shorter lateral spines than nymphs from the southern extension of their range. The nymphs from Panther Creek exhibited a broad mesonotal shield and short lateral spines. Additionally, it was observed in this study that nymphs from the northern extension of their range exhibited shorter genal spines on the head.

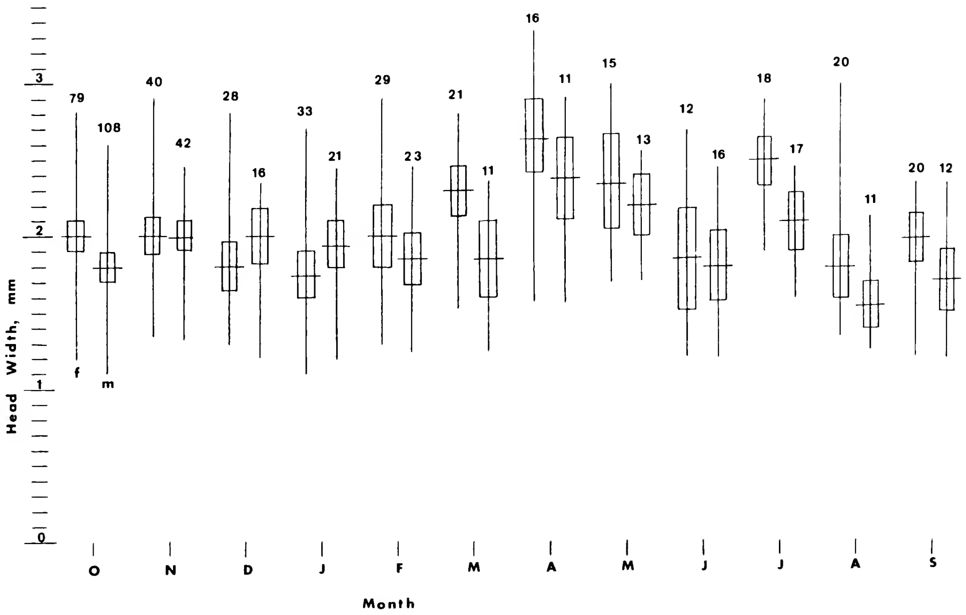

Figure 3. Population range diagram showing monthly head width variations of *Baetisca carolina* nymphs from Panther Creek, Nicholas County, West Virginia. Vertical lines = range, horizontal lines = mean, open rectangle = two standard errors of the mean, f = female, and m = male.

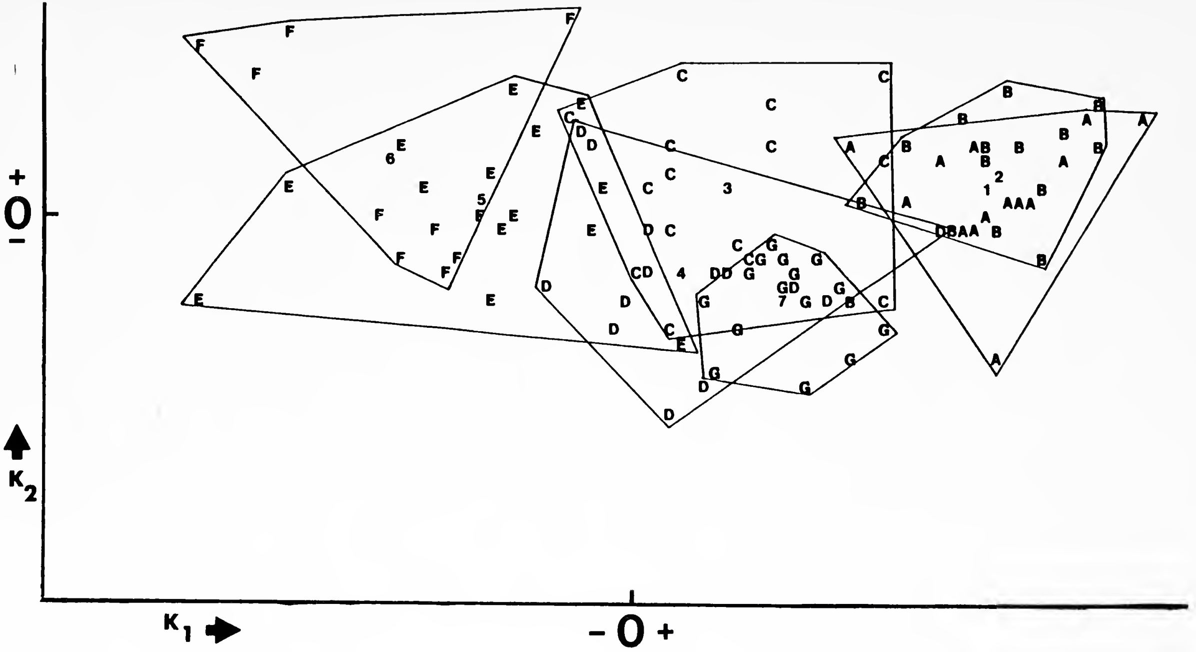

Figure 4. Variates for nymphs of *Baetisca carolina* and *B. berneri* plotted on the first and second canonical axes. Individual nymphs are represented by letters, and numbers represent canonical variate means for the population. A, light colormorph of *B. carolina* from Panther Creek; B, dark colormorph of *B. carolina* from Panther Creek; C, *B. carolina* nymphs from Virginia; D, *B. carolina* nymphs from Tennessee; E, *B. carolina* nymphs from North Carolina; F, *B. carolina* nymphs from Georgia; G, *B. berneri* nymphs from the holotype locality, Laurel Fork, Mingo County, West Virginia.

Nymphal Coloration. Considerable inconsistency was noted in the regularity of the coloration exhibited by *B. carolina* nymphs during the monthly collections (Pettry and Tarter, 1983). During fall and winter months, the majority of the nymphs exhibited a dark body coloration, with dark pigmentation on the legs and on the ventral surface of the head, thorax and abdomen. In spring and summer, as the nymphs grew and approached the emergence period, the dark pigmentation diminished among most of the nymphs. These monthly increases and decreases in percentages of light individuals corresponded to the monthly increases and decreases in the growth pattern shown by nymphs, indicating that body coloration is associated with body size ($r = 0.87$).

Traver (1931) noted considerable color variation in *B. carolina* nymphs in the original description of the species. Also, Traver (1937) noted color variation in *B. thomsenae* (= *carolina*) nymphs. This study confirms Traver's original observations, and additionally indicates that two colormorphs exist in Panther Creek.

ADULT STAGE

Field Studies. Nymphs with developing wing pads were first observed in Panther Creek on April 23. Emergence in the field began between May 15 and 19 and continued through the end of August.

Traver (1931) reported emergence of *B. carolina* in April and May. Traver (1937) observed *B. thomsenae* (= *carolina*) in May and June. The emergence period data reported for other *Baetisca* species are as follows: Pescador and Peters (1974), *B. rogersi,* April through early July; Morris et al. (1978), *B. berneri,* May and early June; Chaffee and Tarter (1979), *B. bajkovi* (= *lacustris*), May.

Exuviae were collected during the emergence period to determine the yearly pattern of emergence. These data indicated a bimodal emergence pattern. The primary peak occurred in May when emergence began, with the other peak in August near the end of the emergence period. The data for early June may not correctly represent the actual emergence pattern. Heavy rains were recorded during this time, 3.85 inches (97.8 mm) fell during the first week of June and undoubtedly washed away nymphal exuviae. The water level of Panther Creek rose four feet during this time. The effect of high water on emergence is unknown; however, emergence continued

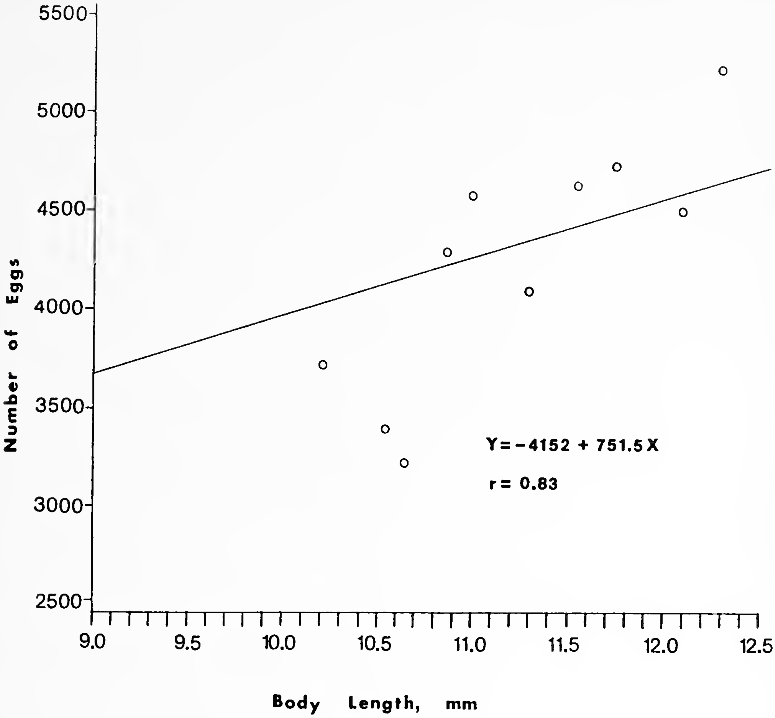

Figure 5. Fecundity-length regression analysis and the coefficient of correlation for adult females of *Baetisca carolina,* Panther Creek, Nicholas County, West Virginia.

since small numbers of exuviae were found. Even though these data can be adversely affected by environmental conditions such as rain, the general emergence pattern is supported by growth data of the nymphs. The two peak emergence periods corresponded to the two growth periods exhibited by the nymphal population (Figure 2).

Rearing and Emergence. Last instar *B. carolina* nymphs were reared in the laboratory beginning in late April. Only one subimago, a female, emerged in the laboratory. This occurred before 1:00 p.m. on May 6, and the subimago died before transforming into an imago.

Subimagos collected in the field successfully completed the transformation to the imaginal stage in the laboratory. Duration of the subimaginal stage of *B. carolina* was recorded for two individuals at laboratory temperatures. A female subimago transformed in 24 hours and 27 minutes, while a male subimago transformed in 20 hours and 29 minutes. The male imago lived 48 hours.

Subimaginal transformation data for other species of the genus *Baetisca* have been reported by other authors. Traver (1931) reported that the subimago stage of *B. carolina* varied between 21 and 24 hours under warm temperatures, while enduring up to 50 hours during cold weather. Berner (1955) observed *B. escambiensis* subimagos transforming to imagos in 40 to 44 hours. Pescador and Peters (1974) reported that the duration of the subimaginal stage of *B. rogersi* ranged from 12 to 30 hours, averaging 21 hours and 21 minutes. Morris et al. (1980) observed that the duration of the subimaginal stage of *B. berneri* was approximately 24 hours. Chaffee and Tarter (1979) reported that *B. bajkovi* (= *lacustris*) subimagos transformed into imagos 13 to 25 hours later.

Fecundity. Direct egg counts for ten *B. carolina* adults ranged from 3271 to 5274 per individual, averaging 4280. A correlation coefficient between fecundity and body size was determined to be 0.83 (Figure 5). Pescador and Peters (1974) reported egg counts from *B. rogersi* adults ranged from 1500 to 2727 per individual, averaging 2168. Morris et al. (1980) reported egg counts from *B. berneri* adults ranged from 1001 to 2375 per individual, averaging 1899. Chaffee and Tarter (1979) reported egg counts from *B. bajkovi* (= *lacustris*) adults ranged from 1508 to 3158 per individual, averaging 2361.

Egg Size. The eggs of *B. carolina* have an average diameter of 0.17 mm. Individual eggs ranged from 0.14 to 0.21 mm. Egg diameter measurements from SEM photomicrographs showed ranges from 130 to 160 microns, averaging approximately 145 microns.

Smith (1935) reported the egg diameter of *B. carolina* and *B. obesa* to be 0.18 mm. Pescador and Peters (1974) reported that newly laid eggs of *B. rogersi* had a diameter of 0.1 to 0.2 mm, while mature eggs had a diameter of 0.2 to 0.3 mm. Morris et al. (1980) reported that eggs of *B. berneri* had an average diameter of 0.18 mm. Chaffee and Tarter (1979) reported that eggs of *B. bajkovi* (= *lacustris*) had average measurements of 0.15 × 0.19 mm.

SUMMARY

The ecological life history of the mayfly *Baetisca carolina* Traver was studied in Panther Creek, Nicholas County, West Virginia,

from October 1981 to September 1982. Nymphs were primarily collected from a sand and small stone substrate. Length-frequency distributions indicate a one year (univoltine) life cycle. Male and female nymphs exhibited the greatest growth in April and July. Females exhibit a definite size superiority. Monthly foregut analysis indicates that nymphs are primarily detritivouous, with other components of the diet including diatoms and filamentous algae. Two colormorphs, light and dark, are present in the population. As nymphal size increases, a greater percentage of the population exhibits light body coloration. Multivariate discriminant analysis was used to separate *B. carolina* from the closely related *B. berneri.* Subimagos emerge in the field from mid-May through the end of August. A bimodal pattern of emergence was observed. Imagos emerged approximately 24 hours later. Direct egg counts ranged from 3271 to 5274 per female; the average was 4280. The correlation coefficient between fecundity and body size was 0.83.

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PHYLOGENETIC IMPLICATIONS OF GROOMING BEHAVIOR IN COCKROACHES (INSECTA: BLATTARIA)*

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Introduction

The use of behavioral data for the investigation and delineation of evolutionary relationships has been increasingly heuristic (Evans, 1952; Speith, 1952; Alexander, 1962; etc.). In insects, grooming behavior seems particularly useful because it is a widespread and prominent part of their behavioral repertory. Comparative studies of several orders have been based on grooming behavior (Szymanski, 1918; Heinz, 1949; Gangwere, 1958; Jander, 1966; Farish, 1972; Valentine, 1973; Valentine and Glorioso, 1979). Lipps (1973) provides an excellent review of grooming literature.

The cockroaches are a diverse group with an extensive nontaxonomic literature. There are many descriptions of the general biology of the order (Gould and Deay, 1938; Roth and Willis, 1954, etc.) and of particular species (Qadri, 1938; Rau, 1940; Dow, 1955; Heslop and Ray, 1959, etc.). Roth and Willis (1954) and McKittrick (1964) summarize many such papers, especially on biology. Our taxonomy follows McKittrick (1964), and is summarized in Table 1.

Unspecified grooming behavior of cockroaches is mentioned by Patton (1941) and Burkholder (1965). Others discuss grooming of particular body parts (Haber, 1920; Mote, Wilcox, and Davis, 1926; Roth and Willis, 1952 and 1954; and Eisner, 1961). A few authors are more detailed: Gangwere (1958), Yoshikawa (1958), Eaton and Farley (1969), and Lipps (1973). The most complete description of roach grooming is by Turner (1913), who describes in excellent detail antennal, palpal, and leg cleaning using the mouth, and the use of a leg to rub the base of the antenna and dorsal surface of the abdomen, all in a roach he called *Periplaneta orientalis,* now placed in the genus *Blatta.*

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The above references give a very incomplete picture of roach grooming. Gangwere (1958) and Lipps (1973) discuss roaches from a generalized view, but the species are not named nor are their individual repertories described. No work investigates the order and tries to characterize grooming patterns within it, and no work describes the complete repertory of even one species.

METHODS

Grooming behavior was recorded during 154 hours of observations on 23 species representing 20 genera and four families of Blattaria (see Table 1). The grooming movements performed by each species are listed in Tables 2 and 3. Terminology follows Valentine and Stouffer (in preparation). Since there are over 3,500 species of cockroaches, a few exceptions to the family patterns we present are to be expected.

Small and large species were maintained in 9 and 12 cm white cardboard medical specimen cups with clear plastic lids. Lightly crumpled paper provided cover, and bits of dog biscuits and small water-soaked cotton balls provided food and water. *Cryptocercus punctulatus* was maintained in a 9 cm cup containing pieces of the log in which it was discovered. This debris provided food and was lightly misted every other day.

Each common species was observed for at least four hours. The longer observation periods listed in Table 1 provided no additional behaviors. Monospecific groups of 5 to 7 individuals were observed for 10 minutes in the maintenance cup with the paper removed. Then, single roaches were observed for not less than 20 minutes. A new cup was used for each species. Species 20 mm long and larger were observed directly; those less than 15 mm were observed with a dissecting microscope. Observations were made at most hours of the day or night, either in artificial or existing natural light. In the cases of *Blaberus craniifer* and *Cryptocercus punctulatus,* the light was fitted with a red cellophane filter. After grooming behavior of groups and individuals had been recorded for at least four hours for a particular species, further grooming was elicited by dusting 3 to 5 roaches of each species with household flour and observing these individuals for an average of an additional 20 minutes.

Table 1. Number of individuals and time spent observing each species

	No. individuals observed	No. hours group observed	No. hours ind. observation	Total number hours observ.
CRYPTOCERCIDAE				
Cryptocercus punctulatus Scudder	2	0	12	12
BLATTIDAE				
Blattinae				
Blatta orientalis Linnaeus	7	1	6	7
Periplaneta australasiae (Fabricius)	6	1	5	6
Periplaneta brunnea Burmeister	6	1	5	6
Periplaneta americana (Linnaeus)	6	1	5	6
BLATTELLIDAE				
Plecopterinae				
Supella longipalpa (Fabricius)	7	1	6	7
Blattellinae				
Blattella germanica (Linnaeus)	7	1	6	7
Xestoblatta immaculata Hebard	5	1	4	5
Nyctiborinae				
Nyctibora lutzi Rehn & Hebard	6	1	5	6
BLABERIDAE				
Zetoborinae				
Schultesia lampyridiformis Roth	12	2	5	7
Blaberinae				
Eublaberus posticus (Erichson)	6	1	5	6
Archimandrita tessellata Rehn	5	1	7	8
Byrsotria fumigata (Guèrin)	4	3	0	3
Blaberus craniifer Burmeister	4	2	8	10
Pycnoscelinae				
Pycnoscelus indicus (Fabricius)	6	1	4	5
Pycnoscelus surinamensis (Linnaeus)	8	2	6	8
Diplopterinae				
Diploptera punctata (Eschscholtz)	7	2	5	7
Panchlorinae				
Panchlora nivea (Linnaeus)	~30	3	0	3
Oxyhaloinae				
Leucophaea maderae (Fabricius)	12	3	8	11
Nauphoeta cinerea (Olivier)	7	1	6	7
Jagrehnia madecassa (Saussure)	6	1	4	5
Gromphadorhina portentosa (Schaum)	6	2	8	10
Perisphaeriinae				
Gyna sculpturata Shelford	~24	2	0	2
		34	116	154

RESULTS

CLEANING. Involves chewing movements of the mouthparts.

Antenna Clean: Two major modes of antenna cleaning were observed: *Assisted* and *Unassisted.* The *Assisted* mode is subdivided into three submodes: *Bipedal, Contralateral,* and *Ipsilateral.*

1. *Assisted.*

a) *Bipedal:* This movement was observed only in *Periplaneta brunnea* of the family Blattidae. Both forelegs simultaneously move upward and grasp one antenna as it and the head are bent downward. The head is then raised and the antenna pulled into the mouth by the crossed forelegs.

b) *Contralateral:* This movement was confined to and observed throughout the families Cryptocercidae, Blattidae, and Blattellidae. The antenna is deflected downward as the contralateral foreleg moves upward and contacts the antenna. The head is raised and the antenna is pulled into the mouth by the leg.

c) *Ipsilateral:* Alternating with *Unassisted,* this movement was observed exclusively in the family Blaberidae. It resembles *Contralateral* except that the ipsilateral foreleg is used.

2. *Unassisted.*

Alternating with *Ipsilateral,* this method was observed exclusively in the Blaberidae. The antenna deflects into the mouth using its intrinsic musculature. There is no leg assistance, but the antenna may occasionally be trapped against the substrate.

Once the antenna is in the mouth, two aspects of antenna cleaning are constant in all species: a single antenna is cleaned at a time, and in species assisting with the foreleg, the antenna is released by the leg as it is grasped by the mouthparts.

Palpus Clean: Palpal cleaning was observed in all species. The labial and maxillary palpi are cleaned similarly. A single palp is curled directly into the mouth from the normal resting position. Either the entire palp or only the tip is cleaned.

Leg Clean: With three exceptions, all species clean all three legs. *Cryptocercus punctulatus* performs no leg cleaning, and two species in the family Blaberidae, *Pycnoscelus surinamensis* and *Leucophaea maderae,* were never observed to clean the hindleg.

1. *Foreleg Clean:* A foreleg is raised and extended forward as the head turns to reach it. The body is supported in a normal resting position by the remaining five legs. The mouthparts contact the leg

at any point and clean it by slowly chewing from the point of contact to the end of the tarsus.

2. *Midleg Clean:* As the ipsilateral foreleg is raised and the head turned backward, a midleg is raised and extended forward under the body and raised foreleg. The body is supported by the ipsilateral hindleg positioned slightly farther forward than usual, the three opposite legs, and sometimes by the side of the abdomen.

3. *Hindleg Clean:* This movement resembles *Midleg Clean.* The foreleg is raised, followed closely by the midleg as the head dips down and back, and the hindleg swings forward underneath the raised fore- and midlegs. The tip of the abdomen is curled laterally toward the head, and the body is supported in a fourpoint stance by the curled abdomen and the three legs of the opposite side. If only the tibial apex or tarsus is cleaned, the midleg may remain in contact with the substrate.

Certain features are common to all leg cleaning in all species. The leg is usually raised from the substrate, and is always held ventrally. Movement of the leg relative to the head is always posterior, back and forth movement in the mouth did not occur. Cleaning may begin at any level from coxa to tarsus, and once begun continues from point of contact to the end of the tarsal claws. The leg or parts of the leg may be cleaned once or several times in succession. There is no set order for legs to be cleaned, and leg cleaning may be interspersed with grooming of other body parts.

Body Clean: Grooming the body with the mouthparts has only two modes in roaches.

1. *Sternum Clean:* Sternal cleaning is well-distributed throughout the families and genera (see Table 2). The body is slightly raised by extension of the legs, and the forelegs are widely spaced. The head bends down under the body until the mouthparts reach the coxae of the forelegs. These and the area between them are cleaned. Similar cleaning of the sternal and coxal area of the meso- and metathorax did not occur.

2. *Pronotum* or *Wing Edge Clean:* This is a much rarer movement than *Sternum Clean,* and was observed infrequently in only six species (see Table 2). The head is turned to the side and either the edge of the pronotum or the wing base just behind it is cleaned.

RUBBING. Involves progressive contact of body parts with other parts, or rarely, with the substrate.

Table 2. Cleaning Movements of Roaches

	CLEANING Antenna Clean	Palpus Clean	Foreleg Clean	Midleg Clean	Hindleg Clean	Sternum Clean	Pronotum or Wing Clean
CRYPTOCERCIDAE							
Cryptocercus punctulatus	C	x					
BLATTIDAE							
Blatta orientalis	C	x	x	x	x		x
Periplaneta australasiae	C	x	x	x	x		
Periplaneta brunnea	B,C	x	x	x	x		
Periplaneta americana	C	x	x	x	x		*
BLATTELLIDAE							
Supella longipalpa	C	x	x	x	x	x	x
Blattella germanica	C	x	x	x	x	x	
Xestoblatta immaculata	C	x	x	x	x		x
Nyctibora lutzi	C	x	x	x	x		*
BLABERIDAE							
Schultesia lampyridiformis	U	x	x	x	x	x	
Eublaberus posticus	U,I	x	x	x	x		
Archimandrita tessellata	U,I	x	x	x	x		
Byrsotria fumigata	U	x	x	x	x		
Blaberus craniifer	U	x	x				x
Pycnoscelus indicus	U,I	x	x	x	x		
Pycnoscelus surinamensis	U,I	x	x	x		x	
Diploptera punctata	I	x	x	x	x	*	
Panchlora nivea	U,I	x	x	x	x		
Leucophaea maderae	I	x	x	x		x	
Nauphoeta cinerea	I	x	x	x	x	x	
Jagrehnia madecassa	I	x	x	x	x		
Gromphadorhina portentosa	I	x	x	x	x	x	
Gyna sculpturata	U	x	x	x	x	x	x

Note: U - unassisted
C - assisted -contralateral
I - assisted - ipsilateral
B - assisted - bilateral
*indicates movements performed only after application of flour

Antenna-Foreleg Rub: This movement was performed by all species observed except *C. punctulatus.* The basal segments of the antenna not reached by the mouthparts during *Antenna Clean* are groomed by rubbing. The base of the antenna is caught in the crook of the tibio-femoral joint, and the foreleg very deliberately and slowly moves down in a scraping motion. This movement is often followed by *Foreleg Clean,* but is not consistently combined with *Antenna Clean.*

Head-Foreleg Rub: Two forms were observed (see Table 3).

1. *Eye-Rub:* This movement was observed in all species but *C. punctulatus.* The foreleg is raised and the area of the tibio-femoral joint contacts the eye just below the antennal base. The leg moves straight down in a short, sharp rub reaching most of the eye surface.

2. *Low Face Rub:* This movement was observed in all species. It is similar to *Eye Rub,* yet distinct. The area of the head contacted is restricted to the lateral mouth region.

Prothorax-Foreleg Rub: Individuals of a single species, *Supella longipalpa,* raise a foreleg so that the femur contacts the lateral margin of the prothorax and performs a quick series of two to five posterior strokes.

Abdomen-Hindleg Rub: This movement is well-distributed throughout the families. Only two blaberid species, *Archimandrita tessellata* and *Gromphadorhina portentosa,* were not observed to perform some type of abdomen rub. Dr. Louis M. Roth, in a most useful review of this manuscript, informs us that some other blaberids omit abdomen or wing rubs. He points out that the bodies of *Laxta* females are often solidly caked with dirt, and the tegmina of *Therea nuptialis* have small setae which retain debris and make the insects less conspicuous.

A hindleg is used to rub the dorsal, ventral, and/or lateral surfaces of the abdomen. The movement is always unilateral: an insect may alternate sides rapidly, but only one hindleg ever touches the body at one time. The direction of the rub is posteriad. Often, but not consistently, abdomen rubbing is followed by hindleg cleaning.

Cercus-Hindleg Rub: Cercus rubbing is present in most of the species observed (Table 2). *Cercus-Hindleg Rub* is a separate and elaborate movement quite distinct from abdomen rubbing. The ipsilateral hindleg rubs any part of the cercus; at times, only the very tip. The abdomen may or may not be curled toward the rubbing leg.

Table 3. Rubbing and positioning movements of roaches

	RUBBING										POSITIONING
	Antenna-Foreleg Rub	Head-Foreleg Rub	Prothorax-Foreleg Rub	Wing-Midleg Rub	Abdomen-Hindleg Rub	Cercus-Hindleg Rub	Wing-Hindleg Rub	Hindleg-Hindleg Rub	Abdomen-Substrate Rub	Wing-Abdomen Rub	Wing Flip
CRYPTOCERCIDAE											
Cryptocercus punctulatus		x			x						
BLATTIDAE											
Blatta orientalis	x	x			x	x				x	
Periplaneta australasiae	x	x			x	x					
Periplaneta brunnea	*	x			x	x					
Periplaneta americana	*	x			x	x				x	
BLATTELLIDAE											
Supella longipalpa	x	x	x	x	x	x	x	x			
Blattella germanica	x	x		x	x	x			x		
Xestoblatta immaculata	x	x		x	x	x					
Nyctibora lutzi	*	x			x	x	*			*	
BLABERIDAE											
Schultesia lampyridiformis	x	x			x			x			x
Eublaberus posticus	*	x			x	*					*
Archimandrita tessellata	x	x								*	*
Byrsotria fumigata	x	x			x	x					
Blaberus craniifer											
Pycnoscelus indicus	x	x			x	x					
Pycnoscelus surinamesis	x	x			x	x				x	x
Diploptera punctata	x	x		x	x				x		
Panchlora nivea	x	x			x	x					
Leucophaea maderae	x	x			x	x				x	x
Nauphoeta cinerea	x	x			x	x				x	x
Jagrehnia madecassa	x	x			x	x				x	
Gromphadorhina portentosa	x	x									
Gyna sculpturata	*	x			x	*					

Some individuals of the more primitive species spend up to two minutes engaged solely in this grooming movement.

Abdomen-Substrate Rub: Two of the smaller species (length less than 15 mm), *Blattella germanica* and *Diploptera punctata,* were observed to occasionally twist the abdomen sideways and drag the edge and part of the dorsal surface against the substrate. The wings are maintained in their normal position or raised a bit, resulting in only the abdomen contacting the substrate.

Hindleg-Hindleg Rub: Individuals of only two species, *S. longipalpa* and *Schultesia lampyridiformis,* place one hindleg slightly further under the body than normal and rub it several times from tibia to tarsus with rapid strokes of the tarsus of the opposite hindleg. Often the movement is reversed, and the other hindleg is rubbed similarly.

Wing-Hindleg Rub: A few individuals of three species, *S. longipalpa, Nyctibora lutzi,* and *L. maderae,* rub the dorsal surface of the closed wings with the tarsus of a hindleg, while the abdomen is in its normal resting position beneath the wings. This movement was always performed while *Abdomen-Hindleg Rub* was in progress.

Wing-Abdomen Rub: Several species in the families Blattellidae and Blaberidae (see Table 2) rub the underside of the closed wings vigorously and elaborately with the abdomen. There are four separate techniques. First, the abdomen may be rubbed from side to side in its normal position below the wings. Second, the abdomen may be flexed strongly, concave to the substrate, and the wings rubbed with only the central bent portion (of the abdomen). Third, the abdomen may be flexed strongly, convex to the substrate, and the tip of the abdomen rubbed in a circular or lateral motion against the underside of the wings. Finally the abdomen may be twisted so that only the lateral edge contacts the wings. When performed, these movements were almost always of longer duration than other grooming, and were usually performed between, or even during periods of extensive locomotion.

Wing Flip: In Blaberidae, a period of wing flipping was sometimes observed in conjunction with *Wing-Abdomen Rub.* The flipping could also be performed alone. Bouts last two to five minutes, with wings either flipped vertically or horizontally.

DISCUSSION

Prior to discussion of specific grooming movements, several generalized comments can be made regarding all species observed.

Except for *Abdomen-Substrate Rub* observed in two species, grooming in roaches is restricted to cleaning, or rubbing one body part with another. Other orthopteroids are known to utilize droplets of fluid in grooming (Allard, 1929). Though some individuals observed in this study placed droplets of clear fluid from the mouth onto the substrate, none utilized the droplet in grooming.

Though isolated grooming movements are often interspersed with periods of general activity, the most extensive and complete bouts are nearly always preceded by periods of relative quiet lasting two to seven minutes. No set sequence of grooming movements is discernible in any individual or species. Any combination or sequence of movements is possible, including repetitions of a particular movement. Larger species ($\geqslant$ 45 mm) display a strong tendency to perform all grooming movements less frequently than the smaller species.

Generally, the use of flour as a stimulus has its greatest effect in simply increasing the frequency of movements in the next grooming bout. However, some species perform movements in the presence of flour which are not observed in its absence. Such movements are noted in Table 2 by an asterisk. Movements that are most consistently affected are basal antennal rubbing, abdomen rubbing, wing-abdomen rubbing, and wing flipping.

An overall inhibiting factor is the presence of barometric low pressure. In advance of fronts and when under low pressure cells, all species exhibit a tendency to remain relatively quiet.

With a single exception, all species quickly became habituated to sunlight and artificial light. Grooming activity is readily performed at any hour of the day or night, even in bright light. *Blaberus craniifer* presents the single exception. In this species, the only grooming performed in daylight or lamplight was antenna and palp cleaning. Whether or not dusted with flour, when exposed to light the animal cleaned only the antennae and palpi, then arranged itself with the head, antennae, and legs drawn under the pronotum and wings, and sat unmoving until darkness fell or it was placed in a dark environment. During dark hours, the animal could be heard moving vigorously around the cup. On numerous occasions, the appearance of the roach's body the next day clearly indicated that leg cleaning and abdomen, cercus, and basal antenna rubbing had been performed. Using a red filter, two additional movements were observed: *Foreleg* and *Pronotum Clean.* Unfortunately, the single specimen died before a complete repertory was observed.

Ordinal Patterns.

The most striking characteristic of grooming in the order Blattaria is the remarkable stereotypy of the movements. In grooming a particular structure, one method usually suffices for all species. Despite varied habitats as living in loose sand, or flowers, or in bird nests (Roth, 1973), roaches groom legs, palpi, head, and abdomen in the same way.

Stereotyped methods and modes of grooming may be explained by considering the generalized anatomy of the group and the natural habitats of the species. The cockroaches are a very ancient order little changed in morphology since their time of dominance in the Carboniferous Period. Fossil and contemporary roaches are anatomically very similar. Since extant species are not substantially different in external morphology from either ancestral species or each other, there has been little or no pressure to evolve new grooming patterns to deal with specialized anatomical constraints. Also, roaches are cosmopolitan in their distribution and superficially diverse in their habitats. Unlike interstitial Diplura (Valentine and Glorioso, 1979), none of these habitats places undue physical restrictions on the animals. Roach habitats are cryptic, but none confines a species exclusively to cramped quarters, therefore there is no evidence for selection favoring open-ended and complex repertories like those of Diplura.

Familial Patterns.

Discussion of *familial* trends in grooming behavior lends greatest insight into roach phylogenetic relationships. Some differences exist at other taxomonic levels (Bobula, MS), but these are either inconsistent or based on small sample sizes.

The grooming movement most useful in interpreting blattarian phylogeny is *Antenna Clean.* Other movements form less clear patterns among groups and hence offer no aid in clarifying general phylogenetic relationships.

Based on trends in *Antenna Clean,* consistent familial differences exist between the families with generalized reproductive behaviors

(Cryptocercidae, Blattidae, Blattellidae) and the more specialized Blaberidae. All roaches except the blaberids (the Polyphagidae were not sampled) assist antennae cleaning using the *Contralateral* mode. Individuals of each of the sampled species of Blaberidae, including a representative of the most primitive subfamily (Zetoborinae: *Schultesia lampyridiformis*) use either the *Ipsilateral* and/or *Unassisted* modes. No individual of any of the observed blaberid species used the *Contralateral* mode.

The constancy of this pattern seems highly significant. Apparently the Blaberidae are the most distinctive and cohesive family of roaches. The grooming data suggest that the Blaberidae, as numerous and superficially diverse as they are, form a specialized group clearly separate from the other roaches. This conclusion is in direct agreement with both McKittrick (1964) and Huber (1974).

The abrupt change in blaberid antennal grooming is probably tied to this recent evolutionary surge. The Blaberidae are the most recently evolved, most complex, most diverse cockroach family (Huber, 1974; McKittrick, 1964). If a new grooming movement were to evolve among the roaches, it would most logically appear, not in the groups which are the least changed from the ancestral forms, but in those which are the most changed, i.e., the Blaberidae. When available, the addition of polyphagid antenna cleaning behavior will further clarify the relationship of Blaberidae to the remaining families. If the mode used by Polyphagidae proves to be *Contralateral,* the Blaberidae would even more clearly appear to be a group apart.

It seems unlikely that Polyphagidae and Blaberidae will have similar antennal cleaning techniques. Polyphagidae is a primitive family, most closely related to the Blattellidae, while the Blaberidae devloped from a group which was already clearly separate from Polyphagidae (McKittrick, 1964). Thereafter, Blaberidae underwent extensive adaptive radiation, diverging even farther from their source group, and presumably from Polyphagidae. Any similarity of the Polyphagidae (a group which has not changed much from its ancestral forms) and the Blaberidae (a group very greatly changed) should be almost coincidental.

The monogeneric family Cryptocercidae forms a special case. Grooming movements recorded from *C. punctulatus* were the fewest of any species: a total of only four movements was recorded in more than twelve hours of observation. One individual of this species was put through two flour trials; neither yielded additional movements. After each flour application, as the roach was replaced in its culture cup, it immediately began to run in, under, and among the debris. This type of behavior was not observed when the roach was replaced without flour. After each flour trial, the greatest part of the flour was removed from the roach in less than one minute. Following the first flour trial, the roach was observed for 30 minutes (during which time no grooming was performed) and then removed and examined closely. Only minute specks of flour were visible on the ventral body surface. After the second flour trial, the period of heightened activity lasted seven minutes. As soon as the roach quieted it was removed and examined closely. The only remaining traces of flour were around the coxal bases. The roach was reexamined one-half hour later; this time, no traces of flour were found.

The most logical conclusion is that the flour was removed from the roach by contact with surrounding debris. Apparently the environment is a significant grooming tool for this species. When the two individuals studied were first collected from rotten logs they appeared very clean and shiny with no obvious adherent particles. Also, the cuticle had a bright shine unlike other roaches, and on handling, felt distinctly waxy. This suggests a special quality which makes it a poor site for adherent particles. Certainly if the roach can be free of fine flour within an hour after returning to its natural habitat, other particles could be similarly removed.

It is unlikely that the data obtained for *Cryptocercus* are skewed due to small sample size. Similar results were obtained from both individuals. Most important, the rapidity with which all flour was removed from the roach suggests that few grooming movements were recorded because few exist. The Cryptocercidae may in fact exhibit a case of evolutionary loss of grooming movements. With the development of a streamlined, waxy cuticle capable of shedding most particles, grooming would become an increasingly unnecessary part of the species behavior, and could easily be lost with no adverse effects on survival. If this is the case, it is interesting to note that the retention of antennal cleaning may be an indication of the importance of this sense organ.

SUMMARY

The grooming behavior of 23 species representing four families of Blattaria was recorded from 154 hours of observation. Specimens were initially observed in an undisturbed state. Several of each spe-

cies were later dusted with household flour and further observed.

Grooming is performed by either *Cleaning* (passage through the mouth parts) or by *Rubbing* a structure with another body part or, rarely, the substrate. Palpi are curled into the mouth for cleaning. Antennae are cleaned by one of four techniques: *Unassisted,* in which the antenna deflects into the mouth by its own musculature, and three types of *Assisted: Bipedal,* in which both forelegs grasp one antenna and pull it into the mouth, *Ipsilateral,* assisted by the foreleg on the same side of the head as the antenna cleaned, and *Contralateral,* assisted by the opposite foreleg. Each leg is cleaned in one mode only; the leg is presented ventrally and pulled posteriad. Some species clean the sternum, and some turn the head sideways to clean the edge of the pronotum and/or tegmen.

All rubbing is unilaterally performed. Rubbing by the ipsilateral foreleg grooms the basal parts of the antennae not reached by the mouthparts, as well as the various head surfaces. The abdomen is extensively rubbed with the ipsilateral hindleg contacting the dorsal, ventral, or lateral edges. The cerci are similarly rubbed. The dorsal surface of the tegmen is occasionally rubbed with the ipsilateral hindleg. Flipping of the wings upward or outward occurs, usually while abdomen rubbing is in progress, but can also occur separately.

Several additional movements not generally characteristic of all Blattaria were infrequently performed by some species (these are included in Tables 2 and 3). Three blattellids and one blaberid occasionally rubbed the underside of the wing edge with the midleg, and one of these blattellids made similar movements with the foreleg against the underside of the pronotum. This same species and a blaberid performed hindleg-hindleg rubbing. Finally, two unrelated species, a blattellid and a blaberid, occasionally dragged the side of the abdomen against the substrate.

Grooming behavior is highly stereotyped in Blattaria. Except for *Antenna Clean,* a particular structure is groomed similarly by all species. Apparently, there has been no selection to evolve unique grooming structures nor positions that relate to the ecological differences of modern roaches. What works for one seems to work for all of those studied.

Cryptocercids form a special case since they have a very restricted repertory, but those grooming movements observed are performed as in other species. The minimal repertory of *Cryptocercus* may be a result of evolutionary loss of grooming movements, related to the development of a more waxy cuticle capable of shedding most particulates more efficiently than that of other roaches, or perhaps this species never evolved more complex grooming.

Antenna Clean is the grooming movement which clearly shows a distinction among roaches. The data suggest that the Blaberidae, though superficially diverse in morphology and habitat, form a specialized, cohesive group separate from other roaches. Cause for the change in mode of antennal cleaning may lie in the recent evolutionary surge of Blaberidae, but the actual selective pressures are not known.

The absence of data from the fifth family, Polyphagidae, is regrettable. Since they are the most primitive family of Blaberoidea, logically they should group with Cryptocercidae, Blattidae, and Blattellidae in antennal cleaning technique.

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THE LARVA OF *DINOPONERA* (HYMENOPTERA: FORMICIDAE: PONERINAE)

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In the *Genera Insectorum* Emery ends his account of the genus *Dinoponera* laconically thus: "C'est le géant des Formicides." Zahl (1959) referred to *Dinoponera gigantea* as "the world's largest ant" and embroidered his account with excellent photographs of eggs, larvae, cocoons, a male and workers; there are no queens in this genus. Kempf in his 1971 revision of the genus gives the length of the worker of this species as "30 mm and over."

The generic name is derived from the Greek *deinos* terrible, fearful, and the generic name *Ponera.* After reading Zahl's 1939 and 1959 articles we readily agree that the name is most appropriate because of the large size, the prominent toothed mandibles, the black color and the potent sting.

The range of the genus is almost limited to Brazil, but it does spill over into adjacent Peru, Bolivia and Argentina.

Our description (1952:607) of the genus and *D. mutica* were based on one tattered integument (probably of Mann's [1916:409] larva) and an unlabeled photograph. The latter was probably made by Mann and used as the basis for his description and drawing (1916: Pl. 7, Fig. 55) of an "immature (?) larva 13 mm long." Our Fig. 4 (1952: Pl. II) is a reconstruction.

The larva of the world's largest ant certainly deserves better treatment than we were able to give it at that time but are now able to render it, thanks to the kindness of Dr. William Overal in Belém, Pará. He supplied us with eggs, larvae of 4 sizes, pupae, cocoons and workers of *D. gigantea.*

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Genus DINOPONERA Roger

REVISED CHARACTERIZATION. Profile pogonomyrmecoid (i.e., diameter greatest near the middle of abdomen, decreasing gradually toward anterior end and more rapidly toward posterior end, which is rounded; thorax more slender than abdomen and forming a neck, which is curved ventrally). Body with numerous (114–160) mammiform tubercles, each with 2–25 short simple hairs; body hairs lacking elsewhere. Cranial hairs lacking. Mandible dinoponeroid (i.e. narrowly subtriangular in anterior view; apical portion curved posteriorly; with or without medial teeth.)

Dinoponera gigantea Perty

MATURE WORKER LARVA. Fig. 1. Length (through spiracles) 18.8 mm; removed from cocoon, contracted 20.5 mm; removed from unfinished cocoon, not contracted 23.6 mm. Profile pogonomyrmecoid, with or without lateral longitudinal welts; with 116 mammiform tubercles distributed as follows: T2, T3 and AIX with 8 tubercles each, T1 and AI–AVIII with 10 tubercles each, AX with 2; each tubercle with 2–25 short simple smooth hairs; ventral pairs of tubercles smaller than the others and with fewer hairs. Leg vestiges present. Anus posteroventral. Somites distinct. Spiracles small. Integument densely spinulose, the spinules rather large and arranged in short to long rows, longest anteroventrally. Body hairs lacking except on tubercles. Cranium transversely subelliptical; integument rugulose; a few rugae bearing minute spinules or papillae. Antennae small; with 3 sensilla each. Head hairs lacking except on venter of labium; integument with about 50 sensilla. Labrum trapezoidal; anterior surface with ventrolateral bosses, each bearing about 24 sensilla; ventral surface densely spinulose, the spinules longer laterally; each half with 1 isolated and 2 contiguous sensilla; entire posterior surface densely spinulose, the spinules rather long and in numerous rather long subtransverse rows, the spinules so long and the rows so close together that the spinules overlap; each half with 4 sensilla in a longitudinal row near middle. Mandible large, apical and subapical teeth heavily sclerotized and curved posteriorly; with a small medial blade bearing a medial tooth; posterior surface spinulose, the spinules minute and isolated or in short rows. Maxilla large and bulging laterally; apex paraboloidal, entire surface densely covered with isolated spinules, the spinules longer ventrally; palp

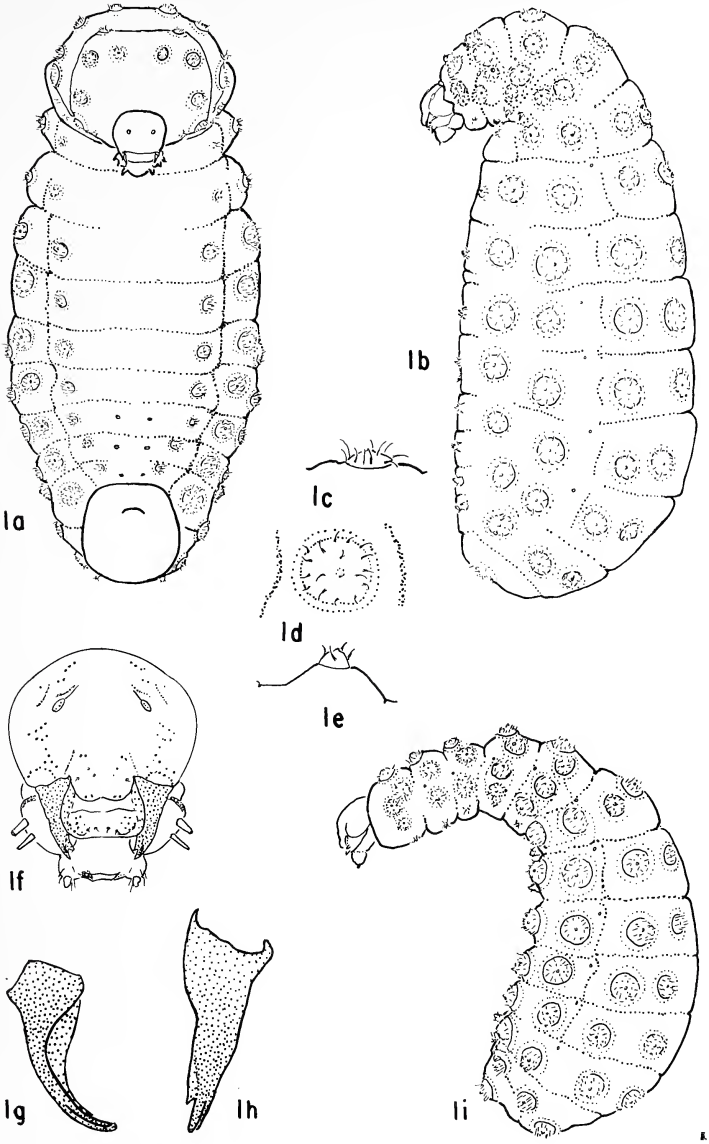

Figure 1. Fourth instar larva. a, Larva (removed from cocoon, contracted) in ventral view, ×4.5; b, larva (removed from unfinished cocoon, not contracted) in side view, ×4.5; c, lateral tubercle in side view, ×9; d, lateral tubercle in surface view, ×9; e, ventral tubercle in side view, ×9; f, head in anterior view, ×16; g, left mandible in lateral view, ×37; h, left mandible in anterior view, ×37; i, early fourth instar larva in side view, ×4.5.

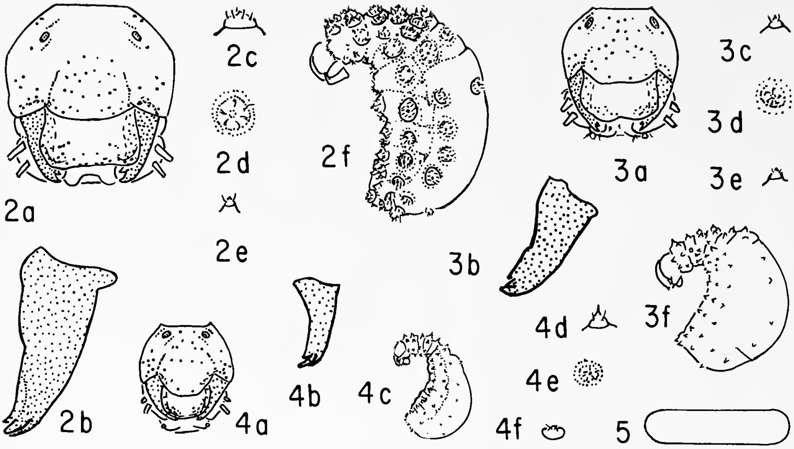

Figure 2. Third instar larva. a, Head in anterior view, ×16; b, left mandible in anterior view, ×37; c, lateral tubercle in side view, ×9; d, lateral tubercle in surface view, ×9; e, ventral tubercle in side view, ×9; f, larva in side view, ×4.5. Figure 3. Second instar larva. a, Head in anterior view, ×16; b, left mandible in anterior view, ×37; c, lateral tubercle in side view, ×9; d, lateral tubercle in surface view, ×9; e, ventral tubercle in side view, ×9; f, larva in side view, ×4.5. Figure 4. First instar larva. a, Head in anterior view, ×16; b, left mandible in anterior view, ×37; c, larva in side view, ×4.5; d, lateral tubercle in side view, ×9; e, lateral tubercle in surface view, ×9; f, ventral tubercle in side view, ×9. Figure 5. Egg, ×4.5.

digitiform with 5 (2 with a spinule each, 1 encapsulated, 2 small and peg-like) apical sensilla; galea digitiform with 2 apical sensilla. Labium with the anterior surface densely spinulose, the spinules isolated or in rows and small to large; with about 6 unbranched smooth hairs, 0.08–0.1 mm long on each ventrolateral area; palp paxilliform with sensilla similar to those on maxillary palp; opening of sericteries wide and salient with a sclerotized bar on each lateral surface. Hypopharynx densely spinulose, the spinules long and in numerous arcuate anastomosing rows, the rows so close together that the spinules overlap.

THIRD INSTAR LARVA. Fig. 2. Length (through spiracles) about 11 mm. Similar to mature larva except as follows. Thorax more slender and gaster more swollen; neck includes T1–T3 and AI and AII. Tubercles on dorsum of AVI–AVIII reduced to a ring of hairs. Six differentiated somites. Cranium subhexagonal; 1.4 times as broad as long; middle 0.4 of dorsal border flat. Antennae near occipital border. Anterior surface of labrum with short rows of minute spinules ventrally, ventral surface with about 6 sensilla. Opening of sericteries a small hole on ventral surface of labium.

SECOND INSTAR LARVA. Fig. 3. Length (through spiracles) about 7.3 mm. Similar to third instar larva except as follows. Only 8 tubercles on AVII and 6 on AIX; tubercles with center cone-shaped. Cranium with occipital surface flat for half its width. Labrum feebly bilobed; posterior surface with minute spinules. Labium with ventral border trilobed; palp a low knob.

FIRST INSTAR LARVA. Fig. 4. Length (through spiracles) about 3.3 mm. Similar to third instar larva except as follows. Tubercles reduced to 6 each on AVII and AVIII and 2 each on AI and AX; tubercles surmounted by a sharp-pointed cone. Integumentary spinules minute. Cranium 1 1/3 times as broad as long; occipital border concave, with a prominent sclerotized horn on each occipital angle. Labial palp a slight elevation.

EGG. Fig. 5. 2.16 by 0.5 mm, ellipsoidal, straight-sided.

Material studied: 8 larvae and 2 eggs from Brazil, courtesy of Dr. William Overal.

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LIFE HISTORY AND ECOLOGY OF *ACRONEURIA CAROLINENSIS* (BANKS) IN PANTHER CREEK, NICHOLAS COUNTY, WEST VIRGINIA (PLECOPTERA: PERLIDAE)*

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Introduction

Life history information is important to sampling techniques and taxonomy, production, feeding, bioassay, environmental disturbance and management studies. There is a basic lack of life history information that is needed by researchers and resource managers (Rosenberg, 1979).

Stoneflies are an important part of the stream ecosystem and are useful as water quality indicators. Few studies concerning the life histories of *Acroneuria* spp. have been carried out. Siegfried and Knight (1978) studied the life history of *Acroneuria* (*Calineuria*) *californica* Banks. Most other ecological data has been limited to *A. abnormis* and *A. lycorias* and concentrates on specific areas such as food habits, drift and predator-prey relations.

The objective of this investigation was to describe the life history of *Acroneuria carolinensis* with specific reference to: 1) naiad age and growth, 2) sex ratio, 3) food preference and 4) emergence.

Taxonomy and Distribution

Illies (1966) presented a review of the taxonomic changes of *Acroneuria carolinensis. Acroneuria carolinensis* was first described as a new species by Banks (1905) as *Perla carolinensis* from Black Mountain, North Carolina. In 1918, Navas placed it in another genus calling the insect *Nostura carolinensis.* Ricker (1935) assigned new nomenclature and designated the insect as *Acroneuria custae.* Claassen (1940) restored the specific name thus recognizing *Acroneuria carolinensis* as valid.

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Acroneuria carolinensis has been recorded from 11 states and three Canadian provinces. It ranges from Manitoba, Ontario and Quebec in southern Canada to Tennessee and South Carolina in the United States (Peckarsky, 1979).

MATERIALS AND METHODS

Panther Creek originates in Nicholas County, 3½ miles (5.6 km) southeast of the Greenbrier County line, near Saxman, West Virginia at an elevation of 3000 feet (914 m). Panther Creek flows northward, emptying into the Gauley River at an elevation of 820 feet (250 m); it has a total fall of 1180 feet (360 m) and a total length of 9.6 miles (15.4 km). The drainage basin area is 16.88 square miles (43.7 m^2) (Reger, 1921).

The study area is located along Route 39, 13.7 miles (22.1 km) west of the junction of Routes 19 and 39 at Summersville, at an elevation of 2200 feet (671 m). Collections were made in a riffle area 161 feet (49 m) below a concrete dam. The riffle was 36 feet (11 m) long and had an average width of 25.6 feet (7.8 m). Substrate consists of rocks with an approximate size range of 6 to 18 inches (15 to 46 cm) in diameter.

Qualitative samples were collected monthly from December 1984 to November 1985. After disturbing the substrate, a fine meshed dredge (mesh size: 4 mm, December–May; 1 mm, June–November) was held immediately below the disturbed area to collect the drifting naiads. Contents of the dredge were emptied into a white enamel pan to facilitate sorting. Naiads were immediately killed and preserved in 70 percent ethyl alcohol.

Temperature of the stream was recorded monthly using a Fisher instantaneous thermometer. During the emergence period, temperature was recorded weekly.

Water chemistry was measured monthly using a Hach chemical kit (Model AL-36B). Dissolved oxygen, carbon dioxide, hardness, alkalinity and pH were measured in the field. All variables were measured in mg/l except for pH.

Total length (excluding antennae and cerci) was measured by placing the naiad on a plastic millimeter ruler and viewing under a binocular dissecting scope. Naiads were measured to the nearest 0.5 mm and placed in 1 mm class intervals. Length-frequency histograms were produced for each month. Number of age classes was determined based on the distribution of the body length.

Population range diagrams (Hubbs and Perlmutter, 1942) were used to show monthly head width variations between males and females. Early instar naiads too small to sex (usually < 6.0 mm) were excluded from the analysis. Head width was measured to the nearest 0.05 mm using an ocular micrometer in a binocular dissecting microscope. Head width was used as a size standard because it changes least during preservation (Britt, 1953). Monthly growth rates were calculated as a percent increase in mean head width from one month to the next for males and females.

An estimation of the number of instars was calculated using the Janetschek method (Janetschek, 1967). Head width frequency histograms were produced for all collections combined. A trend-line for population growth was then calculated using a gliding mean over five successive class frequencies at a time. Gliding means were then subtracted from the frequency for each size class. These periodic maxima and minima were ploted and positive peaks were counted to determine number of instars.

Sex of naiads was determined by examining the posterior margin of the 8th abdominal sternite. A chi-square test was performed on 72 males and 152 females. Deviation from the expected 1:1 sex ratio was tested at the 0.05 confidence level.

Naiad food preference was determined by examining the contents of the foregut. Twelve foreguts were analyzed each month. After the foreguts were removed by dissection, contents of the foregut were gently scraped onto a glass slide and examined under a binocular dissecting scope. Food items were sorted and identified to the lowest taxonomic unit possible. Taxa, number of taxa per foregut and number of foreguts with the item were recorded. The mean number of a particular taxon per foregut and the percentage of foreguts in which that taxon occurred (percent frequency of occurrence) were calculated on a monthly and seasonal basis.

Using a Ward ultraviolet light trap (8 watts), an attempt was made to collect emerging adults at the study area. On 31 May 1984, the trap was set up from 10:00 to 12:00 p.m. During May and June, the banks of Panther Creek were searched for exuviae to determine the emergence period. Distance of exuviae from the stream bank and type of substrate on which they were found were recorded.

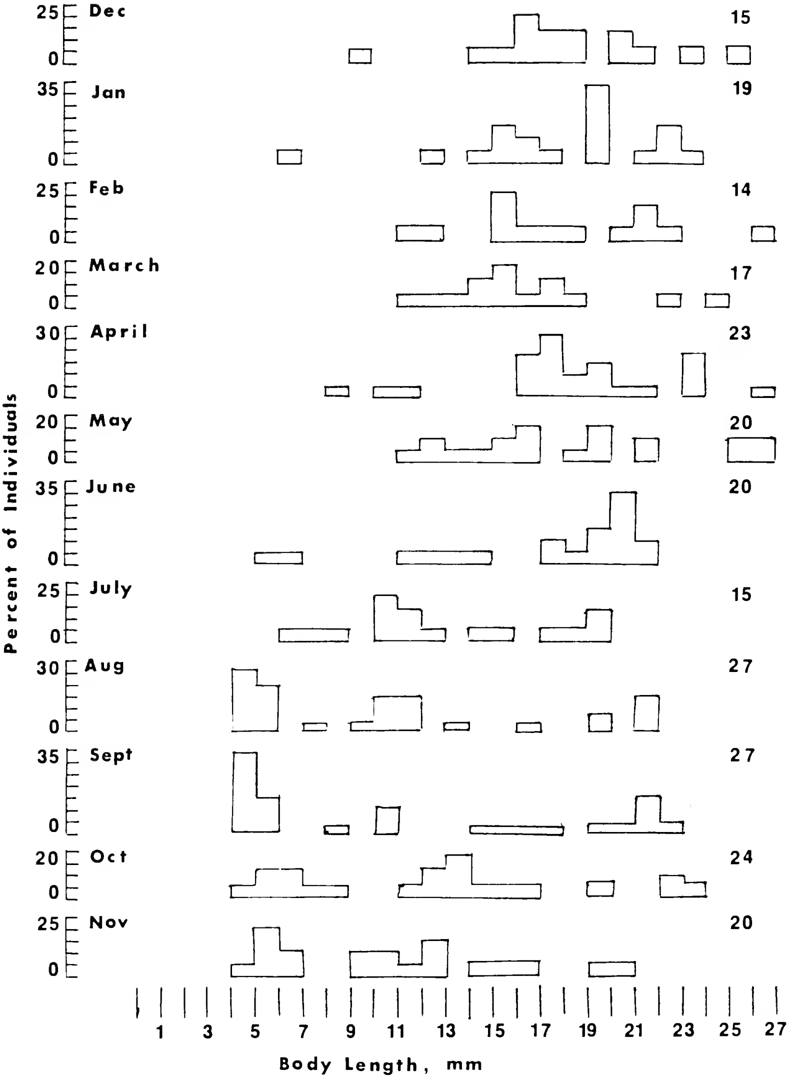

Figure 1. Length-frequency histograms showing monthly distribution of *Acroneuria carolinensis* naiads.

Fecundity was determined by direct egg count. Eggs were dissected out from 19 adults. They were placed in a syracuse watch glass and counted under a binocular dissecting scope. Regression analysis was used to determine the relationship between total body length and number of eggs produced. A correlation coefficient (r) was calculated to determine the strength of the relationship.

The diameter and length of 125 eggs from five adults were measured using an ocular micrometer in a binocular dissecting scope. Eggs were measured to the nearest 0.01 mm. Average egg size was calculated.

Results and Discussion

Stream environment. The mean water temperature at Panther Creek during the study period was 8.3 C. The temperature ranged from 0.0 in January to 16 C in June. During emergence studies, a high temperature of 17 C was recorded on 8 June 1984.

Dissolved oxygen was high, ranging from 7 to 13 mg/l ($\bar{X} = 9.4$ mg/l). Carbon dioxide ranged from 10 to 85 mg/l, with a mean of 61.5 mg/l. Alkalinity ranged from 0.0 to 102.6 mg/l ($\bar{X} = 29.9$ mg/l) during 1982, according to Pettry (1983). Total hardness ranged from 34.2 to 224.9 mg/l ($\bar{X} = 122.8$ mg/l). The pH had a mean value of 6.9 and ranged from 6.3 to 7.2.

Length-frequency histograms. Length-frequency analysis indicated a two-year life cycle (Figure 1). Body length ranged from 3.5 to 26.0 mm. The largest naiads were collected in February, April and May. Larger naiads were absent following the 20 May collection, when emergence had occurred. There was approximately an 11 week egg development period before recruitment of the new age class. The smallest and earliest naiads were first collected in late August. The existence of a 6 mm naiad in January suggested some evidence that a three-year life cycle may be possible. Absence of additional naiads of this size could have been due to the larger mesh size dredge used during the winter collections.

Harper and Magnin (1969) suggested three-year life cycles for *A. abnormis* and *A. lycorias.* They also indicated that the number of naiads collected was too small to make a definite conclusion. Sheldon (1969) reported a life cycle of three years for *Calineuria californica* at an elevation of 2200 m. Heiman and Knight (1975) and Siegfried and Knight (1978) both suggested a two-year life cycle at lower elevation for *C. californica.* Allen and Tarter (1985) reported a two-year life cycle for *Eccoptura xanthanes* (formerly *A. xanthanes*).

Growth. Population range diagrams (Figure 2) showed a wide range in head width. The largest female head width was 6.22 mm and occurred in October. The largest male head width was 5.07 mm and occurred in December. Females exhibited greater mean head widths than males (Figure 2). Males exhibited greatest growth in August (12%) and October (17%). Growth of females was greatest in August (28%) and January (13%). The smallest immatures were first collected in August and had their greatest growth in October (21%). Following emergence there was a marked decrease in mean head width for males in July (26%) and females in June (30%). The population showed a sharp decrease in mean head width in August (48%). This decrease coincided with the recruitment of a new age class.

Calineuria californica exhibited its greatest growth in spring when the stoneflies were still small (Siegfried and Knight, 1978). Growth declined with an increase in size. In this study *C. californica* showed an egg diapause and early instars were not collected until February. In laboratory growth studies with *C. californica,* the greatest growth occurred in the summer, while the least occurred in the winter (Heiman and Knight, 1975).

The Janetschek method (Janetschek, 1967) indicated that *A. carolinensis* naiads underwent 25 instars (Figure 3a and 3c). A general growth trend using gliding means is shown in Figure 3b.

Sex ratio. A chi-square test was applied to 72 male and 152 female *A. carolinensis* naiads. A significant deviation from the expected 1:1 ratio was observed at the 0.05 confidence level.

Foregut analysis. Of the 144 foreguts examined, 78 (54%) contained food items. The highest percentage of empty foreguts occurred in April (75%). On a seasonal basis the percent of empty foreguts never exceeded 50 percent.

Acroneuria carolinensis naiads were carnivorous, with Diptera ($\bar{X} = 6.4$, %FO = 19.4), plecopterans ($\bar{X} = 1$, %FO = 15.9), ephemeropterans ($\bar{X} = 1$, %FO = 12.5) and trichopterans ($\bar{X} = 1.3$, %FO = 5.5) as the most important food items. Diptera was represented by larval chironomid midges. Plecopterans found in the foregut included members from the families Capniidae, Leutridae, Nem-

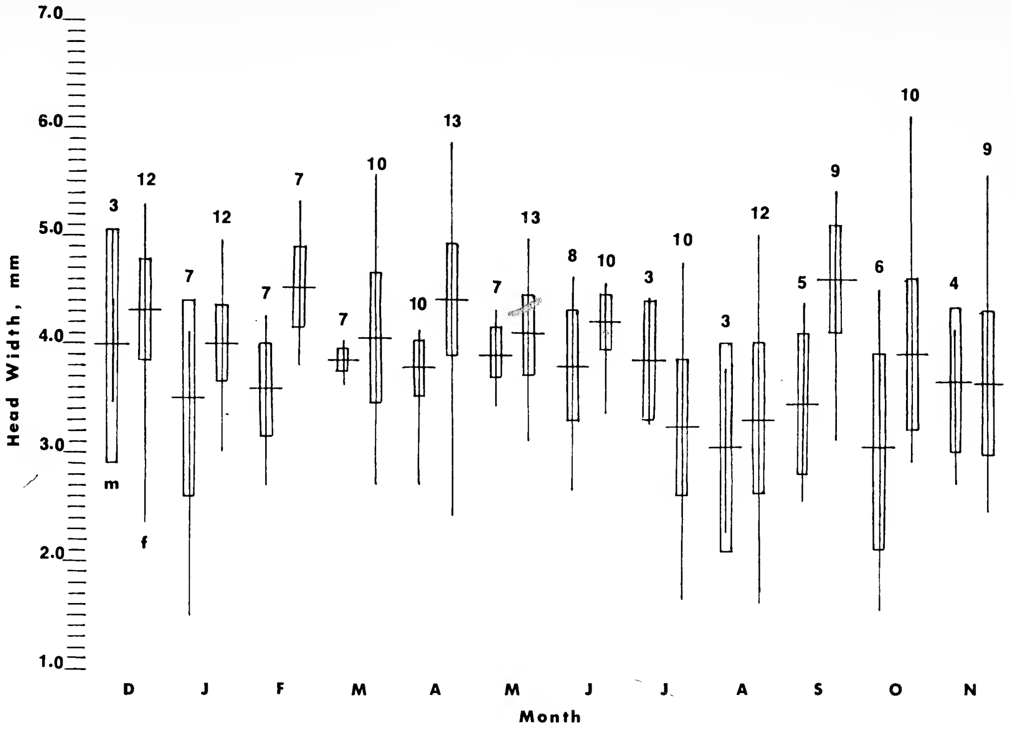

Figure 2. Population range diagrams showing monthly head width variation of *Acroneuria carolinensis* naiads.

ouridae, Taeniopteryidae and Perlodidae. Ephemeropterans included representatives from the genera *Ephemerella, Epeorus, Cloeon, Stenonema* and a member from the family Baetidae. Trichopterans included representatives of the genera *Glossosoma, Hydropsyche* and *Cheumatopsyche.*

Results of monthly foregut analysis are presented in Figure 4. Plecopterans and ephemeropterans made up the principle components of the diet throughout the year. Dipterans became important in the winter and summer, while trichopterans were most important in the summer. Naiads fed most during the winter months with an average of 5.0 food items/stonefly. They fed least during the spring and fall with an average of 1.1 food items/stonefly each season. Siegfried and Knight (1976a, 1976b) and Sheldon (1969) reported dipterans, trichopterans and ephemeropterans as the most important food items for *C. californica.* Sheldon (1969) found that ephemeropterans were a regular component of *C. californica*'s diet and dipterans were important in the winter and summer. Siegfried and Knight (1976a) stated that dipterans were the most important and consistent food item for *C. californica.* Siegfried and Knight (1976b) found that *C. californica* naiads showed no preference for a particular prey and would eat anything available. They also reported a significant correlation between gut diversity and benthic diversity. Sheldon (1969) stated that food consumption was low in the summer. In a laboratory study, Heiman and Knight (1975) found that *C. californica* had its greatest food consumption in the summer, with minimal feeding in the winter, at normal environmental temperatures. Johnson (1981) reported that dipterans and trichopterans were the primary diet for *A. abnormis.* The diet was supplemented with ephemeropterans.

Phoresy. Larvae of a chironomid midge were observed living phoretically with *Acroneuria carolinensis* naiads. The midges occurred on the prothorax or just beneath the mesothoracic wing pad. The phoretic attachment occurred on nine of 241 (3.7%) naiads examined. Dosdall and Mason (1981) reported the chironomid *Nanocladius* (*Plecopteracoluthus*) *branchicolus* living phoretically on *A. lycorias.* They reported varied percentages of the number of stoneflies bearing the chironomids. The percentages of phoretic cases ranged from 10–50 percent.

Rearing and emergence. The attempt to collect emerging adults on 31 May 1984 was unsuccessful. Exuviae were collected up to 4.6

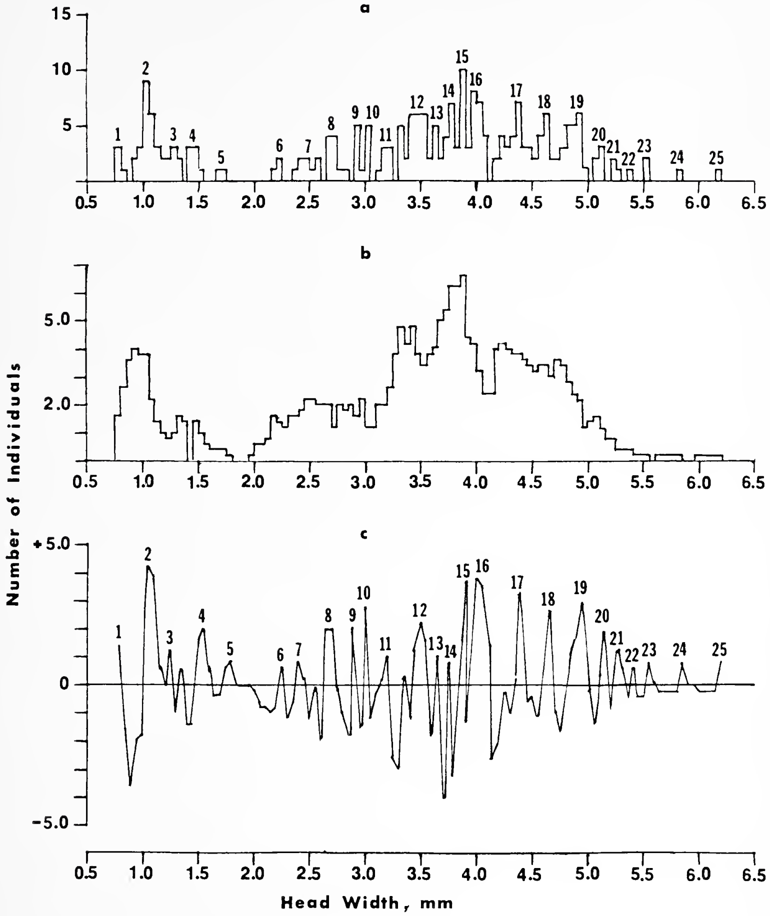

Figure 3. Growth rates of *Acroneuria carolinensis* naiads from Panther Creek, Nicholas County, West Virginia, 1983–1984: a) frequency of size classes; b) trendline of the population, calculated by gliding means over five successive size-class frequencies at a time; c) periodicity of maximum frequency of size.

m from the water surface. They were found clinging to sand, rocks, rhododendron stems and moss. Based on the number of exuviae collected (33), peak emergence was on 8 June 1984; emergence lasted three weeks. The first exuvium was collected on 1 June and the last on 16 June. Emergence peaked with a corresponding peak in

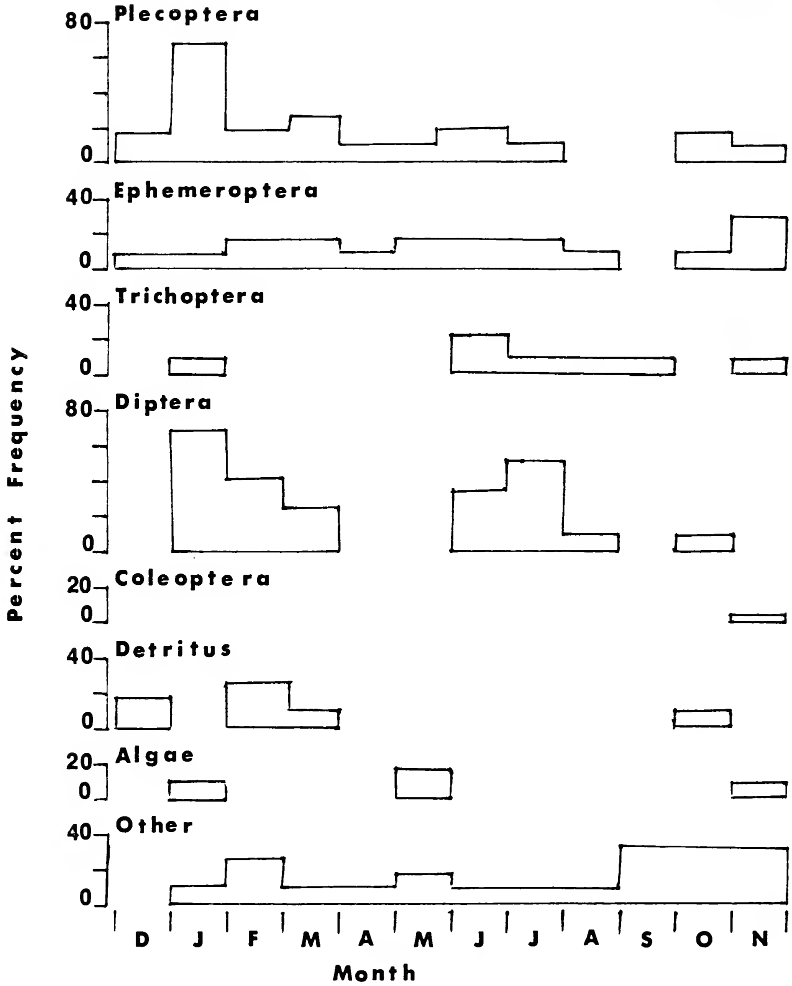

Figure 4. Percentage frequency of food items in foreguts of *Acroneuria carolinensis* naiads each month.

temperature (17° C) (Figure 5). Mingo (1983) reported *A. carolinensis* to be in flight from 12 June to 3 August in Maine. Flight periods for other *Acroneuria* spp. recorded by Mingo (1983) were: *A. abnormis,* 10 June to 14 July; *A. arenosa,* 30 June to 3 August; *A. lycorias,* 10 July. Kondratieff and Despins (1983) reported the following flight periods for *Acroneuria* sp. and related genera from Virginia: *A. arenosa,* late June to early July; *A. abnormis,* throughout June; *Eccoptura xanthanes,* late May through mid-July. Allen and Tarter (1985) reported *E. xanthanes* emerged from 11 June to 14 July in Kentucky.

In a separate study, *A. carolinensis* naiads and adults were to be collected at Panther Creek in the spring of 1985. On 25 May no final instar naiads were collected. On 2 June a single final instar naiad was found after two hours of sampling. These findings suggested that emergence had taken place in mid-May, three weeks earlier than 1984 emergence. The weather in April 1985 was unseasonably warm, and perhaps induced early emergence. Harper and Pilon (1971) studied the emergence of *A. abnormis* for three years (1958, 1959, 1966). They found little temperature difference between the emergence curves, but cooler temperatures in 1958 had delayed emergence for two weeks.

Fecundity. Of the 19 adults examined, only seven contained mature eggs. Therefore, mature eggs and immature eggs of comparable size were counted. Direct egg count resulted in a range of 10 to 800 eggs ($\bar{X} = 239$) per female. There was little correlation between body length and number of eggs ($r = 0.56$).

Egg size. Acroneuria carolinensis eggs were oval in shape. Mean length was 0.43 mm (range 0.38–0.48 mm), mean diameter was 0.33 mm (range 0.29–0.38 mm). Stark and Gaufin (1976) provided electron micrographs of the eggs and gave detailed descriptions. From the material examined by Stark and Gaufin (1976), two types of ova were found. They suspect two closely related species are involved and suggested additional studies of the complex.

SUMMARY

The life history and ecology of *Acroneuria carolinensis* from Panther Creek, Nicholas County, West Virginia were studied from December 1983 to November 1984. Length-frequency distribution indicated a two-year life cycle. The largest naiads (26.0 mm) were collected in February, April and May. Females and males exhibited greatest growth in August (28%) and October (21%), respectively. Naiads underwent 25 instars. A chi-square test applied to 72 males and 152 females showed a deviation (0.05 confidence level) from the expected 1:1 sex ratio. Naiads were carnivorous in their feeding

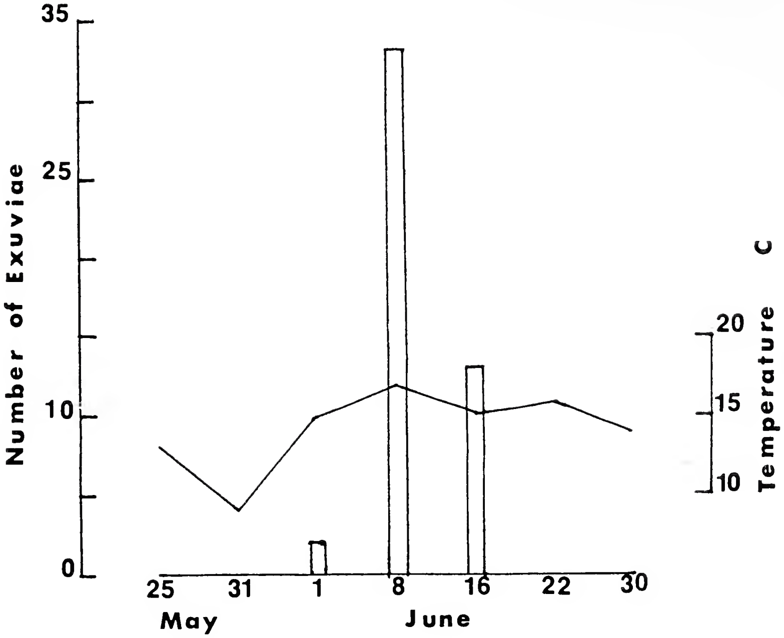

Figure 5. Naiad exuviae collected during May and June, 1984, showing yearly pattern of emergence of *Acroneuria carolinensis.*

habits. Plecopterans ($\bar{X} = 1$, %FO = 15.9) and ephemeropterans ($\bar{X} = 1$, %FO = 12.5) made up the principle components of the diet. Dipterans were important components in the winter and summer, while trichopterans became important in the summer. A phoretic relationship between *A. carolinensis* naiads and a chironomid midge was observed on 3.7 percent of the naiads examined. Emergence was between 1 June and 16 June; peak emergence occurred on 8 June 1984. Direct egg counts for adult females ranged from 10 to 800 eggs ($\bar{X} = 239$) per female. There was little correlation between body length and number of eggs (r = 0.56). Mean egg length was 0.43 mm (range 0.38–0.48) and mean egg diameter was 0.33 mm (range 0.29–0.38).

ACKNOWLEDGMENTS

The authors are especially thankful to the following persons for help in this investigation: Dale Adkins, Dean Adkins, Allan Brant, Creda and Jim Meadows, Amy Messinger, Brian Reeder and Thomas Weaks. Special thanks to Vickie Crager for typing the manuscript.

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A REVISION OF THE NEW WORLD GENUS *CHROMOCRYPTUS* (HYMENOPTERA: ICHNEUMONIDAE).

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Introduction

Taxonomy

Chromocryptus is a strictly New World representative of the cosmopolitan ichneumonid subtribe Ischnina (Gelinae: Mesostenini), as defined by Townes (1969: 158–9). It may be distinguished from other Nearctic and Neotropic ischnines by the following concert of features: (1). Black, red, and white (sometimes mostly red); (2). Wings hyaline to moderately infumate; (3). Clypeus pyramidally raised, often nasute; (4). Mesoscutum largely with coarse punctures or puncto-reticulation and with notauli only faintly defined (fine but well impressed in some males); (5). Hind coxa with a strong subvertical groove externo-ventrally near base; (6). Discocubitus gently arched to weakly angled, sometimes with a vestigial ramellus; (7). Axillus very close to hind margin of hind wing; (8). Propodeal spiracle 1.3–3.0 as long as wide; (9). Propodeal cristae large and well projecting, obtusely cuneate to subligulate, never spiniform; (10). Base of 1st gastric tergite with a lateral expansion that is low and rounded or sometimes prominently subtriangular; (11). Female gaster short and stout, short-fusiform to almost ovoid; (12). Second gastric tergite with abundant large punctures that usually are subadjacent or denser; its setae short but mostly approaching the length of their interspaces; (13). Ovipositor slender to robust, straight, compressed; its sheathed portion 0.35–0.45 as long as fore wing. The foregoing diagnosis easily distinguishes *Chromocryptus* from its

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North and Middle American relatives, but must be used with care in considering the complex South American fauna. A complete description is furnished later in this study antecedent to the key for *Chromocryptus* species.

My concept of *Chromocryptus* agrees with Townes earlier interpretations (1962: 256–7). Some recent authors (Porter 1967: 206–11, Townes 1966: 68) have regarded *Chromocryptus* as a species group within the immense, almost exclusively South American genus *Trachysphyrus* Haliday. In 1969 (179–81), Townes restricted *Chromocryptus* to those "*Trachysphyrus*" in which the axillus vein runs close to the posterior margin of the hind wing. This arrangement still leaves under *Chromocryptus* a heterogeneous and perhaps polyphyletic complex of more than 45 species. I thus prefer to return to Townes' 1962 perception of the genus and to regard it as comprising only those species intimately related to the North American *C. planosae*. This viewpoint has been strengthened by discovery of 5 previously unknown Argentine and Peruvian taxa that agree in most points with *C. planosae*.

RELATIONSHIPS

Chromocryptus probably is related to at least some of the stocks formerly included under *Trachysphyrus* (Porter 1967). It may be particularly close to the central Argentine *Xiphidium* group of *Trachysphyrus* (Porter 1967: 211–15). In both groups the 2nd gastric tergite has large, dense punctures and the base of the petiole shows an at least moderately well developed lateral flange or blunt tooth. The *Xiphidium* group differs from *Chromocryptus* in having the axillus vein far from the hind margin of its wing. Species of the *Xiphidium* group thus belong to *Trachysphyrus,* as most recently defined (Townes 1969: 181–3). However, displacement anteriad of the axillus vein (a derived feature in ichneumonids) probably has occurred independently several times within various evolutionary lines associated with *Trachysphyrus.* Further studies, consequently, might allow expansion of *Chromocryptus* to include those species currently grouped with *Trachysphyrus xiphidium.*

GEOGRAPHIC DISTRIBUTION AND ECOLOGY

Chromocryptus ranges throughout most of the New World from the northeastern United States and California to México, Perú, Argentina, and Brasil. It has not been recorded from the Neantarctic Biotic Province of South America (Chile and adjoining southwest Argentina) nor from any of the West Indian islands.

Of the known species, 6 occur in northern Argentina and/or Brasil, 1 is reported from the Peruvian Coastal Desert, 1 from México and the southern United States, 1 from Florida, 1 from the northeastern United States, and 1 from central California. Habitats occupied by *Chromocryptus* include Temperate Deciduous Forest (*C. planosae*), Floridian Subtropical Evergreen Forest (*C. weemsi* and eastern populations of *C. mesorufus*), Tamaulipan Subtropical Thorn Scrub (western populations of *C. mesorufus*), Chaco-like Tropical Thorn Scrub on the north Peruvian coast (*C. teres*), the northwest Argentine Andean ecotone between Subtropical Cloud Forest, highland Chaco, and Montane Temperate Forests (*C. alvaradoi* and some populations of *C. tomsici*), the northwest Argentine Andean Desert or Prepuna (some populations of *C. tomsici*), the north-central Argentine Dry Chaco (*C. prosopis, C. golbachi*), and very wet subtropical to tropical forests in the south Brasilian biotic zone (*C. huebrichi*).

Wherever it occurs, *Chromocryptus* almost always seems extraordinarily scarce. Specimens which I have observed usually were crawling or flying within the shelter of spiny shrubs. I suspect they may be common in such microhabitats, from which they rarely emerge to enter Malaise Traps and in which it is difficult for the collector to detect and net them.

Hosts

Chromocryptus have been reared most often from tough lepidopterous cocoons attached to bark. Lasiocampidae are the usual hosts, with *C. planosae* recorded from *Epicnaptera* and *Tolype* in the eastern United States and *C. huebrichi* cited from *Titya* near Buenos Aires, Argentina. There is also 1 rearing for *C. planosae* from the arctiid genus *Halisidota.*

Parasitism by *Chromocryptus* is gregarious, with up to 22 specimens emerging from a single host cocoon (Porter 1967: 33–4). This habit also has been recorded for the Chilean *Trachysphyrus horsti* and the Argentine *T. chacorum,* but has not been noted among such commonly reared Holarctic "trachysphyroid" genera as *Itamoplex* and *Buathra.* Pratt (1945: 551) believes *C. planosae* to be polyembryonic.

INFRAGENERIC AFFINITIES

Chromocryptus forms a compact genus in which establishment of subgenera or species groups seems as yet unnecessary. Little has been discovered about the ancestral or derived nature of the states of features used to separate these species, so that phylogenetic analysis within *Chromocryptus* would be premature.

Nonetheless, some idea of relationships within the genus may be derived from the following hierarchically indented schema:

I. Ovipositor stout, its tip not sagittate; fore tibia swollen; clypeus approximately symmetric, convex to bluntly pyramidal .... *C. alvaradoi.*

II. Ovipositor slender and delicate, its tip sagittate; fore tibia not inflated; clypeus asymmetrically and nasutely pyramidal.

   1. Mesopleuron with conspicuous, long, rather regular wrinkles that radiate extensively from speculum; mesoscutum with some smooth areas between puncto-reticulation on both median and lateral lobes .... *C. poecilma, C. teres.*
   2. Mesopleuron without or with only short wrinkles radiating from speculum; mesoscutum usually without smooth areas among the coarse sculpture .... *C. planosae, C. mesorufus, C. weemsi, C. vandykei, C. huebrichi, C. prosopis, C. golbachi,* and *C. tomsici.*

Plausibly, *Chromocryptus alvaradoi* diverged early from the *Chromocryptus* evolutional line. Specializations, possibly associated with parasitism of small hosts and with a newly acquired polyembryonic life style, then led to the origin of a cluster of smaller species with more delicate ovipositors. More recently, this latter category has subdivided into the weakly differentiated *Poecilma* and *Planosae* complexes.

COLLECTIONS EXAMINED

Listed below in alphabetic order are the collections which furnished material for this research and/or in which type specimens are to be deposited. I refer to institutional collections by the name of the city in which they are located and to individual collections by the surname of their owner.

CAMBRIDGE. Museum of Comparative Zoology, Harvard University, Cambridge, MASS 02138.

COLLEGE STATION. Department of Entomology, Texas A & M University, College Station, TX 77843.

GAINESVILLE. Florida State Collection of Arthropods, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P. O. Box 1269, 1911 SW 34th Street, Gainesville Fl 32602.

LAWRENCE. Department of Entomology, Snow Entomological Museum, The University of Kansas, Lawrence, KS 66045.

OTTAWA. Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, Ottawa K1A 06C, CANADA.

PORTER. Collection of Charles C. Porter, 301 North 39th Street, McAllen, TX 78501.

TOWNES. American Entomological Institute, c/o Dr. Virendra Gupta, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, Fl 32602.

Genus CHROMOCRYPTUS

Chromocryptus Ashmead, 1900. Proc. U.S. Natl. Mus. **23**: 41. Type: (*Chromocryptus albopictus* Ashmead) = *planosae* (Fitch).

Mesostenimorpha Viereck, 1913. Proc. U.S. Natl. Mus. **44**: 566. Type: (*Cryptus nebraskensis* Ashmead) =*planosae* (Fitch).

Fore wing 3.4–9.1 mm long. Coloration usually black, red, and white (occasionally mostly red) with hyaline to moderately dusky wings. Flagellum moderately long and slender, a little flattened below toward apex in female, in male with some segments bearing sharp and linear longitudinal tyloids, its 1st segment 3.7–6.2 as long as deep at apex. Mandible rather short and broad with lower tooth often a little shorter than the upper. Clypeus in profile asymmetrically to symmetrically pyramidal, often nasute; its apical margin edentate. Occipital carina sharp and narrow, usually sinuate laterally, reaching the weakly to moderately raised hypostomal carina below. Malar space 0.50–1.0 as long as basal width of mandible. Pronotum a little swollen on dorsal margin and with the submarginal groove vague or absent to shallowly defined; epomia sharp in scrobe and sometimes a little prolonged dorsad, where it occasionally terminates in a weak swelling. Mesoscutum with notaulus weak (sometimes rather strong in male) but traceable 0.5 or more the length of mesoscutum; surface at least in part coarsely and densely punctate, reticulo-punctate, or reticulately wrinkled. Mesopleuron with speculum largely smooth and shining or sometimes much invaded by coarse wrinkling; its surface otherwise wrinkled and/or puncto-reticulate; no ridge on prepectus below. Fore tibia scarcely to palpably inflated. Hind coxa with a sharp and strong subvertical groove externo-ventrally near base. Wing venation: radial cell 3.3–4.4 as long as wide; areolet large, moderately broad to rather high and narrow, its intercubiti slightly to definitely convergent above; 2nd recurrent vertical or reclivous, straight or slightly outcurved dorsad; discocubitus gently arched to broadly angled, sometimes with a vestigial ramellus; mediella beyond base usually weakly arched but fairly strongly arched in some males; axillus very close to and paralleling hind margin of wing. Propodeum: spiracle 1.3–3.0 as long as wide; profile short and high; basal trans-carina traceable and often sharp throughout; apical trans-carina irregular but traceable between cristae, sometimes strong; cristae large and obtusely cuneate to subligulate, often strongly projecting; median longitudinal carinae often traceable but weak in female but stronger in males, where they often define both an areola and a median apical area. First gastric tergite: petiole at base with a low and rounded to often prominent and subtriangular lamella; postpetiole usually strongly expanded, in females 1.7–2.3 as wide apically as long from spiracle to apex and in males 1.2–1.9 as wide; surface of postpetiole at most with vague dorsal carinae and with a few to very many medium sized to large and frequently conspicuous punctures; ventral longitudinal carina defined throughout. Second gastric tergite with abundant, medium sized to large, shallow to (often) sharp punctures that are mostly subadjacent to (often) adjacent; its setae abundant but short and often (but not always) mostly equal to the length of their interspaces. Ovipositor: sheathed portion 0.34–0.45 as long as fore wing; straight, slender to robust, compressed; nodus distinct to obsolete; notch vague to rather large but shallow; dorsal valve with a steep to very gentle taper between notch and apex; tip 0.14–0.21 as high at notch as long from notch to apex; ventral valve on tip with ridges weak and inclivously oblique to sharp and almost vertical.

KEY TO THE SPECIES OF *CHROMOCRYPTUS*

FEMALES

(Female of *C. golbachi* unknown.)

1\. South American species (Perú, Argentina, Brasil) 5

1′. Mexican and North American species 2

2\. Propodeum and mesopleuron largely red; 2nd and 3rd gastric tergites with apical white bands obsolete or absent 3

2′. Propodeum and mesopleuron black and white, without conspicuous red areas; 2nd and 3rd gastric tergites with prominent white apical bands 4

3\. Ground color of head, pronotum, and mesoscutum black; hind face of propodeum with a pair of white bars that reach from cristae to its apical margin; gastric tergites 4–7 with white apical bands and otherwise mostly blackish; punctures on upper 0.3 of mesopleuron mostly adjacent to subadjacent; sheathed portion of ovipositor 0.30 as long as fore wing.... .... 1. *C. planosae* (Fitch)

3′. Ground color of head, pronotum, and mesoscutum red; propodeum red with only a trace of whitish on cristae and area immediately apicad; gastric tergites 4–7 red with white apical bands on 5–7; punctures on upper 0.3 of mesopleuron mostly reticulately confluent; ovipositor 0.40 as long as fore wing .... 2. *C. weemsi* (Porter)

4\. Second and succeeding gastric tergites black with apical band; broad white stripe in anterior 0.6 of sternaulus; hind femur and tibia dusky on apex; hind tarsus partly white .... 3. *C. mesorufus* Cushman

4′. Second and succeeding gastric tergites red with a white apical band; only a trace of white in sternaulus; hind femur and tibia not dusky on apex; no white on hind tarsus.......... .... 4. *C. vandykei* Townes

5\. No white on propodeum; fore wing palpably darkened toward apex, 8.6–9.1 mm long; speculum invaded by coarse wrinkles; fore tibia stout and inflated; propodeal spiracle 2.3–3.0 as long as wide; ovipositor robust, its notch and nodus obsolete, its profile on tip weakly tapering and not sagittate, its ventral valve on tip with strong, almost vertical ridges .... 5. *C. alvaradoi* n. sp.

5′. Hind face of propodeum with a pair of conspicuous white lateral bars between cristae and apical margin; fore wing nearly hyaline, 3.4–6.7 mm long; speculum largely smooth; fore tibia slender and scarcely inflated; propodeal spiracle 1.3–2.1 as long as wide; ovipositor slender and delicate, its notch and nodus usually detectable, its profile on tip more strongly tapering and sagittate, its ventral valve on tip with delicate, inclivously oblique ridges 6

6. Mesoscutum not uniformly reticulo-punctate; mesopleuron with long wrinkles that radiate from speculum; gaster red with variably developed white apical bands on all but 3rd tergite 7

6′. Mesoscutum throughout coarsely reticulo-punctate; mesopleuron with fine reticulo-punctation and wrinkling but without long rugae that radiate extensively from speculum; gaster dull to bright red, sometimes with considerable blackish suffusion, and often with white absent or obsolete on apices of 1st and/or 2nd tergites 8

7. Face mostly white; large white blotch in upper hind corner of mesopleuron; postpetiole with scattered large and strong punctures that become subadjacent laterad and apicad; 2nd gastric tergite with mostly subadjacent to adjacent large and sharp punctures . . . . 6. *C. poecilma* (Porter)

7′. No white on face or in upper hind corner of mesopleuron; postpetiole with only a few small to medium sized and scattered punctures; 2nd gastric tergite with abundant medium sized and shallow punctures that are separated by 1-3× their diameters or more . . . . 7. *C. teres* n. sp.

8. Pair of white stripes on mesoscutum; large anterio-median white blotch on mesopleuron; large, ellipsoid white area on apical 0.5 of lower metapleuron; no white on 1st and 2nd gastric tergites . . . . 8. *C. huebrichi* (Brèthes)

8′. No white on mesoscutum and on mesopleural disc; lower metapleuron at most with a tiny white area at apex; 1st (and sometimes 2nd) gastric tergite with a white apical band 9

9. White flagellar band begins on 6th segment; basal 0.3–0.6 of scutellum white; white apical bands on both 1st and 2nd gastric tergites; 4th gastric tergite with its broad white apical

band abruptly truncate laterally; areolet nearly parallel-sided, the intercubiti scarcely convergent above; propodeal cristae asymmetric, cuneo-ligulate; 2nd gastric tergite with its large punctures mostly subadjacent and surface between punctures with only faint micro-aciculation .... 9. *C. prosopis* n. sp.

9′. White flagellar band begins on 7th segment; basal 0.3 of scutellum white; no white apical band on 2nd gastric tergite; white apical band of 4th gastric tergite nearly complete, not abruptly cut off laterally; areolet not parallel-sided, the intercubiti definitely convergent above; propodeal cristae symmetrically short-ligulate; 2nd gastric tergite with its large punctures in great part practically adjacent and surface between punctures with palpable micro-aciculation........ .... 10. *C. tomsici* n. sp.

MALES

(Males of *C. alvaradoi, C. mesorufus, C. poecilma, C. teres,* and *C. vandykei* unknown).

1. South American species (Argentina, Brasil).................3

1′. North American species.................................2

2. Ground color of head, pronotum, and mesoscutum black; hind face of propodeum with a pair of white blotches from cristae to hind margin; gastric tergites 4–7 with white apical bands and otherwise mostly blackish; punctures on upper 0.3 of mesopleuron at least partly discrete .... 1. *C. planosae* (Fitch)

2′. Ground color of head, pronotum, and mesoscutum red; propodeum red with only a trace of white on cristae and area immediately apicad; gastric tergites 4–7 uniformly red; punctures on upper 0.3 of mesopleuron reticulately confluent... ....2. *C. weemsi* (Porter).

3. Pair of white stripes on mesoscutum; white blotch on clasper; no white on 1st and 2nd gastric tergites, the 4th and following tergites blackish with white apical bands; notauli faint, extending 0.5–0.6 the length of mesoscutum............. .... 8. *C. huebrichi* (Brèthes)

3′. No white stripes on mesoscutum (occasionally a median white blotch); no white on clasper; ground color of gaster usually in large part red, 1st gastric tergite with at least a vague white apical band, 2nd tergite with or without a white band, 3rd tergite with or without a white band, 4th and 5th tergites often with an apical white band; notauli fine but impressed, reaching 0.7–0.8 the length of mesoscutum 4

4. Large white spot on mesoscutum between ends of notauli; postscutellum mostly white; gaster bright red with broad white apical bands on tergites 1–5; mesopleural disc on upper 0.5 with rather fine and longitudinally biased variably reticulate wrinkling and on lower 0.5 uniformly puncto-reticulate; postpetiole 1.8–1.9 as wide apically as long from spiracle to apex .... 11. *C. golbachi* n. sp.

4′. No white on mesoscutum; no white on postscutellum; gaster duller red with white bands not as described above; mesopleural disc uniformly with rather fine and granular puncto-reticulation; postpetiole 1.2–1.7 as wide apically as long from spiracle to apex 5

5. Mesopleuron extensively white; gaster bright to dull red with some dusky staining, with a broad white apical band on tergites 1 and 2, a narrow white band on tergite 3, a broad but laterally aborted white band on 4, and no white on 5th and following tergites; malar space 0.53–0.66 as long as basal width of mandible; postpetiole 1.6 as wide apically as long from spiracle to apex; large punctures on postpetiole uniformly subadjacent to reticulately confluent .... 9. *C. prosopis* n. sp.

5′. Mesopleuron with only a small white area in lower hind corner; gaster red with some dusky suffusion, with white vaguely on apex of 1st tergite, no white apical bands on tergites 2 and 3, with a broad but laterally aborted band on tergite 4, and with white apical bands on 5th and following tergites; malar space 0.80 as long as basal width of mandible; postpetiole 1.2 as wide apically as long from spiracle to apex; large punctures on postpetiole irregularly spaced, not uniformly subadjacent or denser, sometimes mostly sparse .... 10. *C. tomsici* n. sp.

1. *Chromocryptus planosae* (Fitch) (Figs. 1, 2, 6).

Phygadeuon planosae Fitch, 1856. Trans. New York State Agr. Soc. **15**: 501. Holotype ♀: New York (Washington).

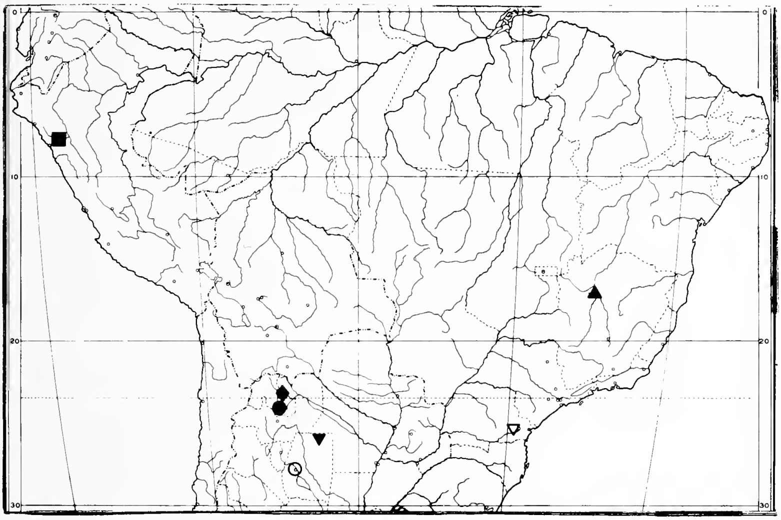
Cryptus nebraskensis Ashmead, 1890. Proc. U.S. Natl. Mus. **12**: 412. Type ♀: West Point, Nebr. (Washington).

Chromocryptus albopictus Ashmead, 1900. Proc. U.S. Natl. Mus. **23**: 41. Type ♀: Urbana, Ill. (Washington).

Agrothereutes (*Itamoplex*) *cressonii* Viereck, 1917. Bull. Connecticut Geol. Natl. Hist. Surv. **22**: 1332. Type ♀: Connecticut (Philadelphia).

Chromocryptus planosae planosae Townes, 1962. Bull. U.S. Natl. Mus. **216**(3): 257.

Trachysphyrus planosae Porter, 1967. Mem. Amer. Ent. Inst. **10**: 207.



1. *C. alvaradoi* (Jujuy Province, Argentina) .... ●
2. *C. poecilma* (Minas Gerais, Brasil)................................ ▲
3. *C. teres* (Simbal near Trujillo, Perú) .... ■
4. *C. huebrichi* (Curitiba, Brasil...also south to eastern Argentina) .... ▽
5. *C. prosopis* (Santiago del Estero, Argentina) .... ○
6. *C. tomsici* (Jujuy Province, Argentina) .... ◆
7. *C. golbachi* (Santiago del Estero Province, Argentina)................ ▼

Fig. 1. Distribution map for *Chromocryptus* in tropical and subtropical South America.

Townes' revisionary study of this taxon (1962: 256–8) summarizes the characters that separate *C. planosae* from other North and Middle American *Chromocryptus*. It defines the species biogeographically as a member of the Temperate Deciduous Forest Biome in eastern North America from Massachusetts south to Pennsylvania west to Michigan, Indiana, Illinois, and Nebraska. It also cites numerous host records for *C. planosae* as a "gregarious parasite" in pupae of the bombycoid genera *Tolype* and *Epicnaptera* (Lasiocampidae) and one rearing from the noctuoid *Halisidota* (Arctiidae).

No additional data have accumulated on *C. planosae*, since the publication of Townes' monograph.

2. *Chromocryptus weemsi* (Porter)
(Figs. 1, 5)

Trachysphyrus weemsi Porter, 1974. Fla. Ent. **57**: 331. Holotype ♀: Sarasota, Florida (Gainesville).

Chromocryptus weemsi Carlson, 1979. Catalog of Hymenoptera in America North of Mexico **1**: 458.

This species is known from 2 females and 1 male collected at Sarasota, Florida in McPhail and Steiner Traps during late winter and early spring (24 February to 14 April). In 1974 (331–5), I described *Chromocryptus weemsi* in relation to its northeast American relative, *C. planosae*. The species are closely allied but seem distinct on the basis of chromatic, sculptural, and proportional features, as summarized in the foregoing key.

3. *Chromocryptus mesorufus* Cushman
(Figs. 1, 7)

Chromocryptus mesorufus Cushman, 1930. Proc. U.S. Natl. Mus. **76**: 2. Holotype ♀: Cuernavaca, México (Washington).

Chromocryptus planosae mesorufus Townes, 1962. Bull. U.S. Natl. Mus. **216**(3): 259.

Trachysphyrus mesorufus Porter, 1977. Psyche **84**(1): 33–5.

Chromocryptus mesorufus shows great affinity to the eastern North American *C. weemsi* and *C. planosae*, as well as to *C. huebrichi* of southern Brasil and northeast Argentina. It occurs in México (Cuernavaca), the Lower Río Grande Valley of south Texas (McAllen), and recently has been reported at Miami, Florida in a blacklight trap (Carlson 1979: 457). The essential sympatry of *C.*

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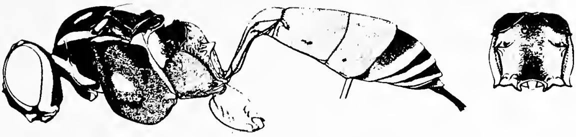

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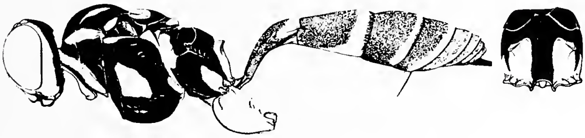

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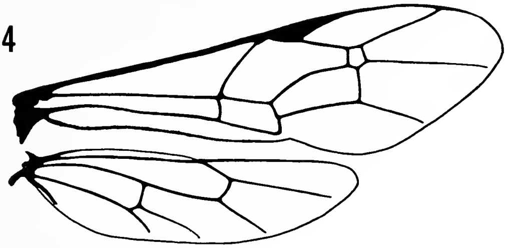

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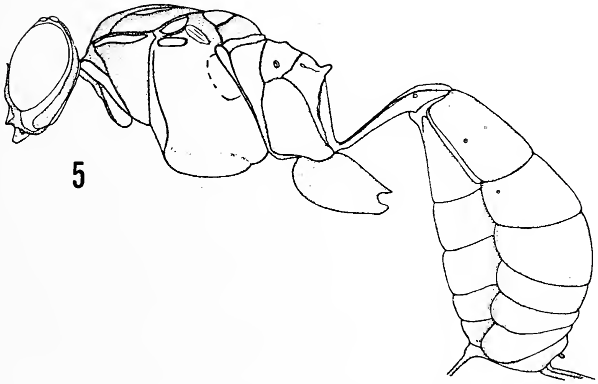


Fig. 2. *Chromocryptus planosae,* ♀. Body in lateral view and propodeum in dorsal view, showing habitus and color pattern. (From Townes 1962: 554). Fig. 3. *Chromocryptus vandykei,* ♀. Body in lateral view and propodeum in dorsal view, showing habitus and color pattern. (From Townes 1962: 554). Fig. 4. *Chromocryptus huebrichi,* ♀. Wings. (From Porter 1967: Fig. 71). Fig. 5. *Chromocryptus weemsi,* ♀. Holotype. Lateral view of body showing habitus and color pattern. (From Porter 1974: 332).

mesorufus and *C. weemsi* in southern Florida seems to confirm the specific distinctness of these close congeners.

A full description of *C. mesorufus* appears in my survey of mesostenine Ichneumonidae in the Lower Río Grande Valley (Porter 1977: 33–5). My Texas specimen was collected on 2 April 1975 at the McAllen Botanical Garden, where I swept it from thorny bushes at a site "dominated by *Prosopis juliflora*" with *Condalia obovata, Celtis pallida, Ehretia anaqua,* and *Baccharis neglecta* in the small tree and shrub stratum.

4. *Chromocryptus vandykei* Townes
(Fig. 3)

Chromocryptus planosae vandykei Townes, 1962. Bull. U.S. Natl. Mus. **216**(3): 258. Holotype ♀: "Havilah", Fresno, California (San Francisco).

Chromocryptus vandykei Carlson, 1979. Catalog of Hymenoptera in America north of Mexico 1: 458.

This is the only *Chromocryptus* of which I have not personally examined material. It remains known only from the unique holotype collected at Havilah, Fresno, County, California on 16 May 1930 by E. C. Van Dyke. It may be identified by reference to the foregoing key and to Townes' original treatment [1962 (3): 258–9].

5. **Chromocryptus alvaradoi** Porter, new species
(Figs. 1, 13)

FEMALE. *Color:* antenna black with some brown staining, especially below toward apex, and with a white band above on flagellomeres 6–9; head and mesosoma black with white markings as follows: orbital ring rather broadly, except for a brief interruption at bottom of eye and sometimes another short break above at level of front ocellus; transverse blotch on clypeus; large blotch on basal 0.5 of mandible; anterior margin of pronotum broadly over about median 0.8; white band on humeral margin of pronotum, which apicad becomes narrower, sometimes irregular, and sometimes suffused with brown; most of tegula; most of subalarum; about basal 0.4–0.3 of scutellum; and sometimes a spot in lower hind corner of mesopleuron; gastric tergites 1–3 varying from mostly red with much blackish staining laterad on 2 and 3 to mostly black with irregular reddish suffusion, the 2nd tergite sometimes with a small white area in its hind corner, and the 3rd tergite with a regular and only sublaterally interrupted or irregular and much fragmented white apical band; tergites 4–7 black with white apical bands that are narrowest dorsad and which become considerably broadened laterally; and tergite 8 black with dorsally interrupted apical white band; fore coxa varying from reddish white with much black staining to black with reduced red suffusion and with a large ventrolateral white blotch as well as a somewhat smaller dorso-lateral white area; mid coxa varying from red with a little dusky to black with some reddish staining and with a large latero-ventral white blotch as well as with smaller and more irregular latero-basal and apico-dorsal whitish areas; hind coxa red, with some black apicad or sometimes mostly black with a large dorso-lateral white blotch at base and with only a little reddish staining (particularly around the white blotch); fore and mid trochanters black with pale brown to whitish narrowly on apex and sometimes with a white spot ventrally on fore trochanter; fore and mid trochantelli shining brown, becoming dusky basad; hind trochanter black with some brown staining and narrowly whitish on apex; hind trochantellus mostly shining brown; femora and tibiae a little dully pale orange; hind femur also blackish on apex and hind tibia likewise with blackish both near base and apex; fore and mid tarsi brownish with considerable dusky staining beyond 1st segment; hind tarsus sometimes wholly black or sometimes with segments 3 and 4 white above on all but apex; wings subhyaline with moderately prominent dusky staining that is most evident on apical 0.2–0.3 of fore wing.

Length of fore wing: 8.4–9.1 mm. *Flagellum:* moderately long and slender, becoming slightly stouter and a little flattened below on about apical 0.3; last flagellomere apically truncate; 1st flagellomere 5.6–6.2 as long as deep at apex. *Clypeus:* in profile strongly high-convex to bluntly pyramidal, only a little asymmetric (basal face convex and approximately as long as the weakly concave apical face); apical margin practically truncate. *Malar space:* 0.73–0.80 as long as basal width of mandible. *Temple:* 0.39–0.44 as long as eye in dorsal view; strongly and directly receding. *Fore tibia:* stout and considerably inflated. *Pronotum:* with a more or less well defined and rather broad and shallow dorsal submarginal groove that becomes narrower and weaker behind. *Mesoscutum:* notauli weak and shallow, traceable 0.5 the length of mesoscutum; surface moderately shining with coarse reticulate wrinkling over a broad area along notauli, on periphery of lateral lobes, and more or less throughout toward apex, but mesad on central and lateral lobes becoming duller and with many moderately large, strong, subadjacent to confluent punctures and definite fine micro-reticulation. *Mesopleuron:* speculum shining with much coarse wrinkling or sometimes also partly smooth and shining; surface otherwise with coarse reticulate wrinkling. *Wing venation:* radial cell 4.0–4.4 as long as wide; areolet large, intercubiti moderately to somewhat strongly convergent above, 2nd abscissa of radius 0.7–0.8 as long as 1st intercubitus; 2nd recurrent weakly inclivous, almost straight; discocubitus at most weakly angled, with or without a stump of a ramellus; nervulus antefurcal; upper part of nervellus 1.8–2.0 as long as lower; axillus close to hind margin of wing. *Propodeum:* short and high, with the basal face gently and convexly sloping rearward and the approximately equal apical face discrete and almost vertically declivous; spiracle 2.3–3.0 as long as wide; basal trans-carina sharp throughout, strongest medially; apical trans-carina weak and irregular, best defined medially; cristae short ligulate, large, stout, conspicuously projecting; median longitudinal carinae irregularly detectable, defining a more or less sharply hexagonal and wider than long areola and very faintly demarking a median apical area; surface coarsely reticulately wrinkled, except with definitely finer wrinkling and some intercalated punctures basad of basal trans-carina. *First gastric tergite:* petiole moderately slender and with a broad, rounded-off subtriangular lateral expansion at base; postpetiole strongly widened, 1.8–2.1 as wide apically as long from spiracle to apex; surface of postpetiole broadly smooth and shining, without dorsal carinae and with a little micro-shagreening (sometimes extensive shagreening) centrally and laterally, and on apical 0.3 with many large, strong, subadjacent or a little sparser to adjacent or restrictedly confluent punctures, as well as with some widely scattered large punctures elsewhere. *Second gastric tergite:* smooth and shining with only faint micro-shagreening and with abundant large, sharp, mostly briefly subadjacent to adjacent or reticulately confluent punctures that emit short, scarcely overlapping setae. *Gaster:* rather short and stout fusiform; 3rd tergite with punctures nearly as strong and dense as those on 2nd, but the following tergites with considerably weaker and sparser punctures. *Ovipositor:* sheathed portion 0.39–0.41 as long as fore wing; straight, stout, markedly compressed; nodus very slightly suggested and with at most a faint trace of a notch; dorsal valve very gradually tapering from nodal area to near apex and then becoming slightly convex in profile on apex; ventral valve on tip with strong and nearly vertical ridges; tip 0.20 as high at nodal area as long from nodal area to apex.

MALE. Unknown.

TYPE MATERIAL. Holotype ♀: ARGENTINA, Jujuy Province, Posta de Lozano, 27-30-XI-1967, C. Porter, E. Willink. Paratype: 1♀, same locality as holotype, 6-XII-1967, C. Porter. Holotype in Florida State Collection of Arthropods; paratype in Collection of Charles C. Porter.

RELATIONSHIPS. *Chromocryptus alvaradoi* deviates markedly from other species of its genus. It shows many chromatic and structural differences from all South and North American congeners. Some of these diagnostic features include the infuscate wings, absence of white markings on the propodeum, greater size, high but not asymmetric clypeus, inflated fore tibia, coarse wrinkling on much of speculum, comparatively long propodeal spiracle, and robust ovipositor with its weakly tapering (instead of sagittiform) tip and vertical ridges on the lower valve.

At Posta de Lozano, this *Chromocryptus* occurs sympatrically with *C. tomsici,* a much smaller species that is closely related to *C. huebrichi* and *C. planosae.* The two form show no evidence of intergradation and confirm their specific integrity by adaptive differences (e.g., ovipositor tip structure) which surely bespeak distinct host preferences.

FIELD NOTES. The type locality is situate on Argentine National Route 9 in Jujuy Province about 25 km north of San Salvador de Jujuy and between the villages of Yala and León. Posta de Lozano faces the entrance to the Quebrada de Humahuaca at about 1600 m altitude. The area supports a singularly diverse vegetation with elements of subtropical wet forest (*Erythrina,* many epiphytic bromeliads), Alder Forest (*Alnus jorullensis*), and, in drier exposed sites, with Chaco communities dominated by *Serjania*-festooned *Acacia* and *Celtis.*

SPECIFIC NAME. For Dr. Carlos Alberto Alvarado, the distinguished Argentine Medical Entomologist and propietor of the Posta de Lozano Motel, a hospitable base for enthralling fieldwork.

6. *Chromocryptus poecilma* (Porter), new combination (Fig. 1)

Trachysphyrus poecilma Porter, 1967. Mem. Amer. Ent. Inst. 10: 210–1. Holotype ♀: Pirapora, Minas Gerais, Brasil (Cambridge).

FEMALE. *Color:* antenna dull brownish black with a large white blotch below on scape and a white band above on flagellomeres 6 (apically)–12 (basally); head and mesosoma black with profuse white markings as follows: basal 0.6 of mandible; most of clypeus; most of face; very broad orbital band which expands across most of temple behind and fills malar space below; propleuron apically; broad anterior margin of pronotum; broad dorsal margin of pronotum, except on median 0.3; pair of stripes on mesoscutum; all but apex of scutellum; tegula; subalarum; anterior margin of mesopleuron dully; very broad oblique band between prepectus at mid-height and lower hind margin of mesopleuron, from which an ellipsoidal branch reaches forward below along sternaulus almost to prepectal carina; large blotch in upper hind corner of mesopleuron; posterior margin of mesopleuron; upper metapleuron; and all of posterio-lateral area of propodeum from crista to hind margin; gaster pale red with broad, complete white apical bands on tergites 1, 2, and 4, as well as with narrower and dorsally incomplete white apical bands on tergites 5–7; fore and mid coxae and trochanters white, legs otherwise mostly pale red, with some dusky on fore and mid apical tarsomeres, toward apex of hind tibia, and more distinctly on hind tarsus which also has a white subapical external area on 1st segment and segments 2–4 wholly white; wings hyaline.

Length of fore wing; 5.6 mm. *Flagellum:* 1st segment 4.8 as long as deep apically. *Malar space:* 1.0 as long as basal width of mandible. *Temple:* 0.30 as long as eye in dorsal view; a little rounded off and strongly receding. *Mesoscutum:* notauli very weak and shallow, vaguely suggested for about 0.6 the length of mesoscutum; surface rather dully shining with some fine micro-reticulation and with abundant, large, strong, subadjacent to adjacent or confluent punctures that average sparsest on lateral lobes but which also become widely spaced for a short distance on central lobe medially, the surface also with more or less well developed oblique wrinkling along notauli and with some reticulate wrinkling over an extensive central area behind. *Mesopleuron:* speculum swollen, smooth and polished; surface otherwise with fine, mostly regular long wrinkles radiating from speculum and gradually fading into reticulo-punctation on anterio-ventral 0.5 of mesopleuron. *Propodeum:* spiracle 1.5 as long as wide; basal trans-carina medially sharp but lower and somewhat irregular sublaterally; apical trans-carina strong, becoming irregular medially; cristae large, strongly projecting, obtusely cuneate; median apical area rather strongly but irregularly defined; surface coarsely reticulately wrinkled. *First gastric tergite:* postpetiole 2.0 as wide apically as long from spiracle to apex; surface of postpetiole shining with fine and distinct micro-reticulation which fades out apically and with scattered large, strong punctures which are most abundant apicad and (especially) laterad, where they average largely subadjacent; setae short and mostly well separated. *Second gastric tergite:* shining with fine, distinct micro-reticulation which becomes stronger laterad and also with abundant large, sharp, mostly subadjacent to adjacent punctures emitting short setae that mostly equal or fall short of the length of their interspaces. *Ovipositor:* tip 0.16 as high at notch as long from notch to apex.

MALE: Unknown.

DISCUSSION. This species is closely related to *C. teres* Porter, but may be distinguished by the characters given in the key. The holotype is the only specimen so far collected.

7. **Chromocryptus teres** Porter, new species
(Figs. 1, 11)

FEMALE. *Color:* antenna dull reddish on scape, pedicel, and first 3 or 4 flagellar segments, grading into black on rest of flagellum, except for white above on most of flagellomeres 7–9 and slightly on base of 10; head and mesosoma black with brownish on some margins and sutures and with profuse white markings as follows: large blotch on base of mandible; most of clypeus; very broad orbital ring with ventro-posterior extension across most of malar space and only a brief gap at bottom of eye anteriorly, broad and medially brownish-interrupted band on pronotal collar dorsally; broad band on most of anterio-lateral margin of pronotum; very broad band on dorso-lateral margin of pronotum; most of tegula; broad white stripe along each notaulus on median 0.7 of mesoscutum; most of scutellum and postscutellum; most of subalarum; very large oblique blotch on anterior 0.5 of mesepisternum from about upper end of prepectal carina almost to sternaulus at its midlength; small spot in lower hind corner of mesepisternum; dull brown tinged area near top of mesepimeron; very large blotch on most of upper metapleuron; large dorsal area on lower metapleuron along pleural carina on apical 0.6 of sclerite; and lateral 0.3 of propodeum, including crista; gaster red: 1st tergite with a broad white apical band that is briefly interrupted on meson; 2nd tergite with weak dusky staining and a prominent, medially well interrupted subapical white band; 3rd tergite with faint dusky staining but no white; 4th tergite with a very broad, laterally incomplete white apical band; and 5th tergite blackish red with a broad, laterally incomplete white apical band; 6th and 7th tergites similar to 5th but with narrower white bands; 8th tergite dull reddish; legs red with black anteriorly on fore coxa, dorso-posteriorly on mid coxa, dorso-anteriorly on fore trochanter, on last 2 or 3 fore and mid tarsomeres, on much of hind trochantellus, inconspicuously toward apex above on hind femur, extensively (especially apicad) on hind tibia, and on much of hind tarsus, as well as with white or whitish anteriorly and posteriorly on fore coxa, dorsally on mid coxa, anteriorly on fore and mid trochanters, and on all of 2nd and most of basal 0.5 of 1st tarsomere; wings hyaline with faint brownish staining.

Length of fore wing; 6.5 mm. *First flagellomere:* 4.4 as long as deep at apex. *Malar space:* 0.9 as long as basal width of mandible. *Temple:* 0.3 as long as eye in dorsal view, anteriorly rounded off and then steeply, directly receding. *Face:* with a large and gently raised, rounded median swelling. *Hypostomal carina:* a weakly elevated flange. *Mesoscutum:* notauli nearly percurrent, extremely shallow; mesoscutal surface shining with coarse, reticulate wrinkling along notauli, between notauli on apical 0.5, and exteriorly on lateral lobes, as well as with some duller micro-reticulate areas centrad on lobes. *Mesopleuron:* speculum swollen, mostly smooth and polished; surface otherwise shining with strong, rather straight to gently sinuate wrinkles radiating extensively from speculum but grading into more puncto-reticulate surface anteriad and ventrad. *Wing venation:* radial cell 3.7 as long as wide; areolet large, intercubiti only weakly convergent above, 2nd abscissa of radius 1.0 as long as 1st intercubitus; 2nd recurrent reclivous, straight; disco-cubitus broadly angulate, without a ramellus; nervulus antefurcal; upper part of nervellus 3.5 as long as lower. *Propodeum:* short, high, basal face gently arched and sloping rearward; apical face discrete, vertical, about as long as basal; spiracle 1.9 as long as wide; basal trans-carina sharp throughout; apical trans-carina irregular but traceable between cristae; cristae short ligulate, large and strongly projecting; median apical area irregularly suggested; median longitudinal carinae and lateral longitudinal carinae vague; surface shining, coarsely reticulately wrinkled, except with strong but finer puncto-reticulation basad of basal trans-carina. *First gastric tergite:* postpetiole 2.0 as wide apically as long from spiracle to apex; surface of petiole shining, finely micro-reticulate on basal 0.7 and polished and nearly smooth on apical 0.3, with only a few small to medium sized, sparse punctures and scattered short setae which only laterally approach the length of their interspaces; flange laterally at base of petiole unusually low, narrow, and rounded in contour. *Second gastric tergite:* rather silky-shining with delicate micro-reticulation, except on the polished apex, and with abundant, medium sized, prominent but shallow punctures which are separated by 1–3× their diameters (densest laterad) and which show some areas of even wider separation mesally and basally; punctures emitting short setae that mostly fall short of the length of their interspaces. *Ovipositor:* sheathed portion 0.36 as long as fore wing; straight, slender, compressed; nodus weakly defined with a broad but shallow notch; dorsal valve with a gentle, direct taper from notch to apex; ventral valve with fine oblique ridges on tip; tip 0.14 as high at notch as long from notch to apex.

MALE. Unknown.

TYPE MATERIAL. Holotype ♀: PERÚ, La Libertad Province, Simbal, 16-VII-1982, C. Porter, T. O'Neill. Holotype in Florida State Collection of Arthropods.

RELATIONSHIPS. This species belongs to the same radiation that includes the North and Middle American *Chromocryptus* as well as *C. poecilma, C. huebrichi, C. prosopis,* and *C. tomsici* from Brasil and Argentina. Its nearest relative and probable vicariant is the south Brasilian *C. poecilma* (Porter 1967: 210–11), which it approaches in mesoscutal and mesopleural sculpture, as well as in many details of coloration. *C. teres* differs from *C. poecilma* by having much sparser punctures on the 2nd gastric tergite and by lacking a white blotch in the upper hind corner of the mesopleuron. The sparse 2nd gastric punctures (separated mostly by 1–3× their diameters) also separate *C. teres* from other members of its species group (2nd gastric punctures subadjacent to adjacent).

FIELD NOTES. The unique holotype was swept from semishaded undergrowth along a dry river bed at Simbal near Trujillo, Perú. This locality, at the lower extreme of a fertile valley in the north Peruvian Coastal Desert, has a natural vegetation dominated by *Prosopis, Acacia, Opuntia, Cereus,* and much other Thorn Scrub (Sonoran-Chaqueñan) vegetation.

SPECIFIC NAME. From the Latin adjective *teres,* "polished, rounded, elegant."

8. *Chromocryptus huebrichi* (Brèthes)
(Figs. 1, 4, 8, 9)

Agrothereutes Huebrichi Brèthes, 1913. An. Mus. Nac. Hist. Natl. Buenos Aires **24**:41. Lectotype ♀ (labeled by Townes, 1965), no data, (Buenos Aires).

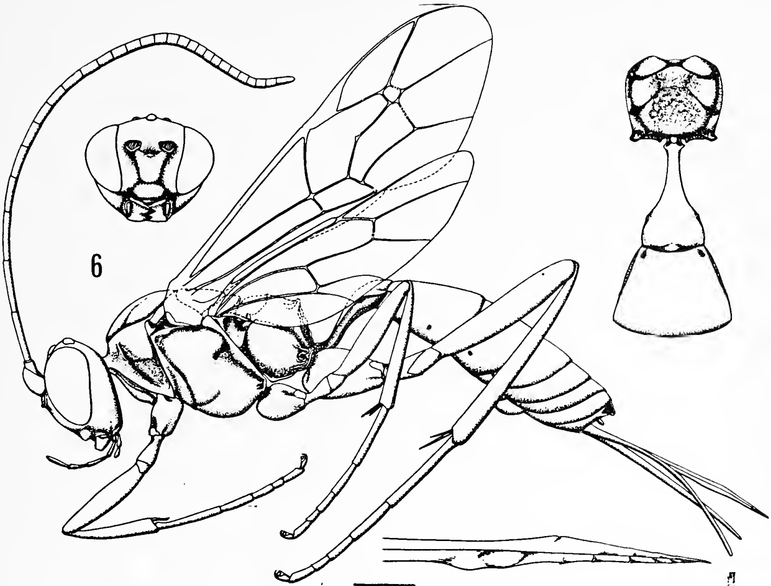
Spilocryptus argentinensis Mallo, 1954. Idia 73-5:30. *Nomen nudum.*

Chromocryptus planosae, new subspecies, Townes, 1962. Bull. U.S. Natl. Mus. **216**(3): 257.

Trachysphyrus planosae huebrichi Townes, 1966. Mem. Amer. Ent. Inst. **8**: 72.

Trachysphyrus huebrichi Porter, 1967. Mem. Amer. Ent. Inst. **10**: 207–10.

FEMALE. *Color:* antenna black, brownish below toward apex, sometimes with a small white spot below on scape and at base of 1st flagellomere, a white band above on flagellomeres 6 (in part) or 7 to 10 or base of 11; head and mesosoma black with profuse white markings as follows: about basal 0.5 of mandible; most of clypeus; orbits very broadly, with a narrow interruption at bottom of eye, and behind expanding to cover most of lower temple and malar space, as well as broadened in front so as to cover most of face except for area above clypeus and below antennal sockets; propleuron apicad; broad margin on anterior margin of pronotum, except near apex; broad band on all but median 0.3 of dorsal margin of pronotum; pair of stripes on mesoscutum; tegula; subalarum; large anterio-median blotch, smaller blotch in lower hind corner, and most of hind margin of mesopleuron; scutellum except near apex; upper metapleuron; ellipsoid blotch on apical 0.5 of lower metapleuron; and broad posterio-lateral bar on propodeum extending from crista to hind margin; gaster pale red; 4th gastric tergite with a



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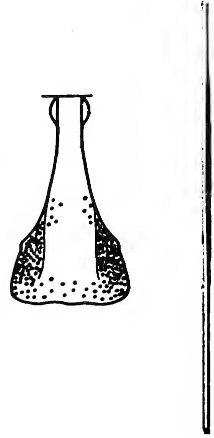

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Fig. 6. *Chromocryptus planosae,* ♀. Habitus sketches of body in lateral view, head in anterior view, and propodeum with first two gastric tergites in dorsal view. (From Townes 1962: 536). Fig. 7. *Chromocryptus mesorufus,* ♀. Gaster in dorsal view, showing color pattern and habitus. (From Porter 1977: 40). Fig. 8. *Chromocryptus huebrichi,* ♀. Ovipositor tip in lateral view. (From Porter 1967: Fig. 32). Fig. 9. *Chromocryptus huebrichi,* ♀. Dorsal view of first gastric tergite. (From Porter 1967: Fig. 103).

white apical band that is preceded by a blackish area; succeeding tergites blackish with dorsally much narrowed white bands; legs pale red: fore and mid coxae and more or less of their trochanters below, white, the trochanters sometimes a little dusky above; hind tibia irregularly dusky toward apex; fore and mid tarsi dusky toward apex; hind tarsus more or less dusky with a usually subapical white band or blotch on 1st segment and with more or less of segments 2–4 white; wings hyaline, sometimes faintly brownish apicad.

Length of fore wing: 5.6–6.7 mm. *First flagellomere:* 5.3–5.5 as long as deep at apex. *Malar space:* 0.9–1.1 as long as basal width of mandible. *Temple:* 0.30–0.40 as long as eye in dorsal view; rounded off and strongly receding. *Mesoscutum:* notauli narrow and very weak except near base, traceable 0.5–0.7 the length of mesoscutum; surface dully shining, throughout coarsely and granularly puncto-reticulate. *Mesopleuron:* speculum swollen, largely smooth and polished; surface otherwise rather finely puncto-reticulate to reticulately wrinkled. *Propodeum:* spiracle 1.7–2.0 as long as wide; basal trans-carina well defined throughout, sometimes a little irregular; apical trans-carina weaker than basal, becoming very indistinct medially; cristae large and stout, obtusely cuneate; median apical area irregularly suggested; surface strongly reticulately wrinkled. *First gastric tergite:* postpetiole 1.7–2.3 as wide apically as long from spiracle to apex; surface of postpetiole smooth and shining with fine, often largely obscure micro-reticulation and with scattered large, sharp punctures which become mostly subadjacent to adjacent over a broad area laterally and which emit short setae that laterally largely equal or a little exceed the length of their interspaces. *Second gastric tergite:* smooth and shining with fine, rather obscure micro-reticulation that becomes stronger laterad and with abundant large, sharp, mostly subadjacent to adjacent punctures that average more crowded and a little smaller toward apex and, especially, laterad, and which emit short setae that mostly equal or exceed the length of their interspaces. *Ovipositor:* tip 0.17–0.21 as high at notch as long from notch to apex.

MALE. Differs from female as follows: *Color:* antenna black except for a large white spot below on scape; clypeus and face almost wholly white; only basal 0.7 of scutellum white; apical 0.5 of 3rd gastric tergite blackish; 4th tergite more generally blackish, its apical white band interrupted medially; succeeding tergites more deeply black than in female, their white apical band broader and not narrowed above; white blotch on clasper; fore and mid trochanters with a brownish stripe above; hind femur slightly dusky near apex; hind tibia dull red, becoming gradually blackish above beyond base, especially on apical 0.5.

Length of fore wing: 5.1 mm. *First flagellomere:* 3.6 as long as deep apically. *Malar space:* 0.7 as long as basal width of mandible. *Temple:* 0.50 as long as eye in dorsal view; rounded off and moderately receding. *Mesoscutum:* surface with stronger, larger, and more discrete punctures than in female, which are mostly adjacent to reticulately confluent on central lobe but which on lateral lobes become partly subadjacent with palpable interspaces. *Propodeum:* spiracle 2.1 as long as wide; basal trans-carina very sharp and high; apical trans-carina a little irregular but strong and sharp; cristae large and strongly projecting short-ligulate; median longitudinal carinae sharp throughout, rather strongly but irregularly defining the median apical area; lateral longitudinal carinae strong and sharp; surface grossly reticulate. *First gastric tergite:* postpetiole 1.4 as wide apically as long from spiracle to apex; surface of postpetiole smooth and shining with only a trace of micro-reticulation, its punctures even larger and sharper than in female but sparser, mostly subadjacent laterad; setae a little longer than in female but mostly well separated. *Second gastric tergite:* with punctures that are even larger, sharper, and denser (mostly subadjacent) than in female.

Specimens Examined. 16♀ and 1♂: ARGENTINA, Buenos Aires Province, Olivos, XI-1952, J. Foerster (Ottawa); BRASIL, Paraná State, Quatro Barros nr. Curitiba, 5-II-1966, H. and M. Townes (Townes).

Relationships. Townes (1966: 72) has regarded *C. huebrichi* as a subspecies of the eastern North American *C. planosae.* The two entities, indeed, are closely related. They share such features as a delicate and sagittate ovipositor tip, lack of smooth areas on the mesocutum, and absence of strong wrinkles radiating from the mesopleural speculum. However, the following characters distinguish *C. huebrichi* from its Nearctic congener: propodeum and mesopleuron black with white markings (versus extensively red as well as with black and white maculation), face mostly white (versus mostly black), lower metapleuron black with a large white blotch (versus mostly red), malar space 0.9–1.1 as long as basal width of mandible (versus 0.8–0.9), propodeal spiracle 1.7–2.0 as long as wide (versus 1.4–1.5), and large punctures widely scattered on median field of postpetiole (versus rather dense).

Chromocryptus huebrichi also much resembles the northwest Argentine *C. tomsici, C. prosopis,* and *C. golbachi.* These species are distinguished in the key but also show some additional differences, as summarized here: female of *C. huebrichi* with 1st flagellomere 5.3–5.5 as long as deep at apex (5.8–6.0 in *C. tomsici*); malar space in female *C. huebrichi* 0.90–1.0 as long as basal width of mandible (0.84–0.85 in *C. tomsici*); propodeal spiracle 1.7–2.0 as long as wide in *C. huebrichi* (1.3–1.5 in *C. prosopis*); female postpetiole with scattered punctures medially in *C. huebrichi* (with dense punctures, even on median field, in *C. tomsici*); no white on male postscutellum in *C. huebrichi* (postscutellum mostly white in *C. golbachi*); malar space 0.70 as long as basal width of mandible in *C. huebrichi* males (0.80 in *C. tomsici,* 0.53–0.66 in *C. prosopis,* and 0.80–0.85 in *C. golbachi*); male postpetiole 1.4 as wide apically as long from spiracle to apex in *C. huebrichi* (1.2 in *C. tomsici,* 1.6 in *C. prosopis,* and 1.8–1.9× in *C. golbachi);* and male postpetiole with large punctures sparse medially in *C. huebrichi* (subadjacent to reticulately confluent in *C. prosopis* and *C. golbachi*).

The above-cited differences show that *C. huebrichi, C. planosae, C. tomsici, C. prosopis,* and *C. golbachi* manifest multiform but often slight phaenotypic divergence. When more specimens are collected, they should furnish evidence about the extent of geographic and intrapopulation variability among these *Chromocryptus* and prove whether this widely distributed *Planosae* group consists mainly of discrete species or of intergrading geographic races.

HABITAT NOTES. Most of the type series was collected near Curitiba, Brasil on the 1000 m high, cool, wet Planalto of Paraná State. This region is characterized floristically by subtropical wet forests of myrtaceous and other angiosperm trees plus *Araucaria* and *Podocarpus.* The forests are broken in places by grasslands, whose biota recalls that of the Argentine pampas.

I have no information as to the precise microhabitats where *C. huebrichi* was collected.

HOSTS. Mallo (1954, as cited above) reared *C. huebrichi* from the lasiocampid moth, *Titya proxima.*

9. **Chromocryptus prosopis** Porter, new species
(Figs. 1, 10)

FEMALE. *Color:* scape and pedicel brownish black, a large white area below on scape; flagellum dark brown with a reddish tint and with a white band above on flagellomeres 6 (beyond base) to 11 (slightly on base); head black with white as follows: on a broad orbital ring, which may be narrowly interrupted at bottom of eye or complete and below expanded so as to cover most of temple; on a large V-shaped median facial area (contiguous dorso-laterally with white orbital ring), on most of clypeus (contiguous above with the white facial blotch); and on basal 0.5 or more or mandible, as well as with more or less well developed light brown areas in anterior white orbital bands, light brownish on antennal sockets, on apical margin of clypeus, on part of mandible, and sometimes elsewhere; mesosoma dull red with extensive dusky to black staining, especially on pronotum and mesoscutum, as well as with white as follows: spot on apex of propleuron; broad band on anterior margin of pronotum, extending almost to apex; very broad band on all but median 0.3 of dorsal margin of pronotum; tegula; subalarum; basal 0.3–0.6 of scutellum; most of upper metapleuron; small white area at apex of lower metapleuron; broad posterio-lateral bar on propodeum from crista to hind margin; gaster dull to bright red with some weak but extensive dusky staining and with white as follows: a broad apical band on 1st tergite, a narrower and somewhat fragmented apical band (broader laterad) on 2nd tergite, and 4th tergite with a very broad white apical band that ends abruptly laterad far from lower margin; fore and mid coxae and trochanters mostly white with some blackish and reddish areas; legs otherwise reddish, paler on fore legs, and with much dusky on tarsi, as well as with 3rd and (sometimes) most of 4th hind tarsomeres white; wings hyaline with a vague brownish tint apicad.

Length of fore wing: 5.8–6.0 mm. *First flagellomere:* 5.0–5.6 as long as deep at apex. *Malar space:* 0.93–1.0 as long as basal width of mandible. *Temple:* 0.36–0.43 as long as eye in dorsal view; anteriorly rounded-off and then very strongly receding. *Mesoscutum:* weakly to very weakly traceable for about 0.5 the length of mesoscutum; surface dully shining and uniformly with strong puncto-reticulation plus (especially medio-posteriad) coarse reticulate wrinkling. *Mesopleuron:* speculum swollen, mostly smooth and polished;

Fig. 10. *Chromocryptus prosopis,* ♀. Holotype. Photograph of entire insect and cocoon from which it emerged.

surface otherwise uniformly, rather finely and granularly puncto-reticulate. *Propodeum:* spiracle 1.3–1.5 as long as wide; basal trans-carina sharp and high throughout; apical trans-carina traceable but weak to obsolete (especially mesad), irregular, its cristae large and stout, cuneo-ligulate, conspicuously projecting; median and lateral longitudinal carinae scarcely suggested, neither the areola nor the median apical area defined; surface largely with strong reticulate wrinkling, but more puncto-reticulate basad of basal trans-carina. *First gastric tergite:* postpetiole 1.8–2.0 as wide apically as long from spiracle to apex; surface of postpetiole smooth and silky-shining with faint micro-aciculation and very large, sharp punctures which become mostly subadjacent laterad but are very sparse elsewhere, punctures emitting short setae which even laterad do not surpass the length of their interspaces; base of petiole with a low and rounded-off lateral flange. *Second gastric tergite:* shining, with a little micro-reticulation and with abundant, mostly subadjacent to somewhat reticulately confluent, sharp, medium sized punctures; its setae short, mostly equalling or falling a little short of the length of their interspaces. *Ovipositor:* tip 0.18–0.20 as high at notch as long from notch to apex.

MALE. Differs from female as follows: *Color:* antenna brownish, more red-tinged below, with white only on scape below; clypeus and face often almost completely pure white; white orbital ring very broad, reaching rearward to occipital carina on lower 0.6 of temple; propleuron largely white; mesopleuron with white irregularly below on prepectus, white on a large blotch in lower front quadrant just distad of prepectal carina, and also white on a broad band that parallels sternaulus below and reaches about 0.6 the distance to apex of mesopleuron; mesepimeron white dorsally; scutellum white on basal 0.7; gaster with a broad white apical band on both 1st and 2nd tergites, a narrower and laterally aborted white apical band on 3rd tergite (or rarely without white on tergite 3), and a broad and laterally aborted white apical band on 4th tergite; fore tibia and tarsus tinged with whitish; 3rd and 4th hind tarsomeres white.

Length of fore wing: 5.3–5.4 mm. *First flagellomere:* 3.8–4.0 as long as deep at apex. *Malar space:* 0.53–0.66 as long as basal width of mandible. *Mesoscutum:* notauli narrow but well defined, traceable about 0.8 the length of mesoscutum; surface coarsely puncto-reticulate throughout. *Propodeum:* spiracle 1.7 as long as wide; median longitudinal carinae weakly to rather strongly defined and more or less vaguely delimiting an areola and a median apical area; lateral longitudinal carinae weak and irregular; surface grossly reticulate. *First gastric tergite:* postpetiole 1.6–1.7 as wide apically as long from spiracle to apex; surface of postpetiole with numerous large, coarse punctures which may be in great part subadjacent but sometimes are irregularly sparser or even mostly sparse; baso-lateral flange of petiole small and weak. *Second gastric tergite:* with even coarser, larger, and denser punctures than in female, most of which are adjacent to reticulo-confluent.

TYPE MATERIAL. Holotype ♀: ARGENTINA, Santiago del Estero Province, Santiago del Estero, reared from cocoon adhering to bark of *Prosopis alba* found by D. Havrylenko during VIII-1963. Paratypes: 2♀ and 5♂, same data as holotype. Holotype in Florida State Collection of Arthropods. Paratypes in Collection of Charles C. Porter (1♀, 1♂), in American Entomological Institute (1♀, 1♂), in the Museum of Comparative Zoology (1♂), in the Snow Entomo-

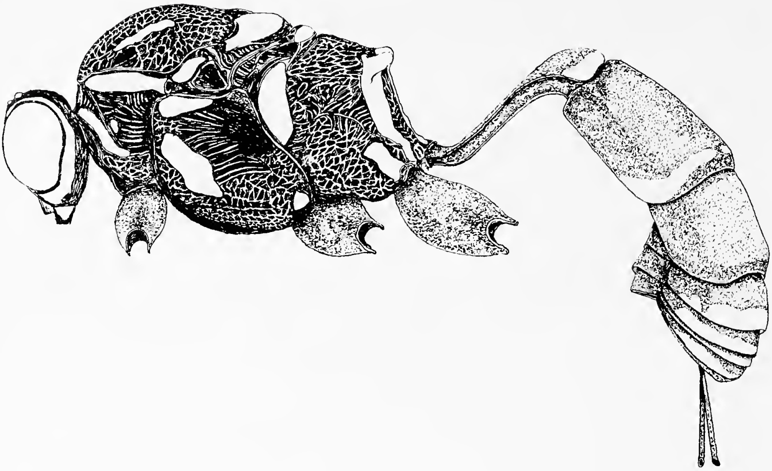

Fig. 11. *Chromocryptus teres.* ♀. Holotype. Body in lateral view, showing habitus and color pattern.

logical Museum of the University of Kansas (1♂), and in the Collection of Texas A&M University (1♂).

RELATIONSHIPS. *Chromocryptus prosopis* is very similar to the nearly sympatric *C. tomsici.* Besides the diagnostic features cited in the key, *C. prosopis* has the 1st female flagellomere 5.0–5.6 as long as deep at apex (5.8–6.0 in *C. tomsici*) and the female malar space 0.93–1.0 as long as the basal width of the mandible (0.84–0.85 in *C. tomsici*).

FIELD NOTES. The type locality is in the Dry Chaco Biome of northern Argentina, a semideciduous subtropical forest and scrub characterized by such plants as *Prosopis, Acacia, Cercidium, Schinopsis, Aspidosperma, Celtis, Condalia, Zizyphus, Trithrinax, Opuntia,* and many other xerophytes. This community in floristic composition and environmental parameters much resembles the south Texas Thorn Scrub, where *Chromocryptus mesorufus* has been collected.

HOSTS. All of the type specimens were reared from a single, large, tough, gray cocoon found on *Prosopis alba* (Leguminosae), a South American mesquite. Gregarious parasitism also has been observed in the North American *Chromocryptus planosae* (Townes 1962: 258).

Specific Name. For the leguminous shrub, *Prosopis,* on which the host of this species feeds.

10. **Chromocryptus tomsici** Porter, new species
(Figs. 1, 12)

Female. *Color:* scape dark reddish brown with a white area beneath, pedicel and flagellum brown to black with white above on flagellomeres 7–10 or sometimes onto base of 11; head black with white on a broad orbital ring that is briefly interrupted at bottom of eye, on a large, V-shaped median facial mark (in some specimens small and irregular), on most of clypeus, and on much of basal 0.5 of mandible; mesosoma black with white as follows: a broad band (sometimes mesally narrowed) on all but apex of anterior margin of pronotum; a band on all but median 0.3 of dorsal margin of pronotum; tegula on basal 0.6 or more; subalarum; basal 0.3 of scutellum; sometimes a tiny spot in lower hind corner of mesopleuron; most of

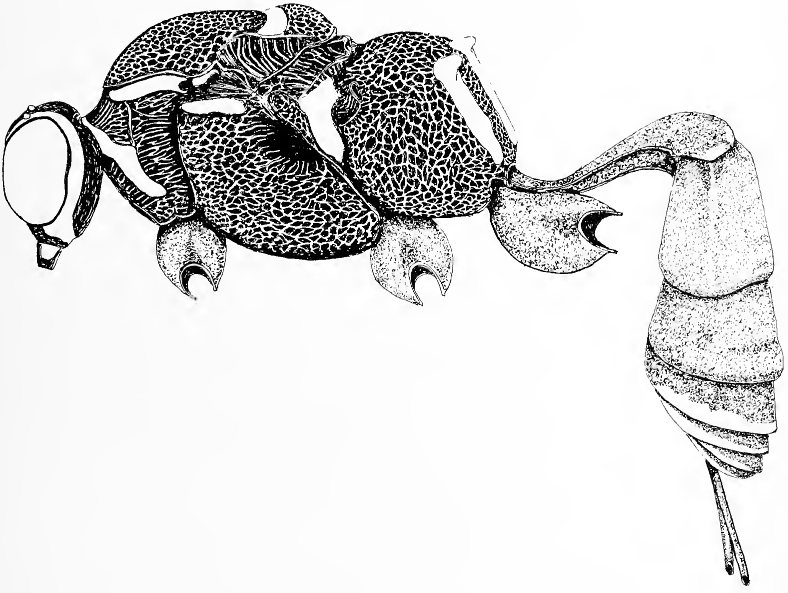

Fig. 12. *Chromocryptus tomsici,* ♀. Holotype. Body in lateral view, showing habitus and color pattern.

upper metapleuron; sometimes a vague suffusion on apex of lower metapleuron; and broad posterio-lateral bar on propodeum from crista to hind margin; gaster red with some blackish staining, especially on 5th and following tergites but sometimes also extensive on 2nd and 3rd tergites, and with the following white: a broad and medially obsolete apical band on 1st tergite; a very broad and nearly complete apical band on 4th tergite; a narrower, laterally widened apical band on 5th tergite; and with still narrower, dorsad broadly interrupted apical bands on following tergites; fore and mid coxae white with extensive black marks; fore and mid trochanters white below and reddish brown above; legs otherwise red with dusky on tarsi, especially on hind tarsus, and with white on 3rd and (sometimes) also on more than basal 0.5 of 4th hind tarsomeres; wings hyaline with faint dusky staining apicad on fore wing.

Length of fore wing: 4.6–5.8 mm. *First flagellomere:* 5.8–6.0 as long as deep at apex. *Malar space:* 0.84–0.85 as long as basal width of mandible. *Temple:* gently rounded and very strongly receding; 0.37–0.40 as long as eye in dorsal view. *Mesoscutum:* notauli very faint, detectable 0.5–0.6 the length of mesoscutum; surface uniformly with strong rugose wrinkling that sometimes grades into dense puncto-reticulation laterad. *Mesopleuron:* speculum swollen, mostly smooth and polished, and with a few (sometimes very few) strong and short wrinkles radiating from its periphery; surface otherwise uniformly strongly but rather finely and granularly reticulately wrinkled. *Propodeum:* spiracle 1.4–1.8 as long as wide; basal trans-carina fine but well developed throughout and sometimes rather strongly raised; apical trans-carina weakly and irregularly traceable throughout; cristae strongly projecting, symmetric, short-ligulate or subligulate; longitudinal carinae obsolete; median apical area sometimes irregularly delimited. *First gastric tergite:* postpetiole 1.8–1.9 as wide apically as long from spiracle to apex; surface of postpetiole silky-shining with at least a little and sometimes with conspicuous micro-reticulation and with abundant very large and coarse punctures that are irregularly distributed but extensively subadjacent on median field and which become even denser laterad; setae rather long, in part equalling the length of their interspaces; base of petiole with a low and subtriangular lateral flange. *Second gastric tergite:* a little dully shining and minutely aciculate, with abundant, uniformly distributed, medium sized, mostly almost sub-

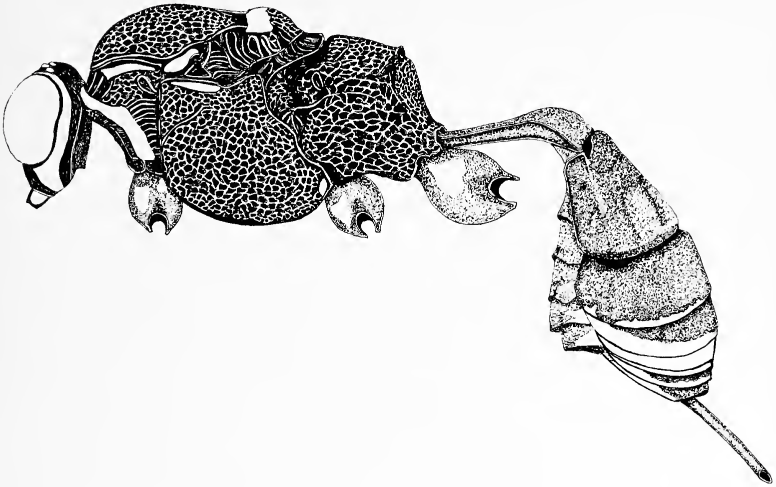

Fig. 13. *Chromocryptus alvaradoi,* ♀. Holotype. Body in lateral view, showing habitus and color pattern.

adjacent to in part reticulately confluent punctures; setae short, mostly about as long as their interspaces. *Ovipositor:* 0.19–0.21 as high at notch as long from notch to apex.

MALE. Differs from female as follows: *Color:* no white on flagellum; face largely white, except for an extensive black spot that reaches dorsad from each anterior tentorial pit and for a median dot below antennal sockets; white spot on apex of propleuron; white on most of basal 0.5 of scutellum; propodeal posterio-lateral white bars broader than in female, leaving only median 0.3 of hind propodeal face black; white vaguely developed on apex of 1st gastric tergite; 4th tergite with a broad white apical band on median 0.5 only; 5th and following tergites with broad and complete white apical bands; 3rd and almost all of 4th hind tarsomere white.

Length of fore wing: 5.3 mm. *First flagellomere:* 4.0 as long as deep at apex. *Malar space:* 0.80 as long as basal width of mandible. *Temple:* 0.44 as long as eye in dorsal view. *Mesoscutum:* notauli fine but definitely impressed, rather sharp, reaching about 0.7 the length of mesoscutum; surface coarsely and uniformly reticulo-punctate. *Mesopleuron:* surface more definitely reticulo-punctate than in female. *Propodeum:* spiracle 1.7 as long as wide; basal trans-carina

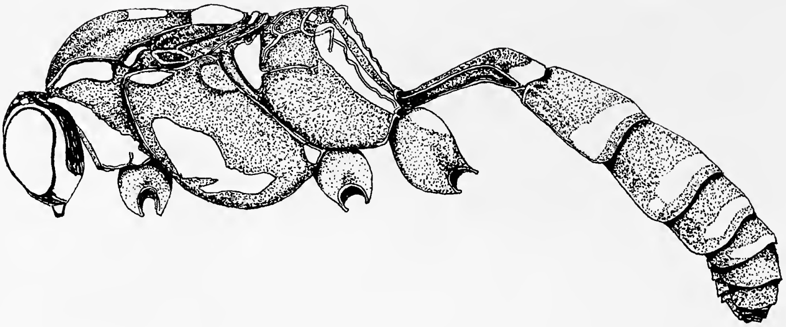

Fig. 14. *Chromocryptus golbachi,* ♂. Holotype. Body in lateral view, showing habitus and color pattern.

very sharp and high; apical trans-carina strong but irregular; cristae short-cuneate, very large and strongly projecting; median longitudinal carinae irregular but well developed, areola and median apical area defined; surface, especially on apical face, very coarsely reticulately wrinkled. *First gastric tergite:* postpetiole 1.2 as wide apically as long from spiracle to apex; surface of postpetiole almost uniformly with large and strong, subadjacent to a little reticulately confluent punctures; setae equal or exceed the length of their interspaces; basal expansion of petiole a low and rounded flange.

TYPE MATERIAL. Holotype ♀: ARGENTINA, Jujuy Province, Posta de Lozano, 21-III-1969, C. Porter. Paratypes: 1♀ and 1♂, ARGENTINA, Jujuy Province, Huacalera, 2800 m, 25-III-1969, C. Porter. Holotype in Florida State Collection of Arthropods. Paratypes in Collection of Charles C. Porter.

RELATIONSHIPS. This species shows close affinity to the Argentine *C. prosopis* and to other members of the *Planosae* complex within *Chromocryptus.* Its diagnostic features are summarized in the key and in the discussions of *C. tomsici* and *C. hübrichi.*

FIELD NOTES. *Chromocryptus tomsici* seems to replace the lowland Chaco *C. prosopis* in the mountains of northwest Argentina. The habitat of the type female, a complex ecotone at 1600 m, already has been discussed under the treatment of *C. alvaradoi.* Huacalera, where the paratypes of *C. tomsici* were collected, is much drier and colder than Posta de Lozano. It belongs to the Prepuna Biome, a high Andean desert characterized by such xerophilous shrubs as *Schinus, Prosopis, Acacia,* and *Cercidium,* as well as by arborescent cacti of the genus *Trichocereus*. Most of my ichneumonids from Huacalera were swept from tall bunch grass along an irrigation ditch near the Hotel Monterrey.

SPECIFIC NAME. For Professor Zlatko Tomsic̆ of the Universidad Nacional de Tucumán, an unfailing and generous friend during my 23 years of aquaintance with the Argentine Republic.

11. **Chromocryptus golbachi** Porter, new species
(Figs. 1, 14)

FEMALE. Unknown.

MALE. *Color:* antenna reddish brown with white on most of scape below; head black with white on a very broad orbital ring (briefly interrupted at bottom of eye), on most of face, on clypeus, and on about basal 0.8 of mandible; mesosoma bright red with blackish extensively in middle of pronotal collar and laterad to or distal of epomia, as well as on some margins and sutures, and with white as follows: on apex of propleuron; very broad band (greatly expanded ventro-laterally) on anterior margin of pronotum; very broad band on all but median 0.3 of dorsal margin of pronotum; a large blotch on mesoscutum between ends of notauli; tegula; subalarum; almost whole scutellum; most of postscutellum; much of ventro-anterior quadrant of mesopleuron distad of prepectal carina; broad and sinuate band following sternaulus from prepectal carina about 0.6 the distance back to hind margin of mesopleuron; small blotch in lower hind corner of mesopleuron; mesepimeron above speculum; all of upper metapleuron; small to large and elongate dorso-apical area on lower metapleuron; very broad, reddish-tinged, ventrally widened lateral bar on propodeum from crista to hind margin; and sometimes incomplete hind margin of apical trans-carina of propodeum; gaster bright red with broad and complete white apical bands on tergites 1 and 2, as well as with equally broad but laterally abbreviated white apical bands on tergites 3–5; fore and mid coxae and trochanters white and often variegated with pale red, especially on coxae; fore and mid trochantelli reddish above and white below; hind coxa red with white on most of dorso-basal 0.5; hind tarsomeres 3 and (sometimes also) 4 white; legs otherwise red, tending to whitish on fore and mid femora, tibiae, and tarsomeres 1–4, dusky on fore and mid 5th tarsomeres; red of hind leg darker and hind tarsus dusky on segments 1–2 and 5 and white on segments 3–4; wings hyaline.

Length of fore wing: 3.4–4.4 mm. *First flagellomere:* 3.7–4.0 as long as deep at apex. *Malar space:* 0.80–0.85 as long as basal width of mandible. *Temple:* 0.36–0.51 as long as eye in dorsal view; rounded-off and strongly receding. *Mesoscutum:* notauli fine but definitely impressed, reaching 0.7–0.8 the length of mesoscutum; surface shining, sometimes almost uniformly with coarse reticulate wrinkling and sometimes with brief smooth interspaces between many of the punctures, especially on lateral lobes. *Mesopleuron:* speculum smooth, polished, and swollen, peripherally with some coarse irregularly to sometimes rather regularly radiating wrinkles; surface otherwise on upper 0.5 complexly and moderately finely reticulately wrinkled (the wrinkling with some longitudinal bias) but on lower 0.5 becoming regularly puncto-reticulate. *Propodeum:* spiracle 1.3–1.7 as long as wide; basal trans-carina sharp and high; apical trans-carina strong and complete, more or less irregular; cristae moderately projecting subligulate to ligulo-cuneate; median longitudinal carinae traceable but irregular, defining a very broad and narrow areola and the usual median apical area; surface, especially on hind face, very coarsely and vermiculately reticulately wrinkled. *First gastric tergite:* postpetiole 1.8–1.9 as wide apically as long from spiracle to apex; surface of postpetiole silky-shining with conspicuous delicate aciculation and with very large and sharp punctures of somewhat irregular distribution but in great part subadjacent to reticulately confluent; setae short and not or barely attaining the length of their interspaces; base of petiole with a rather strong and rounded lateral flange. *Second gastric tergite:* dully shining with widespread fine aciculation and abundant, uniformly distributed large and strong, subadjacent to a little reticulately confluent punctures; setae short, mostly equalling the length of their interspaces.

TYPE MATERIAL. Holotype ♀: ARGENTINA, Santiago del Estero Province, Los Tigres, in Malaise Trap, R. Golbach. Paratype: 1♂, same locality as holotype. Holotype in Florida State Collection of Arthropods; paratype in Collection of Charles C. Porter.

RELATIONSHIPS. This distinctive and brightly colored *Chromocryptus* belongs to the same complex as *C. huebrichi, C. prosopis,* and *C. tomsici.* Most of its diagnostic characters are expounded in the key. Some other features of possible taxonomic importance are its malar space length (0.80–0.85 as long as basal width of mandible, versus 0.53–0.66 as long in *c. prosopis,* 0.70 in *C. huebrichi,* and 0.80 in *C. tomsici*), as well as the presence of some short but strong wrinkles radiating from the specular periphery (such wrinkles are absent in *C. huebrichi* and *C. prosopis* and variably defined in *C. tomsici*).

FIELD NOTES. Los Tigres, in Santiago del Estero Province of the Argentine Dry Chaco Biome, suffers an unusually drastic subtropical semihumid climatic regimen, with long, rainless winters and only sporadically pluvial summers that register thermic maxima of 45–50° C. The ichneumonid fauna of such localities often is large but rarely becomes accessible for capture by hand net. Thus it is not surprising that the types series of *C. golbachi* was collected at Los Tigres in the course of a Malaise Trap survey.

SPECIFIC NAME. For Professor Rodolfo Golbach of the Fundación Miguel Lillo at the Universidad Nacional de Tucumán, who collected the type series and who has done more than any other researcher to document the Argentine entomofauna.

ACKNOWLEDGMENTS

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My collecting in the Lower Río Grande Valley of Texas has been facilitated by annual permits issued under authority of the Texas Parks and Wildlife Department.

SUMMARY

The mesostenine genus *Chromocryptus* comprises trachysphyroid ichneumonids with pyramidal clypeus; strongly sculptured mesoscutum; axillus near hind margin of wing; 1st gastric tergite with a palpable basolateral expansion; 2nd gastric tergite with large, dense punctures; and with a short, straight, compressed ovipositor. There are 11 species: *Chromocryptus planosae* (Fitch) in the northeastern United States; *C. weemsi* (Porter) in Florida; *C. mesorufus* Cushman in Florida, Texas, and México; *C. vandykei* Townes in California; *C. teres* n. sp. in Perú's Coastal Desert; *C. alvaradoi* n. sp., *C. golbachi* n. sp., *C. prosopis* n. sp., and *C. tomsici* n. sp. in northwest and north-central Argentina; *C. huebrichi* (Brèthes) in south Brasil and adjacent Argentina; and *C. poecilma* (Porter) from Minas Gerais, Brasil. Biomes inhabited by different species of *Chromocryptus* include Temperate Deciduous Forest, Tropical Wet Forest, Subtropical Cloud Forest, lowland Subtropical Thorn Scrub, and high Andean Desert. Several *Chromocryptus* have been reared as apparently polyembryonic parasites from moth cocoons (mostly Lasiocampidae) attached to bark.

Much of the material on which this revision is based was collected in northern Argentina during frequent periods of collaboration with the Fundación Miguel Lillo and the Facultad de Ciencias Naturales of the Universidad Nacional de Tucumán. I am particularly grateful to Professor Rodolfo Golbach and to Dr. Abraham Willink of these institutions.

Finally, I thank Mr. Thomas J. O'Neill of Fordham University for his consummate skill in preparing many of the illustrations for this article and for his assistance on several South American fieldtrips.

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THE LARVA OF *PROATTA* (HYMENOPTERA: FORMICIDAE)

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When Forel established (1912) the genus *Proatta* he placed it in the tribe Attini, but later (1917) he removed it to a new tribe Proattini. Wheeler (1922) kept it there, but Emery in the Genera Insectorum (1922) placed it alone in the subtribe Proattini of the tribe Attini. Weber (1958): "While it is true that *Proatta butteli* is strikingly like an attine, this is taken here to be an example of convergence in worker morphology and not necessarily an indication of phylogenetic relationships. The spinosity is especially like that of *Mycocepurus,...*There is no evidence that *Proatta* is a fungus-grower and it is not considered here to be a member of the Attini."

For years we have yearned for larvae of *Proatta* in the hope that they might solve the problem. Hence we were very happy when Mr. M. W. Moffett generously sent us a supply—so happy, in fact, that we processed them immediately.

Genus *Proatta* Forel

Profile attoid, but only slightly curved. Somites indistinct. Body hairs sparse, generally distributed. Antennae minute; slightly above midlength of cranium. Head hairs sparse, generally distributed. Mouth parts small. Mandible amblyoponoid, feebly sclerotized.

Proatta butteli Forel

Figure 1

Length (through spiracles) 2–2.6 mm. Profile attoid. Spiracles small, decreasing slightly posteriorly. Integument with rather long

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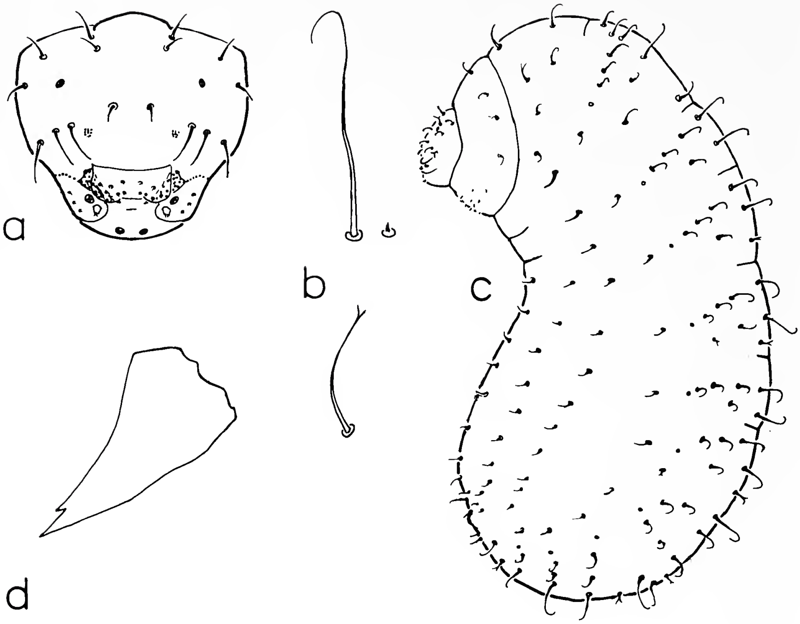

Figure 1. *Proatta butelli* larva. a, Head in anterior view, ×122; b, 3 types of body hairs, ×400; c, larva in side view, ×42; d, left mandible in anterior view, ×640.

rows of spinules. Body hairs sparse; generally distributed. Of 3 types: (1) 0.025–0.1 mm long, unbranched, smooth, slender, with tip more or less curved; (2) about 0.025 mm long, few, with bifid tip; (3) about 0.006 mm long, unbranched, smooth, few, on venter of thorax. Cranium subheptagonal, about 1½ times broader than long. Antennae just above midlength of cranium; minute; with 3 sensilla each. Head hairs few; 0.013–0.056 mm long, unbranched, smooth, slightly curved. Mouth parts small. Labrum trilobed; anterior surface of each lateral lobe with 2–3 sensilla near ventral border; middle lobe with a cluster of 3–4 sensilla near each ventrolateral corner. Mandible amblyoponoid; moderately sclerotized; moderately stout; apex a short slender tooth; a small subapical medial tooth. Maxilla adnate; subovoidal in anterior view; palp a small skewed peg with 5 (1 apical, 3 subapical and 1 basal) sensilla; galea a slender frustum with 2 apical sensilla. Labial palp a slight elevation with 5 sensilla; an isolated sensillum between each palp and the opening of the sericteries; the latter a short transverse slit. (Material studied:

Table 1. Comparison of *Proatta, Myrmicocrypta* and higher attines.

Character	*Proatta*	*Myrmicocrypta*	Higher attines
Profile	attoid (but slightly curved)	attoid (but slightly curved)	attoid (strongly curved)
Somites	indistinct	indistinct	indistinct
Spiracle line	with a posterior curve	with a posterior curve	J-shaped
Body hairs	sparse, short generally distributed	short and restricted	short and restricted
Cranium	genae not lobose	genae not lobose	genae lobose
Head hairs	few, generally distributed	few, below level of antennae	few to numerous, generally distributed
Mouth parts	small	small	small
Mandibles	amblyoponoid; feebly sclerotized; no spinules	amblyoponoid; feebly sclerotized; coarse spinules on basal 2/3	attoid; feebly sclerotized; coarsely spinulose
Maxillae	short, wide and adnate	short, wide and free	long, narrow and adnate

numerous larvae from Botanical Gardens, Singapore, courtesy of M. W. Moffett.)

The solution to the problem of relationship can be best provided in a table (Table 1) comparing simultaneously the larvae of *Proatta, Myrmicocrypta* [which Wheeler regarded (1910:329) as the most primitive of the fungus-growing ants] and the most specialized (*Cyphomyrmex, Trachymyrmex, Mycetosoritis, Acromyrmex* and *Atta*). For a full understanding of the table one should refer to our 1948 and 1976 papers.

So what is the answer? We conclude that the larva of *Proatta* is definitely attine. We have a prejudice against attaching a small monotypic genus found locally in the Oriental Realm to a large wide-spread tribe in the Neotropical Realm; hence we had hoped that the larva would be either strongly attine or strongly non-attine. It is neither, but it is as good an attine as *Myrmicocrypta.* It lacks the coarse spinules on the mandibles, which is an attine character, but so does *Apterostigma,* which is otherwise like the higher attines.

The weightiest evidence is said to be that *Proatta* is not known to be a fungus-grower; but is it really necessary that the ancestral attine already have that habit?

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CLEPTOPARASITISM OF *AMMOPHILA HARTI* (FERNALD) (HYMENOPTERA: SPHECIDAE) BY *SENOTAINIA VIGILANS* ALLEN, WITH OBSERVATIONS ON *PHROSINELLA AURIFACIES* DOWNES (DIPTERA: SARCOPHAGIDAE)*

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Introduction

Cleptoparasites utilize a host's food or prey for the rearing of their own young (Evans, 1970; Matthews and Matthews, 1978). They are often an integral part of fossorial and xylicolous solitary wasp nesting aggregations and, as such, have been reported in the wasp literature for many years (e.g., Peckham and Peckham, 1898; Fabré, 1916; Rau and Rau, 1918; Ristich, 1953, 1956; Evans, 1963, 1966, 1970; Kurczewski and Harris, 1968; Peckham, 1977; Evans, et al., 1980; Wcislo, 1984). Some of the more important cleptoparasites belong to the tribe Miltogrammini (Diptera: Sarcophagidae) (Allen, 1926; Evans, 1970), and these may be grouped into two categories based on their manner of host-location: (1) hole searchers and (2) satellite flies (Ristich, 1956; Evans, 1970). Regardless of which host-locating method is employed, cleptoparasites place an environmental pressure on the reproduction of the wasps. Wasps can reduce the deleterious effects of cleptoparasitism by evolving effective counter-cleptoparasitic behaviors (see Spofford, et al., 1986). Progressive provisioning of nests, in which the female wasp provides food to the larva over a period of days and therefore comes into close contact with her developing young, is believed to have evolved in part as a response to cleptoparasitism (Evans, 1966, 1970; Evans and Eberhard, 1970).

Ammophila harti (Fernald), a simultaneous progressive provisioner, was found in association with two miltogrammine cleptoparasites; *Senotainia vigilans* Allen and *Phrosinella aurifacies*

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Downes. This provided us with the opportunity to examine: (1) the effects of cleptoparasitism on the reproductive success of a progressive provisioner; (2) the behavioral strategies of the flies in attempting to parasitize *A. harti* nests; (3) the actual means by which cleptoparasitism is reduced; and, (4) the behavioral responses of *A. harti* to the presence of the flies.

STUDY SITE AND METHODS

The study was conducted near Auburn, Cayuga County, NY, between 2 June–29 Aug 1982 and 21 June–22 Aug 1983. A description of the site is given elsewhere (Hager and Kurczewski, 1985, 1986). The behavior of *P. aurifacies* and *S. vigilans* was recorded in order to obtain average hourly, daily and seasonal activity rates. These rates are reported in mean number observed behaviors/sample hr to account for differences in sampling effort. The data for the two years are pooled. To provide greater biological significance, calendar date is adjusted to reproductive date with reproductive date 1 corresponding to the first day of *A. harti* nesting activity.

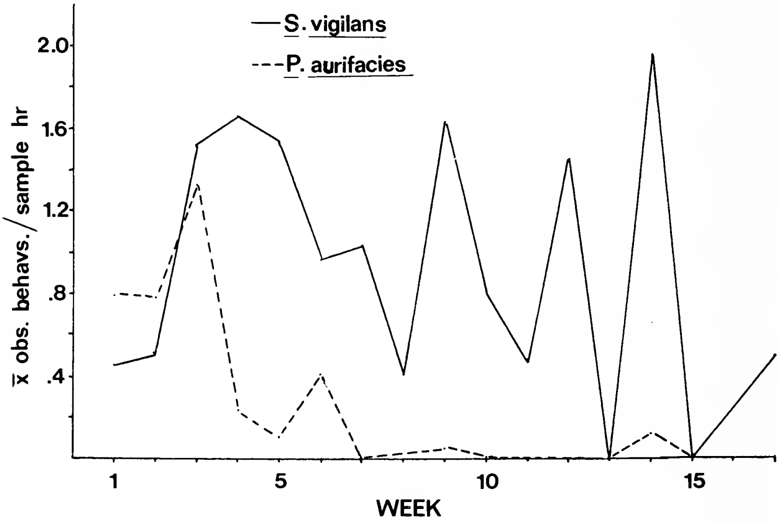

Figure 1. Weekly activity (mean no. observed behaviors/sample hr) of *Senotainia vigilans* and *Phrosinella aurifacies* in *Ammophila harti* nesting aggregation, combined for 1982 and 1983. Week 1 corresponds to first week of *A. harti* nesting.

The cleptoparasitic behavior of *S. vigilans* was divided into two categories: (1) landing on the prey and (2) entering nests. *A. harti*'s response to the presence of this fly was observed and classified as: (1) no response (wasp continued to normally provision the nest) or (2) response (wasp deviated from her normal provisioning pattern). We observed the following responses: (1) freeze-stop (Alcock, 1975), (2) flight, (3) prey abandonment, and (4) nest cleaning.

Nests suspected of being parasitized were excavated within 24–48 hr of the observed fly activity and the rates of parasitism determined. Wasp larvae and fly maggots were removed from nests and placed in sand-filled, plastic 35 mm film canisters to simulate the cell environment. Larvae and maggots were fed quiescent caterpillars taken from provisioning females or obtained from nearby vegetation and killed by freezing. Overwintering puparia and cocoons were placed in perforated containers in a punctured bucket (to allow drainage) and buried in the sand at approximately the mean cell depth of *A. harti*. The bucket was removed in March and brought into the lab to obtain emergence records.

RESULTS

Phrosinella aurifacies

P. aurifacies was most active during June and July in association with the first generation of *A. harti* (Fig. 1). There was a sharp decline in *P. aurifacies* activity as the season progressed (ANOVA $F = 12.43$, 14 df, $p < 0.01$, $r^2 = 0.45$). A few flies were observed sporadically in August and September. Daily activity of *P. aurifacies* during the first generation of *A. harti* was uniformly distributed (Fig. 2).

P. aurifacies was observed walking circuitously on the tumuli of *A. harti* nests. The flies investigated any disturbed sand areas, including entrances to other wasp nests and footprints. No larviposition was observed in an *A. harti* nest entrance or in or on the tumulus, nor were any maggots or puparia found in or near the cell of an excavated nest. Only one fly was observed exiting an open *A. harti* nest. When dug the next day, the cell of this nest was empty and no evidence of flies was found in its vicinity. *A. harti* occasionally chased away flies circling on tumuli of nests under construction.

The abundance of *P. aurifacies* during the first generation coincided with the construction of the deepest *A. harti* cells. Regression analysis between *P. aurifacies* activity and cell depth yielded an r^2 value of 0.42 (ANOVA $F = 10.28$, $p < 0.01$).

Senotainia vigilans

S. vigilans was present throughout the nesting season of *A. harti* (Fig. 1). During the first generation of *A. harti, S. vigilans* was more active in the morning than in the afternoon (Fig. 2). This coincided with the period of greatest activity of first generation females of *A. harti* and other wasps present in the sand pit. In the second generation of *A. harti, S. vigilans* was equally active in both the morning and afternoon (Fig. 2).

S. vigilans was attracted to movement and, therefore, trailed wasps constructing, inspecting, or provisioning nests. Flies either hovered 2–15 cm above and behind a female while darting close to the wasp or her prey, or perched on a nearby elevated site (e.g., pebble, plant) and watched the wasp from there. In attempting to larviposit on the prey, *S. vigilans* exhibited two, not mutually exclusive, behaviors: (1) landing on the prey at the nest entrance or as it was being taken inside; and (2) entering the nest (following the provisioning wasp into a nest). (see Spofford, et al., 1986.)

Of 105 observations of *S. vigilans* attracted to *A. harti* provisioning their nests, flies landed on the prey 25.7% (27 of 105) of the time. Some *S. vigilans* landed and larviposited on prey during transport to the nest, but most landed on the prey either while the wasp was opening the nest or as she took the prey inside.

Flies entered the wasps' burrows 47 (44.8%) times. It was uncertain whether or not entering flies larviposited on the prey or in the burrow, or left without larvipositing. Some flies did not travel far into the burrow and most reappeared less than 2 sec after entry. Two flies reappeared in entrances shortly after the wasps, indicating that they had "crossed paths" in the burrow. Flies attracted to provisioning *A. harti* did not attempt to larviposit 29.5% (31 of 105) of the time. These flies either continued to hover, were distracted by another wasp in the vicinity, or were eluded by the wasp (see counter-cleptoparasitic behavior).

The success frequency of the "landing" strategy was high (Table 1). Larviposition occurred 20 of 27 (74.1%) times when the fly landed on the prey. It could not be ascertained if larviposition actually occurred when a fly entered the nest because the fly was not visible. Therefore the presumed parasitism numbers (≈ success fre-

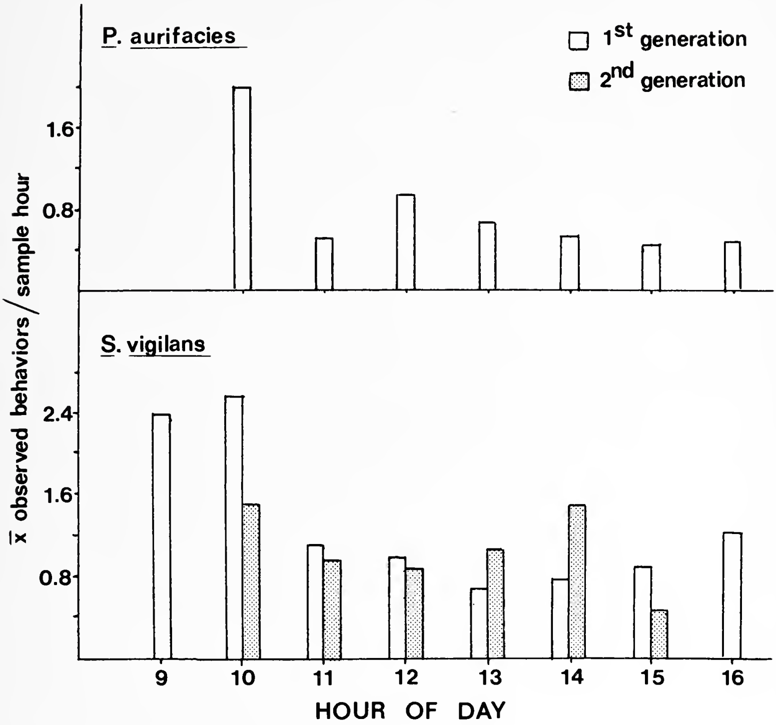

Figure 2. Hourly activity of *Senotainia vigilans* and *Phrosinella aurifacies* during first and second generations of *Ammophila harti*, combined for 1982 and 1983. There are no data for *P. aurifacies* during *A. harti's* second generation due to low population.

quency) for the entering behavior may not reflect actual larviposition. A nest that contained decaying prey remains and/or puparia near the cell was presumed to have been parasitized and those in which a maggot or maggots were found were obviously parasitized.

Four larvipositions by *S. vigilans* were successful when the attack occurred on the initial prey placed in the cell. None of the 16 attacks which occurred on a subsequent provisioning of a nest were successful. If entering behavior is included, the success frequency of cleptoparasitism on first provisioning drops to 72.7% (8 of 11) and successful attacks on subsequent provisioning increases to 7.1% (2 of 28). In total, only 25.6% of the attacks resulted in successful parasitism (10 of 39). When all of the nests constructed by females in which a prey was placed (≈ used nests; see Hager and Kurczewski, 1986) are considered, *S. vigilans* successfully parasitized 1.63% (4 of 245) of the nests, while another 2.45% (6 of 245) of the nests were presumed parasitized, making a total of 4.08% (10 of 245) parasitized used nests.

Of eight *A. harti* cells containing *S. vigilans* maggots, three each also contained a wasp larva, four had prey only, and one cell contained two maggots and prey. From the nests with prey only, two flies emerged the following June and three others failed to emerge. In the cells also containing a wasp larva, the maggots disappeared within a day. Either the wasp larva consumed the maggot(s) or it outcompeted the maggot(s), resulting in its(their) starvation. One wasp larva actively moved from a fresh prey on which it was feeding to a prey that was parasitized. Three hr later, the maggot could not be found.

Counter-cleptoparasitic behavior

A provisioning wasp responded to the presence of an *S. vigilans* by either "freezing" on the sand for up to 10 min ($\bar{x} = 4.3 \pm 3.6$ min, $N = 9$), flying to surrounding vegetation for up to 15 min ($\bar{x} = 6.6 \pm 5.2$ min, $N = 13$), or alternating periods of "freezing" with low hopping flights near her nest. *A. harti* sometimes turned and faced *S. vigilans* before freezing. At other times, the wasp would fly at the trailing flies. Success of "freezing" depended upon the number of flies present and the number of active wasps in the vicinity. In periods of high nesting density and activity, flies were easily distracted by the movements of other wasps and "freezing" was effective. Flights to vegetation were successful for the same reason.

Prey abandonment was observed once under continuous pressure from five trailing *S. vigilans.* Unsuccessful in evading the flies (several landed on the prey), the wasp crawled up vegetation and abandoned her prey. She proceeded to her nest, opened it, searched for her prey, but never relocated it. Six *S. vigilans* and a hyperparasite, *Perilampus hyalinus* Say (Perilampidae), were reared from this prey (see Spofford and Kurczewski, 1984).

Another response by *A. harti* to the presence of *S. vigilans* was nest cleaning (see Hager and Kurczewski, 1986). The number of times a wasp entered and removed sand from her burrow was a function of her activity (inspecting or provisioning) and the absence or presence of cleptoparasitic flies. In the absence of flies, the mean number of trips into the burrow for sand removal was 4.7 ± 4.51 (range 1–26, N = 94). With flies present, either hovering behind or perching nearby, the intensity of the cleaning behavior increased significantly to 9.5 ± 4.97 trips (range 1–17, N = 23; t = 52.28, 115 df, $p < 0.05$).

Discussion

The main advantage of progressive provisioning is generally considered to be the greater protection from enemies afforded the egg or larva due to the prolonged presence of the female (Evans, 1966). The female may remove or destroy cleptoparasites or provide more food to a parasitized nest and thus prevent starvation of the larva. Since most provisioning trips to a nest occur after the egg has hatched, the cleptoparasite will usually be introduced to a larva. In this case, the larva may be able to outcompete the maggot (cleptoparasite) and thus indirectly kill it, or it may directly destroy the maggot by feeding upon it.

With this in mind, we can now consider several predictions for the effects of cleptoparasitism on *A. harti:* (1) cleptoparasites will almost always be successful if they attack the initial prey in a cell (while the wasp is still in the egg stage); (2) successful cleptoparasitism should decrease as the larva matures; and, (3) the larva may be the essential component in cleptoparasitic defense by consuming or outcompeting the maggot (cleptoparasite).

P. aurifacies, a closed nest searcher, had little or no effect on the reproductive success of *A. harti.* Cells were found to be deeper in the first generation when *P. aurifacies* was present, but the significance of this correlation remains questionable. Other factors (e.g., soil moisture) may influence cell depth. Reasons for why hole-searching cleptoparasites are not successful in parasitizing *A. harti* include: (1) the stone used to close the nest entrance provides a physical barrier to a burrowing maggot deposited in the entrance; (2) removal of the tumulus from the vicinity of the entrance may aid in its concealment and therefore *P. aurifacies* may be unable to detect (locate) the entrance; and, (3) *A. harti* cleans the burrow and, in so doing, may remove any maggots placed therein.

Senotainia vigilans, on the other hand, had limited success in cleptoparasitizing *A. harti* nests. This success depended upon the

Table 1. Success frequency of two behavioral strategies exhibited by *Senotainia vigilans* in attempting to parasitize the provisions of *Ammophila harti.*

	Behavior					
	Landing on prey		Entering nest		Total	
	Success.	Unsucc.	Success.	Unsucc.	Success.	Unsucc.
Observed parasitism[1]	3(3)[3]	4(0)	1(1)	0	4(4)	4(0)
Presumed parasitism[2]	1(1)	13(0)	5(3)	12(3)	6(4)	25(3)
Total observations	21(4)		18(7)			
Percentage of successful parasitism for fly attacks on initial provisionings	4/4 = 100%		4/7 = 57%		8/11 = 72.7%	
Percentage of successful parasitism for fly attacks on subsequent provisionings	0/16 = 0%		2/12 = 16.7%		2/28 = 7.1%	
Percentage of total successful parasitism	4/20 = 20%		6/19 = 31.6%		10/39 = 25.6%	

[1] Observed parasitism = presence of maggot in cell.

[2] Presumed parasitism = presence of decayed prey remains and/or fly puparia in or near cell.

[3] Number in parenthesis indicates number of times cleptoparasitic attempt was associated with initial provisioning of nest.

stage of the developing wasp at the time of maggot deposition; eggs and young larvae were most vulnerable (Table 1). The two nests presumed parasitized that were attacked after an initial provisioning may have contained young larvae.

In an attempt to test whether the female or the larva is responsible for the elimination of maggots after their introduction into a nest, four cells each containing a larva and maggot(s) were placed in individual rearing tins, thereby removing any influence the mother may have had on the cleptoparasitized nest. All of the maggots disappeared within hours, regardless of whether any extra prey were added to a cell. This suggests that the larva either starves the maggot indirectly by consuming the food or eats the maggot. One advantage of progressive provisioning in *A. harti* therefore appears to be the larva's ability to outcompete the cleptoparasite. The mother's ability to defend her larvae against cleptoparasitism may play a lesser role. Evans (1966, 1970) has noted in *Bembix belfragei* Cresson the cooccurence of larva and maggots, all of which were able to reach maturity by feeding on prey provided by the female.

The total frequency of successful cleptoparasitism of used nests was 4.08%. If all of the provisioned nests found empty or with remains are considered to have been cleptoparasitized (which is highly unlikely), then 20% of the nests were cleptoparasitized. This is compared to the 57.9% *S. vigilans* parasitism of a mass provisioner, *Tachysphex terminatus* (F. Smith), at the same site (Spofford, et al., 1986). Evans (1966) did not report any quantitative data on cleptoparasitic loads for progressive provisioning Nyssoninae but did note that cleptoparasitism was less than that for mass provisioners of this subfamily. Although cleptoparasitic frequencies for other wasps are scarce, the pattern still emerges that those species not exhibiting progressive provisioning suffer a higher cleptoparasitism—from 20% [*Philanthus zebratus nitens* Cresson (Evans, 1970)] to 50% [*Sphecius speciosus* (Drury) (Reinhard, 1929; Evans, 1966)].

Behavioral adaptations other than the manner of provisioning may also reduce cleptoparasitism. Nests may be provisioned at times of the day or season different from the diurnal and seasonal activity patterns of the flies. Such rhythmical modification is not well documented. Evans et al. (1980) found *Crabro monticola* (Packard) and *Crabro largior* Fox bringing prey to their nests early in the morning, before satellite flies were active. Certain pompilids and sphecids are less afflicted than related species because they overwinter in the adult stage and nest during the first warm spring days when few or no cleptoparasites are present (O'Brien and Kurczewski, 1982; Alm and Kurczewski, 1984). There was no daily or seasonal adjustment in provisioning times by *A. harti* related to peak fly activity. *S. vigilans* is a generalized cleptoparasite and many other fossorial wasp species were present at the study site.

Diversionary provisioning flights may be a means of deterring trailing satellite and related flies (Evans, 1963, 1970; Alcock, 1975; Matthews et al., 1979; Evans, et al., 1980, McCorquodale, 1984). Female wasps may perform elaborate flight manuevers incapable of being followed by the flies, they may take a long time in reaching the nest which may result in the fly losing interest, or they may freeze in a populated area and the fly may become distracted by another wasp. The latter two behaviors were observed frequently in *A. harti*. *A. harti* may exhibit these behaviors more often when initially provisioning a nest or when provisioning a young larva than when provisioning an older larva, but our data are insufficient to support this. Wasp species exhibiting progressive provisioning may not have evolved elaborate diversionary flights or other such "pre-parasitic" behaviors because of the ability of their larvae to outcompete maggots introduced into the cells ("post-parasitic" behavior).

Nest cleaning may be designed to rid the burrow of cleptoparasites. It is possible that *S. vigilans* larviposits after it enters the burrow and the maggot may then crawl downward into the cell. However, it is more plausible that the fly is attempting to contact the prey as it is carried down the burrow, based upon the behavior observed above ground. Burrow cleaning may remove any maggots so deposited. Evans (1966) observed debris being removed from nests of several *Bembix* species and suggested that this behavior prevents maggots from maturing on the excess food remains not consumed by the larva or may even remove maggots already present in the debris. The sand removed via the burrow cleaning of *A. harti* needs to be examined for the presence of maggots, although presence of maggots in the sand merely proves that *S. vigilans* will deposit maggots in the burrow and not that the function of burrow cleaning is to remove maggots. An alternative function of nest cleaning may be to facilitate the transport of prey to the cell by removing sand that might otherwise block the burrow. The presence of the adult fly may serve as a cue that stimulates further burrow cleaning. This then enables the wasp to bring the prey in more quickly during the next provisioning and decreases the exposure time of the prey to cleptoparasites.

Nesting in aggregations may reduce cleptoparasitism through the selfish herd effect (Wcislo, 1984). *A. harti* may nest in one location not only because it contains all of the physical requirements but also because those individuals nesting in a congested area may limit the amount of cleptoparasitism of their nests. Wcislo (1984) suggests that this works best against hole-searching cleptoparasites but we feel it can be extended to include satellite flies. *S. vigilans* was often distracted from following a provisioning wasp by the movements of another wasp nearby. A wasp adopting the strategy of remaining still after having been spotted by a satellite fly may have an increased chance of evading the fly when it is within a nesting aggregation.

ACKNOWLEDGMENTS

We thank N. E. Woodley and W. L. Downes, Jr. for identifying the flies, A. S. Menke for confirming the wasp species, and M. G. Spofford for assistance in the field. We also thank W. M. Shields for reviewing the manuscript and offering useful comments. This work was partly funded in 1982 and 1983 by Grants-in-Aid of Research from Sigma Xi, the Scientific Research Society.

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A REVISION OF *COSMIOCRYPTUS* IN THE COASTAL DESERT OF PERÚ AND NORTH CHILE (HYMENOPTERA: ICHNEUMONIDAE)

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Introduction

Taxonomy and Relationships

Cosmiocryptus, as here defined, ranges from Ecuador to Perú, Bolivia, Brasil, Argentina, and the Neantarctic regions of Chile. Like its close relative *Trachsphyrus,* this genus prefers Andean (up to at least 4000 m), semiarid, and temperate habitats, but also has a few specialized representatives in tropical South America below the equator and outside the Amazon Basin.

Cosmiocryptus includes at least 50 described species (Porter 1967) plus as many as 100 still undescribed representatives. My concept of *Cosmiocryptus* (NEW STATUS) includes most of the species placed by Townes (1969: 179–81) under *Chromocryptus,* with the exception of *Chromocryptus* itself (which I recognize as a separate genus restricted to species intimately related to *Phygadeuon Planosae* Fitch). It should be noted that Townes (1969: 181) tentatively synonymizes *Cosmiocryptus* with *Trachysphyrus.* However, *Cosmiocryptus* does not fit in *Trachysphyrus,* as defined either by Townes or by me, since its type species has the axillus vein "parallel to the anal margin of the hind wing" (Townes 1969: 159) and so will run in Townes key (1969: 159–65) to *Chromocryptus.*

Cosmiocryptus is a heterogeneous assemblage of perhaps diverse affinities. Some of its species superficially resemble Holarctic members of the related genera *Itamoplex* and *Caenocryptus.* Others may be close to the large but as yet little studied temperate Australian and Tasmanian "trachysphyroid" fauna. It is thus not possible

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to give an exhaustive generic description of *Cosmiocryptus* but species in the Coastal Desert may be recognized by the following combination of characters: Axillus close to anal margin of hind wing; base of 1st gastric tergite without a lateral tooth; mediella moderately arched to almost straight; mandible stout with lower tooth not longer than upper; hind coxa with a strong subvertical groove externo-ventrally near base; propodeal cristae never elongately spiniform; 1st gastric tergite rarely with large and dense punctures.

Ecology and Host Records

Cosmiocryptus often are found on the branches of shrubs or trees or in herbaceous vegetation. Information about habitat preferences of many species is given under the discussion of each taxon.

The only rearing record for *Cosmiocryptus* in the Coastal Desert is from a species of *Megalopyge* (Lepidoptera: Megalopygidae).

COLLECTIONS

Listed below in alphabetic order are collections which furnished material for this study and/or in which type and voucher specimens are or are to be deposited. I refer to institutional collections by the name of the city where they are located and to individual collections by the surname of the owner. Specimens of *Cosmiocryptus violaceipennis,* of *C. diplatys,* and of *C. weyrauchi* will be distributed to Arica, Cambridge, College Station, Gainesville, Lawrence, Porter, Townes, and Gainesville.

ARICA. Centro de Investigacíon y Capacitacíon Agricola, Departamento de Agricultura, Universidad de Tarapacá, Arica, CHILE.

CAMBRIDGE. Museum of Comparative Zoology, Harvard University, Cambridge, MASS 02138.

COLLEGE STATION. Department of Entomology, Texas A & M University, College Station, TX 77843.

GAINESVILLE. Florida State Collection of Arthropods, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P.O. Box 1269, 1911 SW 34th Street, Gainesville, FL 32602.

LAWRENCE. Department of Entomology, Snow Entomological Museum, The University of Kansas, Lawrence, KS 66045

PORTER. Collection of Charles C. Porter, 301 North 39th Street, McAllen, TX 78501.

TOWNES. American Entomological Institute, c/o Dr. Virendra Gupta, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P.O. Box 1269, Gainesville, FL 32602.

WASHINGTON. Department of Entomology, U.S. National Museum, NHB 168, Washington, DC 20560

Genus *COSMIOCRYPTUS*

Cosmiocryptus Cameron, 1902. Trans. Amer. Ent. Soc. **28**: 371. Type: *Cosmiocryptus violaceipennis* Cameron

Neocryptopteryx Blanchard, 1947. Commun. Zool. Mus. Hist. Nat. Montevideo **2**(42): 1. Type: *Neocryptopteryx orientalis* Blanchard. New synonym.

KEY TO THE COASTAL DESERT *COSMIOCRYPTUS*

FEMALES

1. Gaster solid red or red with black staining; flagellum black with a white band; clypeus low to moderately raised, symmetrically to asymmetrically convex in profile 2

1′. Gaster variously patterned with red, black, and white; flagellum not black and white; clypeus strongly raised, bluntly and asymmetrically pyramidal in profile 7

2. Epomia turned mesad above and enclosing a triangular area; mesoscutum shining and with much gross punctation and wrinkling along notauli and on peripheries of lateral lobes but duller and more finely punctured centrad on lobes; propodeal cristae very strongly projecting cuneate to ligulate; ventro-lateral carina absent on 1st gastric tergite; sheathed portion of ovipositor 0.8–0.9 as long as fore wing, gently upcurved .... 2. *C. huascar* (Porter)

2′. Epomia not turned mesad at its upper end; mesoscutum uniformly more or less shining, without or with rather weak wrinkling along notauli and not more strongly sculptured on peripheries of lateral lobes; propodeal cristae more or less strong, moderately projecting, subligulate or subcuneate; ventro-lateral carina distinct throughout on petiole; sheathed portion of ovipositor 0.4–0.6 as long as fore wing, straight 3

3. Apical margin of clypeus produced and with a pair of tubercles on median 0.3; malar space 0.9 as long as basal width of mandible; 2nd gastric tergite smooth and shining, slightly micro-reticulate, with very sparse setae .... 8. *C. weyrauchi* Porter

3′. Apical margin of clypeus not tuberculate; malar space often less than 0.9 basal width of mandible; 2nd gastric tergite with micro-reticulation often stronger and setae often denser than described above 4

4. First flagellomere 6.2–7.8 as long as deep at apex; temple 0.6–0.8 as long as eye in dorsal view; sheathed portion of ovipositor 0.6 as long as fore wing; both dorsal and ventral valves of ovipositor broadly and strongly flattened on tip, dorsal valve profile between notch and apex gently concave .... 5. *C. diplatys* (Porter)

4′. First flagellomere 5.0–6.0 as long as deep at apex; temple 0.4–0.5 as long as eye in dorsal view; sheathed portion of ovipositor 0.4–0.5 as long as fore wing; ovipositor valves at most moderately flattened on tip, the dorsal valve with a straight or slightly convex taper between notch and apex 5

5. Fore tibia stout but not inflated; postpetiole 1.5 as wide apically as long from spiracle to apex; ovipositor slender with nodus very weak, tip 0.16 as high at notch as long from notch to apex; dorsal valve minutely tuberculate on tip .... 7. *C. leptaechma* n. sp.

5′. Fore tibia palpably inflated; postpetiole 1.5–2.0 as wide apically as long from spiracle to apex; ovipositor more robust with distinct nodus, its tip 0.22–0.28 as high at notch as long from notch to apex 6

6. First flagellomere 5.5–6.0 as long as deep at apex; mesopleuron grossly reticulate but always with a shining and discretely punctate swelling above along prepectus opposite speculum; 2nd gastric tergite with distinct finely granular micro-reticulation and with short setae that largely approach the length of their interspaces; ovipositor stout, moderately compressed, profile of its basal valve between nodus and apex basally straight or a little concavely flattened and then convex toward tip .... 4. *C. violaceipennis* (Cameron)

6′. First flagellomere 5.0 as long as deep at apex; mesopleuron strongly, but not grossly, reticulately wrinkled, without a raised or shiny area opposite speculum along prepectal carina; 2nd gastric tergite finely reticulate but with setae much shorter than their interspaces; ovipositor strongly compressed, with a high nodus, dorsal valve directly tapering between notch and apex................6. *C. aricae* n. sp.

7. Speculum uniformly punctate, mesopleuron otherwise with fine reticulate wrinkling; 2nd abscissa of radius 0.5 as long as 1st intercubitus; 2nd recurrent straight or slightly reclivous, palpably outcurved above; mediella gently arched; apical trans-carina of propodeum fine and sharp, looped far forward medially; postpetiole 1.1–1.3 as wide apically as long from spiracle to apex; 2nd gastric tergite dully shining with uniform delicate microreticulation; ovipositor slender and compressed, tip 0.22–0.23 as high at notch as long from notch to apex; wings hyaline; antennae blackish................ .... 1. *C. occidens* n. sp.

7′. Speculum largely smooth and shining, rest of mesopleuron grossly sculptured; 2nd abscissa of radius 0.8 as long as 1st intercubitus; 2nd recurrent gently inclivous, almost straight, not outcurved above; apical trans-carina of propodeum obsolete; postpetiole 1.7 as wide apically as long from spiracle to apex; 2nd gastric tergite smooth and conspicuously shining with faint micro-reticulation that practically fades out toward apex; ovipositor robust, tip 0.30 as high at notch as long from notch to apex; antennae reddish; wings black .... 3. *C. leucetrum* n. sp.

MALES

(Males of *Cosmiocryptus leucetrum, C. aricae* and of *C. leptaechma* unknown).

1. Mediella rather strongly arched; 2nd recurrent palpably outcurved above; temple 0.5–0.6 as long as eye in dorsal view; postpetiole 0.5–0.9 as wide apically as long from spiracle to apex; 2nd gastric tergite dully shining with uniform microreticulation; gaster black, red, and white .... 1. *C. occidens* n. sp.

1′. Mediella straight; 2nd recurrent not outcurved on upper 0.5; temple 0.6–1.0 as long as eye in dorsal view; postpetiole 0.9–1.4 as wide apically as long from spiracle to apex; 2nd gastric tergite smooth and shining with variably developed delicate microreticulation, solid red or red and blackish...2

2. Flagellum without white band; propodeal cristae large, strongly projecting ligulate or subligulate; epomia bent mesad above, where it delimits an appressed triangular area; malar space 0.9 as long as basal width of mandible.................... ....2. *C. huascar* (Porter)

2′. Flagellum marked with white; propodeal cristae well developed, broadly subligulate, not so prominently projecting as in the previous species; epomia strong but not modified at its upper end; malar space 0.6–0.8 as long as basal width of mandible 3

3. Median 0.3 of clypeus produced and with a pair of blunt tubercles; 1st flagellomere 2.6–3.0 as long as deep at apex; in most specimens setae of 2nd gastric tergite average palpably shorter than the length of their interspaces ....8. *C. weyrauchi* (Porter)

3′. Clypeal apex etuberculate; 1st flagellomere 3.7–5.0 as long as deep at apex; setae of 2nd gastric tergite consistently exceed the length of their interspaces 4

4. Mesoscutum strongly shining with abundant but delicate punctation and wrinkling; flagellum with only the 3rd tyloid (counting from base) unusually broad, the rest ovoid to linear..... ....5. *C. diplatys* (Porter)

4′. Mesoscutum rather dully shining, with abundant dense punctures and wrinkles; flagellum with at least 2nd and usually 1st–3rd tyloids broadly oval ....4. *C. violaceipennis* (Cameron)

1. **Cosmiocryptus occidens** Porter, new species

(Fig. 1)

FEMALE. *Color:* scape dull reddish brown, antenna otherwise nearly black; head and mesosoma black with brown staining on mandibles, a dull to pure white spot on base of mandible, and a brownish white to mostly white area on clypeus, as well as with the

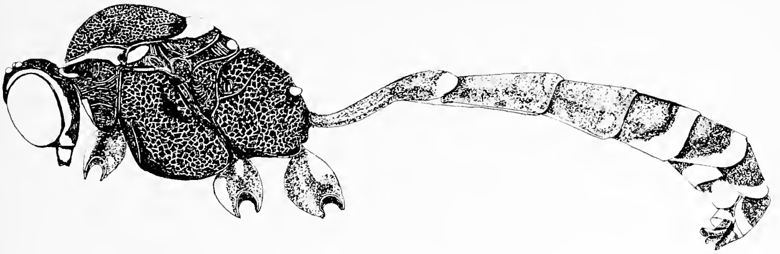

Fig. 1. *Cosmiocryptus occidens*, ♂. Paratype. Lateral view of whole insect, showing color pattern and habitus.

following mostly pure white ornamentation: orbital ring, broken only at bottom of eye; blotch in malar space (sometimes merging with hind orbital band); broad band on pronotal collar; sometimes blotch on anterior-ventral margin of pronotum near mid-height; broad line on dorsal margin of pronotum near mid-height; broad line on dorsal margin of pronotum, interrupted only in front between bases of notauli; about outer 0.5 to almost all of tegula; sometimes small triangular spot on each anterior corner of scutellum; sometimes pair of tiny dots on postscutellum; tips of propodeal cristae; and a tiny dot on subalarum; 1st gastric tergite red with some faint dusky staining that becomes darker near base; 2nd tergite dull red with slight dusky staining; 3rd tergite dull red and more or less conspicuously dusky tinged, sometimes grading into blackish on apical 0.3 and throughout laterad; 4th tergite black with some reddish basally or sometimes mostly red and always with a very broad white apical band which becomes even broader laterad; 5th and 6th tergites black with a very broad white apical band; succeeding tergites black with extensive, irregular white markings; legs red, duller on tibiae and tarsi, sometimes with a tiny white dot near base on hind coxa; wings hyaline with fore wing faintly brownish tinged.

Length of fore wing: 7.0–7.1 mm. *First flagellomere:* 6.8–7.7 as long as deep at apex. *Clypeus:* rather high, strongly blunt-pyramidal in profile; apical margin very weakly convex. *Malar space:* 1.0 as long as basal width of mandible. *Temple:* 0.23–0.33 as long as eye in dorsal view; precipitously receding and slightly rounded off. *Cephalic carinae.* occipital carina sharp but scarcely raised; hypostomal carina only slightly higher than occipital. *Fore tibia:* rather slender, with a weak swelling near basal 0.3. *Pronotum:* dorsal margin weakly swollen; submarginal groove narrow and obsolete; epomia sharp and strong in scrobe, prolonged briefly below, unmodified above. *Mesoscutum:* notauli narrow, shallow but conspicuous, extending about 0.7 the length of mesoscutum; surface at most dully shining, finely but strongly reticulo-rugose to reticulo-punctate on central lobe and on an extensive area behind end of notauli, more coarsely and transversely wrinkled immediately along notauli, sometimes on lateral lobes a little more shining in comparison to rest of mesoscutum and with fine but sharp puncto-reticulation that includes many almost discrete punctures. *Mesopleuron:* speculum slightly differentiated, more shining than rest of surface, with uniform and comparatively coarse punctation; surface otherwise with uniform finely reticulate wrinkling. *Wing venation:* radial cell 3.3–3.5 as long as wide; areolet large; intercubiti strongly convergent above; 2nd abscissa of radius 0.5 as long as 1st intercubitus; 2nd recurrent straight or a little reclivous below, definitely outcurved above; discocubitus broadly angled, with a long ramellus; mediella gently arched; nervellus broken well below middle, upper part 3.5 as long as lower. *Propodeum:* short and high, faces subequal, basal sloping, apical discrete and nearly vertical; spiracle 2.0 as long as wide; area basalis weakly defined; basal trans-carina strong and sharp throughout, much raised medially; apical trans-carina fine and sharp, sometimes weakened laterad, medially thrust far forward; cristae of moderate size, briefly ligulate, projecting; median longitudinal carina delimiting a broadly hexagonal areola; lateral longitudinal carina scarcely suggested; surface dully shining, basad of basal trans-carina puncto-reticulate, rugose between trans-carinae, a little more finely reticulate on apical face. *First gastric tergite:* 1.1–1.3 as wide apically as long from spiracle to apex; ventro-lateral carina fine and sharp throughout; dorso-lateral carina very sharp on postpetiole but gradually weakening basad on petiole; dorsal carinae prominent but blunt and enclosing a low median elevation toward apex of petiole and on base of postpetiole; surface of postpetiole dully shining except more polished on apical 0.3 and with delicate micro-reticulation that fades out near apex. *Second gastric tergite:* dully shining with uniform delicate microreticulation and a few minute, obscure punctures emitting short, widely scattered setae. *Ovipositor:* sheathed portion 0.6 as long as fore wing;

only slightly upcurved, slender, compressed; nodus only gently raised, with a minute notch; ventral valve with fine, well spaced oblique ridges on tip, tip 0.23 as high at notch as long from notch to apex.

MALE. *Color:* differs from female as follows: white spot beneath on scape; white markings on head broader; tegula wholly white; often most of scutellum and postscutellum white; almost percurrent white line on subalarum; 1st gastric tergite with a broad white band on apex; 2nd and 3rd tergites with laterally abbreviated white apical bands, with that of 3rd tergite comparatively weak or irregular (or sometimes all tergites with complete white apical bands); 5th tergite red on basal 0.4; 7th tergite black with a broad white apical band; clasper brownish with a large black spot; fore and mid tarsi dusky, hind tarsus blackish; hind tibia tinged with dusky above, especially toward apex; fore and mid coxae with a black area dorsally that is bounded anteriorly by a large white area and posteriorly by a smaller white area; hind coxa with a large white blotch dorsally on basal 0.5 and sometimes with a little brownish staining apically; fore and mid trochanters white with a broad and nearly percurrent black stripe above; mid trochantellus red as in female but with considerable blackish above.

Length of fore wing: 5.3–7.3 mm. *First flagellomere:* 4.4–4.5 as long as deep at apex. *Malar space;* 0.9 as long as basal width of mandible. *Temple:* 0.5–0.6 as long as eye in dorsal view. *Mesoscutum:* notauli sometimes traceable but faint, sometimes as strong as in female. *Mesopleuron:* speculum often more polished than in female, with some smooth interspaces among the punctures. *Wing venation:* ramellus sometimes very short; mediella quite strongly arched, its upper part 2.4 as long as the lower part. *Propodeum:* basal face strongly declivous; apical face nearly vertical, well differentiated from basal face and 0.7 as long as basal face; spiracle 1.5–1.7 as long as wide; basal trans-carina sometimes becoming a little irregular laterad, but as strongly raised on meson as in female; apical trans-carina fine and gently to rather strongly curved forward on median 0.3–0.6 but weak to obsolete laterad; cristae prominent robustly cuneate; longitudinal carinae scarcely suggested. *First gastric tergite:* postpetiole weakly expanded apicad, 0.5–0.9 as wide apically as long from spiracle to apex; ventro-lateral carina strong throughout, except sometimes weaker below spiracle; dorso-lateral carina weakly and irregularly defined; dorsal carinae absent; surface with coarser and more granular micro-reticulation than in female; setae largely surpassing the length of their interspaces, much longer and denser than in female.

TYPE MATERIAL. Holotype ♀: PERÚ, Lima Province, San Gerónimo, 5-VII-1976, C. Porter. Paratypes: 1♀, 3♂: PERÚ, Lima Province, Matucana, 2389 m, 28-30-VI-1974, C. Porter, L. Stange, 7-9-VII-1975, C. Porter; La Libertad Province, Samne nr. Trujillo, 1500 m, 12-17-VII-1975, C. Porter, L. Stange. Holotype in Florida State Collection of Arthropods. Paratypes in Florida State Collection of Arthropods (1♂), Collection of Henry K. Townes (1♂), and Collection of Charles C. Porter (1♀, 1♂).

RELATIONSHIPS. *Cosmiocryptus occidens* belongs to the *Rufitibia* group within its genus (Porter 1967: 124–6) and is very closely related to the central Andean *C. townesorum* Porter (1967: 135–7).[1] Probably, these 2 species are vicariants which differentiated, in the Puna and Coastal Desert respectively, while late Tertiary and Pleistocene climatic changes alternately prevented and encouraged dispersal of xerophilous biota across the highest Andean cordilleras. A similar relationship seems to obtain between the ephialtine ichneumonids *Itoplectis niobe* Schrottky (mostly restricted to above 2500 m in Perú) and *Itoplectis phoenogaster* Porter (a closely related *Itoplectis* endemic to the Coastal Desert below 2500 m, as discussed by Porter 1979: 180–1).

Cosmiocryptus townesorum differs from *C. occidens* in lacking a white band on the female flagellum, in its absence of red markings, longer temple (0.4–0.5 as long as eye in dorsal view vs. 0.2–0.3 in *C. occidens*), and conspicuously upcurved ovipositor (ovipositor only slightly upcurved in *C. occidens*).

FIELD NOTES. *Cosmiocryptus occidens* inhabits moist areas with subtropical to prepuna climates (1500 to 2389 m altitude) in fertile river valleys along much of the Peruvian coast. I have taken it by sweeping dense herbaceous undergrowth along irrigation ditches and also while beating the large composite shrub, *Baccharis*. *Cosmiocryptus* and numerous other Hymenoptera often are attracted to *Baccharis*, where they feed on honeydew produced by the many

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[1] New combination.

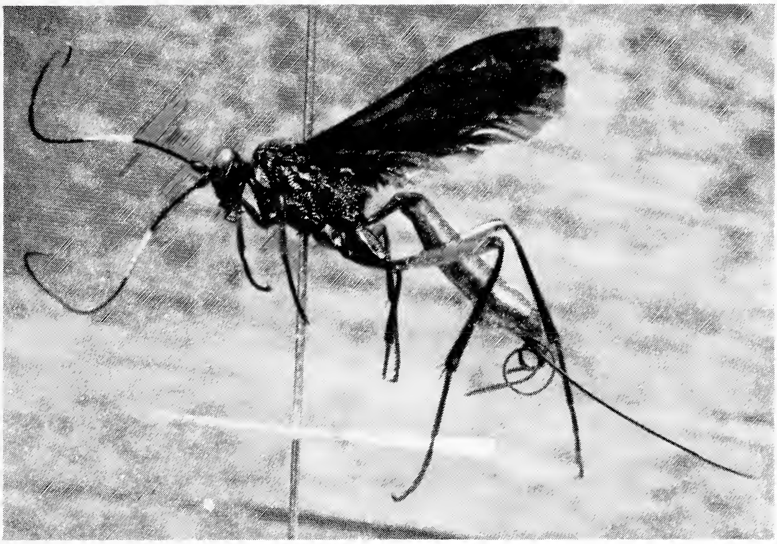

Fig. 2. *Cosmiocryptus huascar,* ♀. Photograph of whole insect in lateral view.

homopterous sap suckers which usually infest this common streamside plant.

SPECIFIC NAME. From the Latin adjective *occidens,* "west or sunset".

2. *Cosmiocryptus huascar* (Porter), new combination (Fig. 2, 3, 4).

Trachysphyrus huascar Porter, 1967. Mem. Amer. Ent. Inst. 10: 122–4. Holotype ♀: Perú, Largos, 3500 m, 23-III-1960, W. Weyrauch (Tucumán).

I described this species (Porter 1967: 122–24) from 5 females and 1 male collected between 2389 m and 3500 m in the Andes of central and western Perú. An additional 4 females now are reported from Matucana, Perú and their analysis permits the following amendments and additions to my original description.

Length of fore wing: 10.5–14.4 mm. *First flagellomere:* 5.9–6.7 as long as deep at apex. *Malar space:* 0.9–1.3 as long as basal width of mandible. *Clypeus:* apical margin nearly straight. *Temple:* 0.5–0.6 as long as eye in dorsal view. *Mesoscutum:* notauli reaching up to

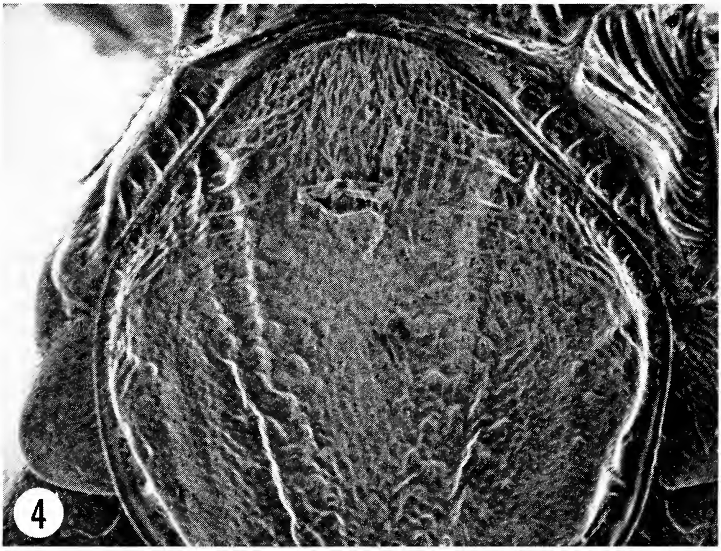

Fig. 3. *Cosmiocryptus huascar,* ♀. SEM Photograph (42×), showing anteriolateral part of thorax.

Fig. 4. *Cosmiocryptus huascar,* ♀. SEM Photograph (55×), showing pronotum and most of mesoscutum in dorsal view.

0.8 the length of mesoscutum. *Wing venation:* ramellus often short but distinct. *Propodeum:* cristae often very strongly projecting cuneate to ligulate. *Ovipositor:* notch sometimes obsolete; tip 0.14–0.17 as high at notch as long from notch to apex.

NEW SPECIMENS EXAMINED. 4♀: PERÚ, Lima Province, Matucana, 2389 m, 28-30-VI-1974, C. Porter, L. Stange.

VARIATION. Although its range extends from the central Andes at Cuzco and Urubamba to the west Andean slopes near Lima, *C. huascar* shows little variation in the characters studied and offers no phaenotypically aberrant local populations. These facts and its ability to live at altitudes of up to 3500 m suggest that this species is a recent (i.e. post-Pleistocene) arrival on the upper fringes of the Coastal Desert.

FIELD NOTES. Specimens of *C. huascar* collected at Matucana were found near the Rimac River, as they flew at low altitude over grassy areas or visited *Baccharis* soaked with homopteran honeydew.

3. **Cosmiocryptus leucetrum** Porter, new species
(Fig. 5)

FEMALE. *Color:* antenna shining reddish brown, with dusky staining that becomes more prominent apicad; head and mesosoma black with reddish brown on much of mandible, on large clypeal blotch, and on much of scutellum, as well as with a narrow white line on much of frontal orbit and a broader white line that extends along rear of vertical orbit and almost all of hind orbit; 1st gastric tergite dark red with blackish near base and again faintly on apical margin; 2nd tergite dark red with inconspicuous blackish staining; 3rd tergite white, except becoming pale brown laterad, and black on basal 0.3; exposed portion of tergites 4–7 white with lateral faint brown suffusion; and tergite 8 black with a little white dorsobasally; legs mostly shining dull red with tibiae and tarsi duller and slightly dusky; wings medium blackish with subdued metallic reflections.

Length of fore wing: 11.3 mm. *First flagellomere:* 6.3 as long as deep at apex. *Clypeus:* strongly and a little asymmetrically blunt-pyramidal in profile; apical margin gently but definitely convex. *Malar space:* 1.0 as long as basal width of mandible. *Temple:* 0.5 as long as eye in dorsal view; receding and only slightly rounded off. *Cephalic carinae:* sharp and low, occipital carina joining the only

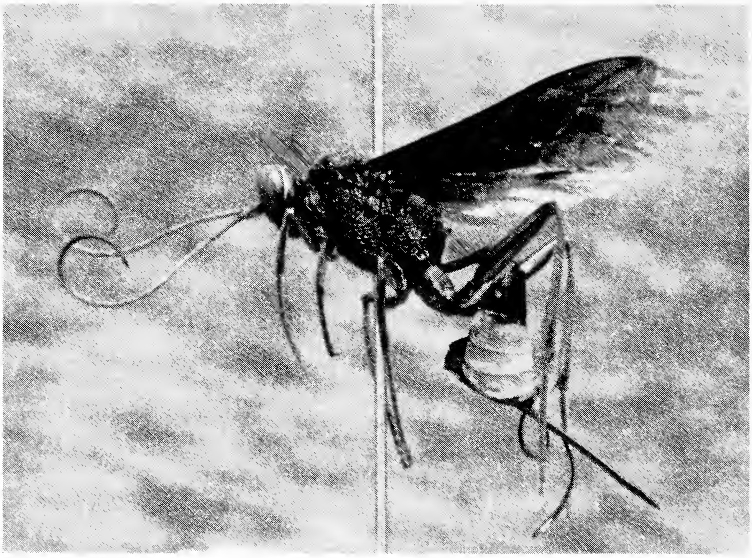

Fig. 5. *Cosmiocryptus leucetrum,* ♀. Holotype. Photograph of entire insect in lateral view.

weakly raised hypostomal carina below. *Fore tibia:* moderately stout, slightly inflated on median 0.3. *Pronotum:* submarginal groove broad, shallow, reticulate; epomia sharp in scrobe, practically effaced below scrobe, dorsally terminating in a broad but low and inconspicuous swelling. *Mesoscutum:* notauli shallow but coarsely reticulate, traceable about 0.8 length of mesoscutum; surface shining with coarse and crowded reticulation and puncto-reticulation; punctures best defined mesad on lobes (especially on lateral lobes) and wrinkling coarsest along notauli and between them rearward. *Mesopleuron:* speculum swollen, puncto-reticulate peripherally and mostly smooth and shining centrad; surface otherwise with extremely coarse reticulate wrinkling. *Wing venation:* radial cell 3.7 as long as wide; areolet large, intercubiti moderately converging above, 2nd abscissa of radius 0.8 as long as 1st intercubitus; 2nd recurrent gently inclivous, almost straight; disco-cubitus slightly angled, with a vestigial ramellus; upper part of nervellus 3.0 as long as lower. *Propodeum:* short and high; faces subequal, the basal arcuately sloping rearward, the apical well differentiated and vertical; spiracle

2.3 as long as wide; basal trans-carina high but irregular on mid section, obsolete laterad; apical trans-carina obsolete; cristae medium sized, broad, short but well projecting, truncately ligulate; longitudinal carinae obsolete; surface with reticulate wrinkling that is strong to coarse on apical face and on much of basal face between trans-carinae (particularly on a broad arc in position of basal trans-carina) and which becomes contrastingly weaker only basad of basal trans-carina. *1st gastric tergite:* postpetiole 1.7 as wide apically as long from spiracle to apex; ventro-lateral carinae strong and sharp throughout; dorso-lateral carinae fine but sharp throughout; dorsal carinae represented by the beveled margins of a broad and low median elevation that becomes detectable toward apex of petiole and continues onto much of postpetiole; surface of postpetiole shining, smooth and polished on about apical 0.3 but otherwise with delicate micro-reticulation and with a few tiny punctures that emit short, sparse, inconspicuous setae. *2nd gastric tergite:* nearly smooth and conspicuously shining, with delicate micro-reticulation that practically fades out toward apex, as well as with scattered tiny punctures that emit short and very sparse setae. *Ovipositor:* unusually robust; sheathed portion 0.53 as long as fore wing; nodus low but distinct, with a tiny notch; dorsal valve with a slightly concave taper from notch for about 0.7 the distance to apex and more convexly tapered on apical 0.3; ventral valve with strong, oblique ridges on tip; tip 0.30 as high at notch as long from notch to apex.

MALE. Unknown.

TYPE MATERIAL. Holotype ♀: PERÚ, Lima Province, Cupiche, 10 km E. Chosica, 25-VI-2-VII-1974, C. Porter, L. Stange. Holotype in Florida State Collection of Arthropods.

RELATIONSHIPS. *Cosmiocryptus leucetrum* belongs to the *Albomarginatus* group within its genus as defined by Porter (1967: 150–3). In this subgroup, it seems most closely allied to *C. uspallatae* Porter,[2] which occurs in the deserts of western Argentina from Mendoza north to Salta Province (Porter 1967: 167, 1975: 211). Features shared by *C. leucetrum* and *C. uspallatae* include their rather pyramidal clypeus, strongly receding temples, very long 1st flagellomere (at least 6.0 as long as deep at apex), only finely reticulate 2nd gastric tergite, relatively long ovipositor (at least 0.50 as

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[2] New combination.

long as fore wing), and stout ovipositor tip (0.30 or more as high at notch as long from notch to apex). *C. leucetrum* differs from *C. uspallatae* in its longer malar space (1.0 vs. 0.8–0.9 as long as basal width of mandible), longer notauli (traceable 0.8 length of mesoscutum vs. 0.3), more coarsely sculptured mesoscutum, extremely coarse mesopleural wrinkling, shorter radial cell (3.7 vs. 4.2–4.3 as long as wide), longer propodeal spiracle (2.3 as long as wide vs. 1.4–1.7), absence of white on the flagellum, partly red gaster, and dull red (vs. mostly pale orange) legs.

FIELD NOTES. The unique holotype was swept from *Baccharis* growing on sandy soil within the flood plain of the lower Rimac River.

SPECIFIC NAME. *Leucetrum,* used here as a noun in apposition, is derived and latinized from the Greek adjective *leukos,* "white", and the Greek noun *ētron*, "abdomen".

4. *Cosmiocryptus violaceipennis* Cameron
(Fig. 6, 7)

Cosmiocryptus violaceipennis Cameron, 1902. Trans. Amer. Ent. Soc. **28**: 372. Holotype ♀: Perú, Callao (London).

I redescribed *C. violaceipennis* (Porter 1967: 218–20) on the basis of 3 females and 1 male collected at Callao (a female cotype), Matucana, and Cañete in the central Coastal Desert and adjacent west Andean slopes. Subsequent collection of 5 more females and 6 new males, obtained not only close to Lima (Rimac Valley, Santa Eulalia Valley) but also in the northern coastal region near Trujillo (Samne), permits further redescription of *C. violaceipennis.*

FEMALE. *Color:* sometimes blackish on as much as apical 0.5 of hind femur.

Length of fore wing: 7.9–12.1 mm. *First flagellomere:* 5.5–6.0 as long as deep at apex. *Mesopleuron:* swollen area along prepectal carina opposite speculum always conspicuous but invaded to a variable extent by punctures and wrinkles. *Wing venation:* ramellus strong and elongate; radial cell 3.8–4.3 as long as wide; 2nd abscissa of radius 0.6–0.7 as long as 1st intercubitus. *First gastric tergite:* postpetiole 1.5–2.0 as wide apically as long from spiracle to apex. *Ovipositor:* sheathed portion 0.40–0.48 as long as fore wing; tip 0.21–0.28 as high at notch as long from notch to apex.

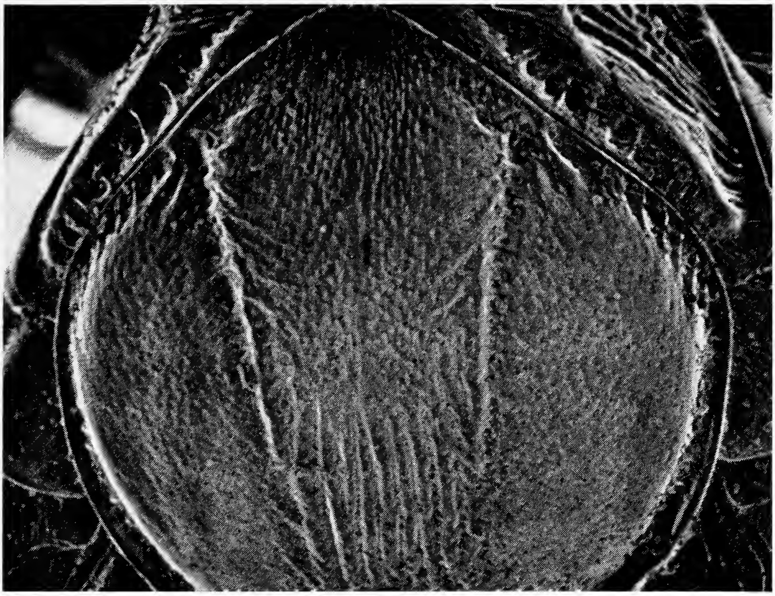


Fig. 6. *Cosmiocryptus violaceipennis,* ♀. SEM Photograph (50×), showing pronotum and most of mesoscutum in dorsal view.

MALE. *Color:* flagellum with white band beginning on segments 9 or 10 and ending on segments 14, 15, or 16; scape sometimes with a large white spot below or sometimes completely dark; clypeus varying from wholly black to mostly white; sometimes with a pair of white spots mesad on pronotal collar; sometimes a white spot on tegula; scutellum sometimes with a white spot; fore coxae and/or trochanters sometimes extensively white; fore and mid legs sometimes more conspicuously reddish brown than in female; hind tarsomeres 3–4 sometimes partly white.

Length of fore wing: 8.7–10.6 mm. *First flagellomere:* 3.7–4.5 as long as deep at apex. *Tyloids:* at least the 2nd (counting from base of flagellum), and usually the 1st and 3rd also, broadly oval. *Temple:* 0.6–0.7 as long as eye in dorsal view. *First gastric tergite:* postpetiole 0.9–1.4 as wide apically as long from spiracle to apex.

NEW SPECIMENS EXAMINED. 5♀ and 6♂: PERÚ, Lima Province, San Gerónimo, Valle del Río Santa Eulalia, 28-VI-1976, C.

Porter, C. Calmbacher; Matucana, 2389 m, 28-30-VI-1974, C. Porter, L. Stange, 4-5-VII-1976, C. Porter; La Libertad Province, Samne, 40 km NE Trujillo, ca. 1500 m, 12-17-VII-1975, C. Porter, L. Stange.

RELATIONSHIPS. This species, along with *C. weyrauchi, C. diplatys, C. leptaechma,* and *C. aricae,* forms a distinctive subgroup that is endemic to the Coastal Desert and adjacent Andean slopes (between sealevel and 3400 m) in most of Perú and in Tarapacá

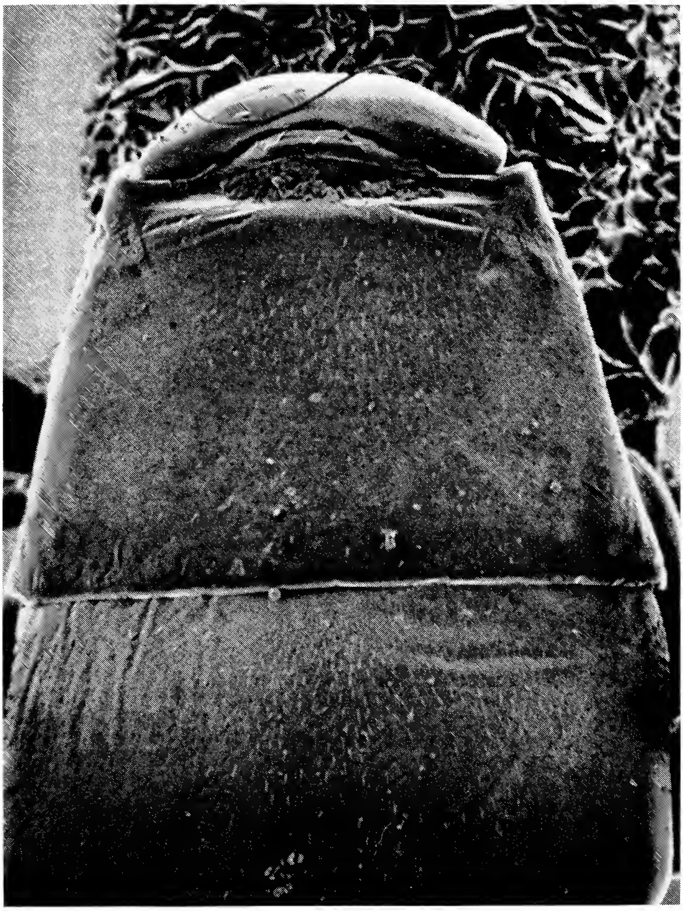


Fig. 7. *Cosmiocryptus violaceipennis,* ♀. SEM Photograph (110×), showing rear of propodeum and much of first 3 gastric tergites in dorsal view.

Province of north Chile. The *Violaceipennis* group (Porter 1967: 217–18 apparently has no close relatives elsewhere in South America. It thus may have evolved *in situ* during the last half of the Tertiary, when a rain shadow created by the uplifting Andes allowed development in what is now the Coastal Desert of a thorn scrub vegetation (similar to the Argentine Chaco) and favorable for comparatively dry-adapted ichneumonids, such as *Cosmiocryptus* and *Trachysphyrus.*

The ancient progenitor of the *Violaceipennis* group might well have reached the Coastal Desert from the Argentine and Bolivian Chaco, while the Andes still were low enough to allow easy dispersal between the arid parts of south-central South America and similar communities then developing on the Pacific coast (Solbrig 1976: 38).

FIELD NOTES. Most of my specimens of *C. violaceipennis* were taken while sweeping herbaceous vegetation along rivers or irrigation ditches. The species does not seem to visit *Baccharis* as often as its relatives.

HOST. *C. violaceipennis* has been reared from *"Megalopyge* prob. *amitina",* a megalopygid moth.

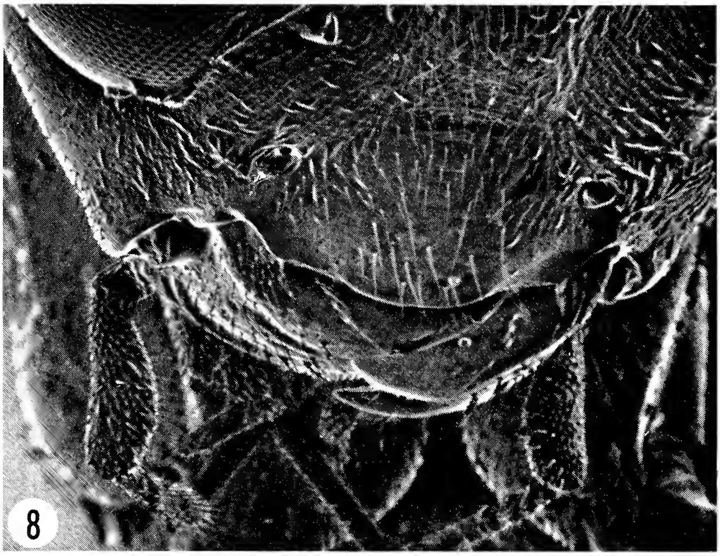
5. *Cosmiocryptus diplatys* (Porter), new combination (Fig. 8, 9, 10).

Trachysphyrus diplatys Porter, 1967. Mem. Amer. Ent. Inst. **10**: 222–4. Holotype ♀: Perú, Matucana, 2400 m, 23-VI-1955, W. Weyrauch (Tucumán).

C. diplatys was described from a unique female (Porter 1967: 222–24). Subsequent collecting has added 14 females and 50 males to this number, but has not extended the species' range beyond Matucana, Perú. Herewith I give a revised description of the female and characterize the male for the first time.

FEMALE. *Color:* antenna black with a white annulus on flagellomeres 4 or 5 to 8, 9, or 10; mandible usually all black; gaster sometimes with extensive but irregular black staining; often with some red on fore and mid trochantelli and on bases of their femora.

Length of fore wings: 8.1–12.8 mm. *Flagellum:* long, slender, cylindric; 1st flagellomere 6.2–7.8 as long as deep at apex. *Malar space:* 0.70–0.90 as long as basal width of mandible. *Temple:* 0.6–0.8 as long as eye in dorsal view; rather strongly receding. *Wing venation:* radial cell 3.7–4.1 as long as wide; 2nd abscissa of radius



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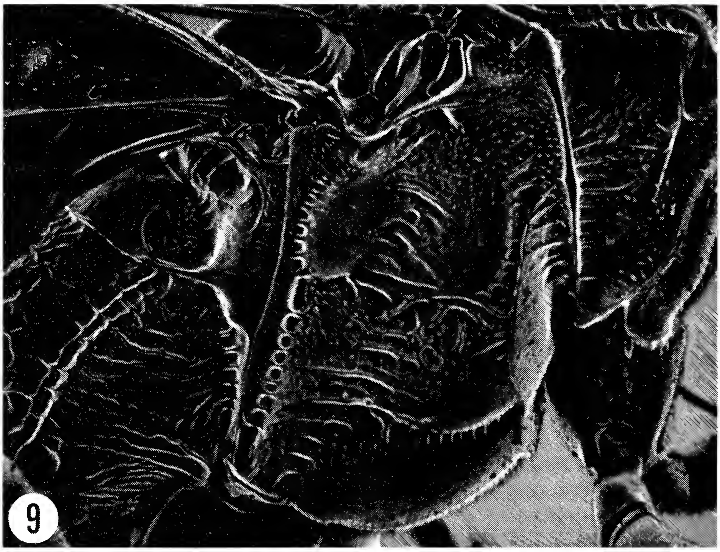

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Fig. 8. *Cosmiocryptus diplatys,* ♀. SEM Photograph (110×), showing clypeus and adjacent areas in anterior view.

Fig. 9. *Cosmiocryptus diplatys,* ♀. SEM Photograph (35×), showing greater part of mesosoma in lateral view.

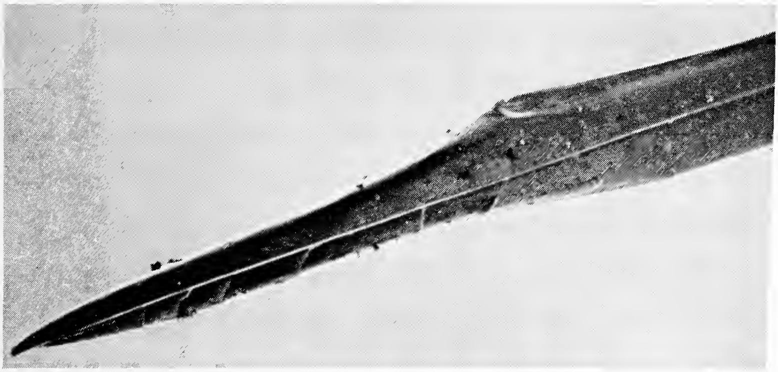


Fig. 10. *Cosmiocryptus diplatys*, ♀. SEM Photograph (85×), showing ovipositor tip in lateral view.

0.6–0.7 as long as 1st intercubitus; ramellus sometimes strong. *Propodeum:* cristae subligulate to subcuneate; wrinkles between the trans-carinae varying from mostly longitudinal to quite irregular. *First gastric tergite:* postpetiole 1.5–2.3 as wide apically as long from spiracle to apex. *Ovipositor:* sheathed portion 0.55–0.63 as long as fore wing; tip 0.20–0.23 as high at notch as long from notch to apex.

MALE. Differs from female as follows: *Color:* white flagellar annulus (often weak below) on segments 7, 8, 9, or 10 to 14 or 15; white orbital bands broader and more extensive than in female; small white spot on tegula.

Length of fore wing: 7.3–12.0 mm. *Flagellum:* 1st segment 3.9–5.0 as long as deep at apex; only the 3rd tyloid (counting from base) unusually broad, the rest ovoid to linear. *Front:* weakly excavated. *Clypeus:* much as in female, very low in profile with rounded apical margin. *Malar space:* 0.67–0.80 as long as basal width of mandible. *Temple:* 0.7–1.0 as long as eye in dorsal view; more strongly rounded-off than in female. *Mesoscutum:* more sparsely punctate than in female, even more shining, sometimes without longitudinal wrinkles mesad between ends of notauli. *Propodeum:* a little longer and lower in profile than in female; cristae strong and bluntly cuneate; sculpture (also of mesosoma) generally weaker than in female, with more or less extensive smooth areas, often including most of areola. *First gastric tergite:* postpetiole 1.0–1.3 as wide apically as long from spiracle to apex. *Second gastric tergite:* with abundant tiny, superficial punctures which emit rather long setae that mostly equal or surpass the length of their interspaces.

NEW SPECIMENS EXAMINED. 14♀ and 50♂: PERÚ, Lima Province, Matucana, 2389 m, 15-VI-1979, C. Porter, 27-30-VI-1976, C. Porter, C. Calmbacher, 28-30-VI-1974, C. Porter, L. Stange, 4-5-VII-1976, C. Porter, C. Calmbacher.

RELATIONSHIPS. Females of *C. diplatys* easily may be distinguished from all sympatric congeners by their conspicuously flattened and otherwise strangely modified ovipositor tip (Fig. 10). The males much resemble those of *C. violaceipennis* but have the mesoscutum more shining and more sparsely punctate and show a different tyloidal conformation.

FIELD NOTES. I have repeatedly found this species common at Matucana toward the upper end of the Rimac Valley in seasonally humid west Andean Prepuna. Most specimens were netted from *Baccharis* along the main river, its tributaries, and irrigation ditches. They seemed attracted by the homopteran honeydew covering *Baccharis* foliage. Also they may have been looking for hosts among the larger lepidopterous cocoons (Psychidae, Saturniidae, etc.) suspended from the *Baccharis*.

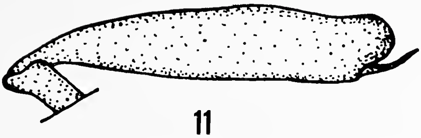
This species is known only from Mantucana. However, there are many entomologically unexplored river valleys along the Peruvian coast and *C. diplatys* eventually should appear in some of these.

6. **Cosmiocryptus aricae** Porter, new species
(Fig. 11, 12).

This *Cosmiocryptus* appears to be a southern vicariant of the central and north Peruvian *C. violaceipennis* (Cameron). It may be distinguished as follows from its northern relative.

FEMALE. *Color:* similar to *T. violaceipennis* (black antenna with white band; mostly black head and mesosoma; blackish wings; red gaster) except for the presence of a dull white area above the base of each mandible interiorly.

Length of fore wing: 6.0 mm. *First flagellomere:* 5.0 as long as deep at apex. *Fore tibia:* stout and definitely inflated. *Mesopleuron:* speculum shining but punctured and wrinkled; surface otherwise strongly and irregularly (but not grossly) wrinkled throughout, lacking a polished and swollen area above along prepectal carina facing speculum. *Wing venation:* radial cell 4.5 as long as wide.



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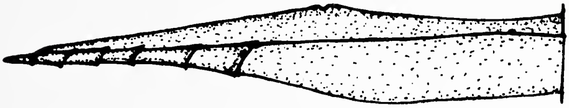

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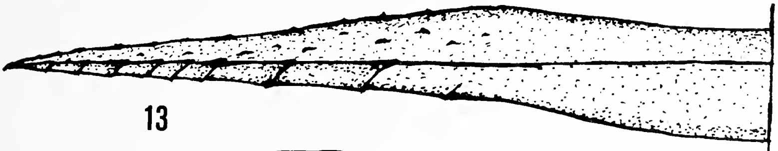

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Fig. 11. *Cosmiocryptus aricae,* ♀. Holotype. Fore tibia in lateral view.

Fig. 12. *Cosmiocryptus aricae,* ♀. Holotype. Ovipositor tip in lateral view.

Fig. 13. *Cosmiocryptus leptaechma,* ♀. Holotype. Ovipositor tip in lateral view.

Fig. 14. *Cosmiocryptus leptaechma,* ♀. Holotype. Fore tibia in lateral view.

Propodeum: spiracle 1.4 as long as wide; cristae subligulate, rather low; surface more densely and less grossly reticulo-rugose than in *T. violaceipennis. First gastric tergite:* no flange at base; postpetiole 1.7 as wide apically as long from spiracle to apex. *Second gastric tergite:* setae sparse and inconspicuous, largely much shorter than the length of their interspaces. *Ovipositor:* strongly compressed; sheathed portion 0.5 as long as fore wing; nodus rather prominently elevated and with a sharp but tiny notch; dorsal valve with a fairly strong, direct taper between notch and apex.

MALE. Unknown.

TYPE MATERIAL. Holotype ♀: CHILE, Tarapacá Province, Chapiquiña, 3170 m, I-1977, in Malaise Trap, C. Porter. Holotype in Florida State Collection of Arthropods.

RELATIONSHIPS. This species shows great superficial resemblance to *C. violaceipennis* but may be distinguished by the features given in the preceding diagnosis and emphasized in the key. The distinctive ovipositor tip of *C. aricae* suggests that its host preferences may differ from those of other sympatric *Violaceipennis* group species.

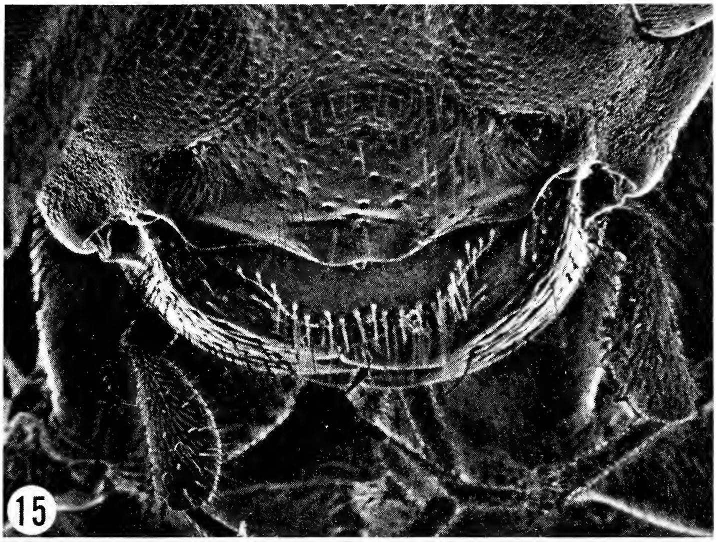
FIELD NOTES. The Malaise Trap used at Chapiquiña, a Puna locality more than 3000 m above Arica, was placed across a small stream bordered by dense, tall bunch grass and, more distantly, by alfalfa fields and *Eucalyptus* plantations.

SPECIFIC NAME. *Aricae* is a latinized genitive singular derived from the Chilean city of Arica.

7. **Cosmiocryptus leptaechma** Porter, new species (Fig. 13, 14).

FEMALE. *Color:* antenna black with a white band above on flagellomeres 3–10; head and mesosoma black; a white line briefly on facial orbit opposite antennal socket, a short white line on orbit at top of eye, and a white line on about median 0.4 of hind orbit; fore and mid legs black with faint reddish brown staining, especially apicad on femora; hind leg with coxa, trochanter, trochantellus, and most of femur red; weakly blackish on apical 0.8 of hind femur and uniformly black on tibia and tarsus; gaster red; wings blackish with metallic blue and purple reflections.

Length of fore wing: 9.4 mm. *Flagellum:* long, slender, cylindric; 1st flagellomere 6.0 as long as deep at apex. *Front:* moderately excavated. *Clypeus:* gently and almost symmetrically convex in profile; apical margin gently convex. *Malar space:* 0.8 as long as basal width of mandible. *Temple:* 0.4 as long as eye in dorsal view; strongly receding and gently convex. *Fore tibia:* stout but not at all inflated. *Wing venation:* radial cell 3.6 as long as wide. *Propodeum:* spiracle 2.0 as long as wide; propodeal surface as grossly but less reticulately or irregularly wrinkled than in *violaceipennis. First gastric tergite:* postpetiole 1.5 as wide at apex as long from spiracle to apex. *Second gastric tergite:* strongly shining with faint but palpable micro-reticulation or shagreening (more polished than in *T. violaceipennis*); punctures very sparse and faint, their setae much more widely spaced than the lengths of the interspaces. *Ovipositor:* sheathed portion 0.5 as long as fore wing; straight, rather slender, strongly compressed; nodus very low, weakly defined, with a small



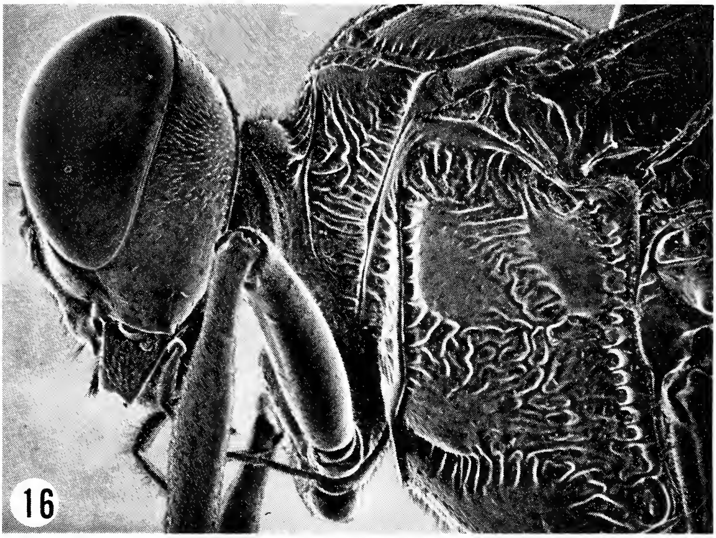


Fig. 15. *Cosmiocryptus weyrauchi,* ♀. SEM Photograph (70×), showing head and adjacent areas in anterior view.

Fig. 16. *Cosmiocryptus weyrauchi,* ♀. SEM Photograph (25×), showing head, prothorax, and mesothorax in lateral view.

and shallow notch; dorsal valve with sparse but conspicuous tiny tubercles and with a very gradual and nearly direct taper between notch and apex; tip 0.16 as high at notch as long from notch to apex.

MALE. Unknown.

TYPE MATERIAL. Holotype ♀: PERÚ. Lima Province, Matucana, 2389 m, 28-30-VI-1977, C. Porter, L. Stange. Holotype in Florida State Collection of Arthropods.

RELATIONSHIPS. This species is closely related to *C. violaceipennis* and *C. aricae.* The very slender, microtuberculate ovipositor tip and uniflated fore tibia constitute the best diagnostic features of *C. leptaechma.* Also distinctive are its low and almost symmetrically convex clypeal profile and strongly shining 2nd gastric tergite with only faint micro-reticulation and widely scattered setae.

FIELD NOTES. *Cosmiocryptus leptaechma* can not be distinguished at sight from other members of the *Violaceipennis* species group. I thus offer no specific information about the circumstances of its capture at Matucana, Perú.

SPECIFIC NAME. *Leptaechma,* used here as a noun in apposition, is derived and latinized from the Greek adjective *leptos,* "delicate", and the Greek noun *aichmē*, "spear point".

8. *Cosmiocryptus weyrauchi* (Porter), new combination (Fig. 15, 16, 17, 18, 19).

Trachysphyrus weyrauchi Porter, 1967. Mem. Amer. Ent. Inst. **10**: 220-2. Holotype ♀: Perú, "Huarochiri", 3400 m, 5-VIII-1961, W. Weyrauch (Tucumán).

In 1967 (Porter: 220-22) I described *T. weyrauchi* from 1 Peruvian female and 2 males collected in Tarapacá Province of north Chile. More recent fieldwork has added 6 females and 16 males, permitting some additions and modifications with regard to the original diagnosis.

FEMALE. *Color:* white flagellar annulus sometimes beginning on 1st segment; gaster in a few specimens with extensive black staining (but always with conspicuous red areas); sometimes with at least a little red on coxae, trochanters, and femora basally; hind leg often wholly or almost wholly black.

Length of fore wing: 9.5-11.0 mm. *First flagellomere:* 5.0-6.2 as long as deep at apex. *Malar space:* 0.86-0.90 as long as basal width

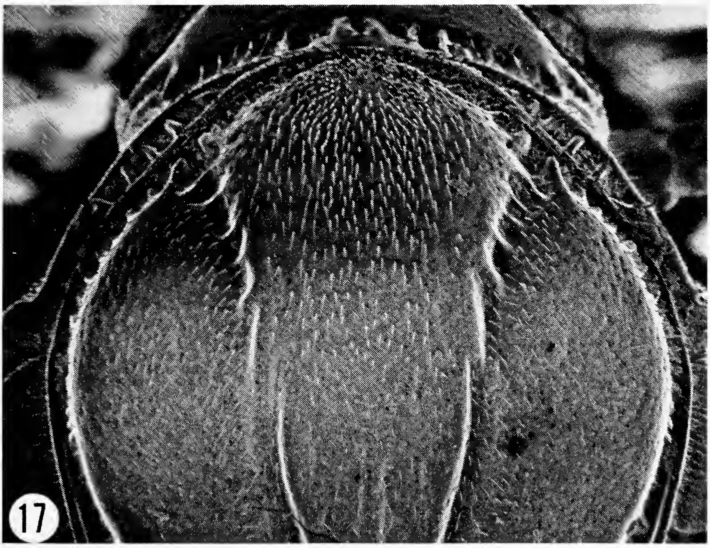


Fig. 17. *Cosmiocryptus weyrauchi,* ♀. SEM Photograph (55×), showing pronotum and most of mesoscutum in dorsal view.

Fig. 18. *Cosmiocryptus weyrauchi,* ♀. SEM Photograph (45×), showing rear of mesopleuron, propodeum, and most of first gastric tergite in lateral view.

of mandible. *Temple:* 0.5–0.6 as long as eye in dorsal view. *Mesopleuron:* often smooth and polished even in lower front quadrant. *Wing venation:* radial cell 3.8–4.4 as long as wide. *Propodeum:* spiracle 2.2–2.3 as long as wide. *First gastric tergite:* postpetiole 1.7–2.0 as wide apically as long from spiracle to apex. *Ovipositor:* sheathed portion 0.5–0.6 as long as fore wing; nodus often rather prominent; tip 0.23–0.30 as high at notch as long from notch to apex.

MALE. *Color:* white flagellar annulus on segments 5, 6, 7, 8 or 9 to 13, 14, or 15; mid coxa occasionally marked with red.

Length of fore wing: 4.8–9.4 mm. *Flagellum:* tyloids all much longer than broad, the 1st 3 linear (counting from base of antenna); 1st flagellomere 2.6–3.2 as long as deep at apex. *Malar space:* 0.70–0.84 as long as basal width of mandible. *Temple:* 0.6–0.8 as long as eye in dorsal view. *Mesoscutum:* notauli traceable up to 0.6 length of mesoscutum. *Mesopleuron:* in small specimens sometimes almost wholly smooth and polished. *Propodeum:* surface in small specimens often extensively smooth and shining; cristae often as strong as in female. *First gastric tergite:* postpetiole 1.3–1.8 as wide at apex as long from spiracle to apex. *Second gastric tergite:* setae generally shorter than the length of their interspaces, but in 1 specimen mostly approaching interstitial length.

NEW SPECIMENS EXAMINED. 6♀ and 16♂: PERÚ, Lima Province, Matucana, 2389 m, 28-30-VI-1974, C. Porter, L. Stange; CHILE, Tarapacá Province, Belén, 3170 m, 18-19-VII-1976, C. Porter, C. Calmbacher, H. Vargas; Chapiquiña, 3170 m, I-1977, Malaise Trap, C. Porter, IX-1977, Malaise Trap, C. Porter, 5-6-VII-1977, C. Porter, G. Díaz, 17-20-VII-1976, 3370 m, C. Porter, C. Calmbacher, 21-VII-1977, C. Porter, 3-VIII-1975, C. Porter, A. Matta; Socoroma, 3000 m, 28-VI-1977, C. Porter, VII-1977, Malaise Trap, C. Porter, 7-VII-1977, C. Porter, G. Díaz.

RELATIONSHIPS. The bituberculate clypeus, usually rather sparse setae on the 2nd gastric tergite, and uniformly elongate tyloids distinguish this conspicuous and somewhat aberrant species from all other members of its subgroup.

FIELD NOTES. *Cosmiocryptus weyrauchi* frequents tall vegetation, such as *Baccharis* and bunch grass, but also may be found on or near the ground among various grasses and forbes, including alfalfa and oregano.

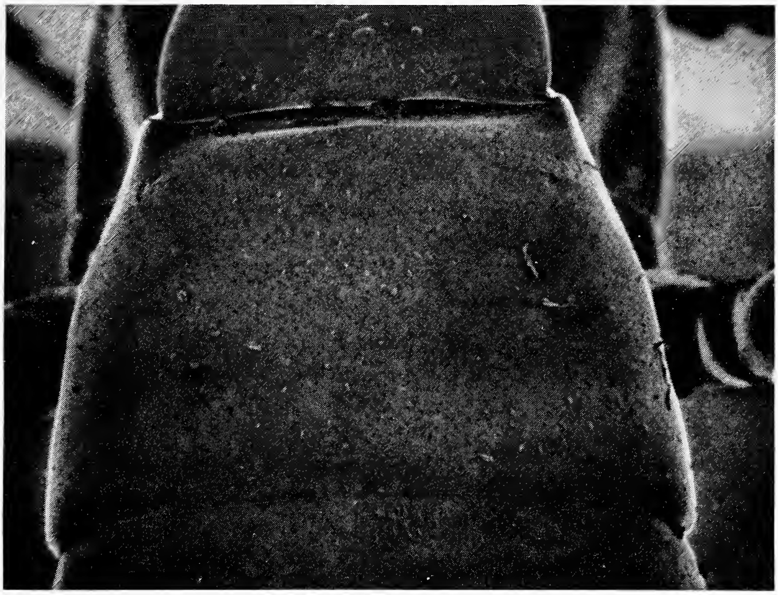


Fig. 19. *Cosmiocryptus weyrauchi*, ♀. SEM Photograph (45×), showing second gastric tergite and adjoining areas in dorsal view.

ACKNOWLEDGMENTS

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Mr. Jaime Zung of Fordham University prepared the Scanning Electron Microscope photographs. I am appreciative of his patience in obtaining excellent pictures without the standard gold coating. Mr. Zung worked under Dr. E. Ruth Witkus, Professor and former chairman of Fordham Biology.

SUMMARY

The mesostenine genus *Cosmiocryptus* ranges from Ecuador to Tierra del Fuego in Andean, temperate, xeric, subtropical, marginally tropical, and Neantarctic biomes. It has 8 species in the Coastal Desert, of which 7 (*C. violaceipennis, C. weyrauchi, C. diplatys, C. aricae, C. leptaechma, C. leucetrum,* and *C. occidens*) seem to be endemic, while the eighth, *C. huascar,* ranges across the Peruvian Andes as far as Cuzco. As here characterized, *Cosmiocryptus* includes mesostenine ichneumonids related to *Trachysphyrus* but with the axillus vein almost appressed to the anal margin of the hind wing. It is also related to *Chromocryptus* but usually lacks large punctures on the 2nd gastric tergite and a baso-lateral expansion on the 1st tergite. Herein described are 4 new species of *Cosmiocryptus: C. occidens* and *C. leucetrum* from north-central Perú plus *C. aricae* and *C. leptaechma* from north Chile.

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ON THE SIGNIFICANCE OF PSEUDOFEMALE BEHAVIOR IN THE NEOTROPICAL COCKROACH GENERA *BLABERUS, ARCHIMANDRITA* AND *BYRSOTRIA*

BY PETER W. WENDELKEN[1] AND ROBERT H. BARTH, JR.[2]

The basic constituents of successful courtship behavior in most species of cockroaches studied thus far are as follows: (1) The male contacts the female. (2) The male courts the female and gives a "full wing raising display," elevating his wings to a nearly vertical position and turning away from the female. (3) The female shows the "mounting and feeding" response. She straddles the male's exposed abdomen and moves forward. As she mounts, the female's mouthparts and palps are closely applied to the male's abdominal tergites and are worked vigorously. (In some species, the female feeds upon secretions of specialized tergal glands.) (4) The male backs beneath the mounting and feeding female, extending his abdomen backward in copulatory thrusts. (5) Genital connection is achieved and the pair execute a turning operation to assume the opposed copulatory position (male and female facing in opposite directions). The opposed position persists throughout copulation which may last for an hour or more (Barth 1968a, Wendelken 1976, Simon and Barth 1977a). Females and males are generally suspected of producing sex pheromones of varying degrees of volatility which function in the release of certain aspects of courtship behavior. The relative contributions of chemical and tactile stimuli to the release of the various stages in the courtship sequence vary considerably among different species (Barth 1968a). As a rule, female sex pheromones are important in release of male courtship behavior, including the full wing raising display (Barth 1968a, 1970; Wendelken 1976; Simon and Barth 1977b). And male sex pheromones are believed to be involved in release of the female mounting and feeding response which serves to position the female such that the male may achieve genital connection (Roth and Dateo 1966, Barth 1968a). The tactile stimuli produced by the female's mounting and feeding response play an

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important role in the release of the male's backing movements and copulatory thrusts (Barth 1964, 1968a; Wendelken 1976; Simon and Barth 1977a).

In cockroaches, the term "homosexual behavior" has been used in reference to the behavior of males directing male courtship patterns toward other males (Barth 1964). "Pseudofemale behavior" has been used to designate the appearance in the male of motor patterns which are characteristic of female sexual behavior—i.e., the "mounting and feeding" response. Pseudofemale mounting and feeding release backing and copulatory thrusts by the displaying male. However, genital connection is only rarely achieved and in such cases lasts only a few seconds (Barth 1964). Homosexual and pseudofemale behavior are of widespread occurrence in cockroaches. Homosexual behavior may be at least partially explicable in terms of female sex pheromone becoming attached to the cuticle of males exposed to females. The female sex pheromone would tend to release courtship behavior in males coming into antennal contact with these pheromone-tinged males. Thus, to some extent, homosexual behavior may be an artifact of the courtship situation (Roth and Willis 1952, Simon and Barth 1977b).

No satisfactory explanation has been advanced to account for the perplexing prevalence of pseudofemale behavior in cockroaches. The elementary form of male mounting and feeding behavior, as described above, has been reported for the following species: *Periplaneta americana* (L.) (Roth and Willis 1952, Barth 1970, Simon and Barth 1977a); *Periplaneta brunnea* Burmeister and *Periplaneta fuliginosa* (Serville) (Barth 1970, Simon and Barth 1977a); *Periplaneta japonica* and *Periplaneta australasiae* (F.) (Simon and Barth 1977a); *Blatta orientalis* L. (Roth and Willis 1952, Barth 1970, Simon and Barth 1977a); *Supella longipalpa* (F.) (Roth 1952); *Latiblattella angustifrons* Hebard (Willis 1970); *Eurycotis floridana* (Walker) (Barth 1968b); *Blattella germanica* (L.) (Roth and Willis 1952); *Parcoblatta fulvescens* (Saussure and Zehntner) (Wendelken and Barth 1971); *Byrsotria fumigata* (Guérin) (Barth 1964); *Leucophaea maderae* (F.) and *Nauphoeta cinerea* (Olivier) (Roth and Barth 1967). This list is not necessarily all inclusive but it does indicate the widespread occurrence of the elementary form of pseudofemale behavior in cockroaches. In none of these instances was pseudofemale behavior described as being a component of the male repertoire of aggressive behavior.

This paper discusses the significance of a previously unreported form of pseudofemale behavior in the neotropical cockroach genera *Blaberus, Archimandrita,* and *Byrsotria.* These genera belong to the Tribe Blaberini (Blaberidae, Blaberinae) according to Roth (1970a).

MATERIALS AND METHODS

Stock cultures were maintained as described by Barth (1964) for *Byrsotria fumigata.* Observations of behavior were made during the dark phase of a 12 hour day/night cycle under red illumination in specially designed observation chambers constructed of transparent lucite plastic (39.5 × 26.8 × 14.5 cm deep) with a removable center partition dividing the chamber into two halves allowing segregation of the sexes prior to an observation period (for details, see Barth 1964).

COURTSHIP IN TRIBE BLABERINI

Very elaborate and complex preliminary male courtship behavior is found in *Blaberus discoidalis* Serville, *B. parabolicus* Walker, *B. giganteus* (L.), *B. craniifer* Burmeister, *Archimandrita tessellata* Rehn, and *Byrsotria fumigata.* In addition, in these species there is frequently vigorous aggressive behavior between males at the site of courtship of a female. These phenomena are considered to be a consequence of sexual selection acting on the males. "Sexual selection" here refers to a selective advantage for characters producing a competitively unequal advantage in both epigamic and intrasexual interactions associated with mating behavior. In spite of the complexities of male behavior in these species, the terminal events leading to copulation (the copulation sequence) follow a basic cockroach pattern (Wendelken 1976). Preliminary male courtship behaviors are released by a female sex pheromone (Barth 1964, 1970; Wendelken 1976). If a courted female is receptive, she signals receptivity by moving or turning toward the courting male and simultaneously antennating him. This receptive female behavior releases the male's culminating courtship display: the "full wing raising display." In the full wing raising display, the male pivots 180 degrees to face away from the female and simultaneously raises his wings to a vertical position. The receptive female, in probable response to a male sex pheromone, then proceeds to "mount and feed" in a forward direction over the exposed dorsal surface of the male's abdomen (Wendelken 1976). She straddles the male's abdomen as she mounts and makes "feeding" movements with her mouthparts on the male's exposed abdominal tergites. (Unlike certain cockroach species the males do not possess macroscopically visible tergal glands in these species.) As she mounts the male backs beneath her. When her feeding activities reach the region of the first tergite, the male makes rhythmic protrusions of his hooked right phallomere. Genital connection is achieved and the pair performs a turning operation which results in the opposed copulatory position (Wendelken 1976).

It should be emphasized that the sequence of events initiated by a female's display of receptive behavior toward a courting male will ordinarily proceed quickly to copulation in the absence of disruption by other animals. In the family Blaberidae, the ovoviviparous reproductive cycle is distinguished by oviposition of the ootheca into a brood sac where incubation proceeds until hatching occurs about one to three months later. A female which copulates loses the capacity for sexual receptivity until after parturition.

RESULTS

In these species, aggression between males in courtship situations is very intense and often violent. However, there is little in the way of aggressive interactions between males and females. Among themselves, males engage in fighting, chasing, and fleeing. Pseudofemale behavior was found to play a conspicuous role in the overall context of male-male aggression as outlined below.

Courting males frequently interfere with the courtship of rival males. Interference may take place at any stage of courtship. The more disruptive forms of intervention are enumerated as follows: (1) Frequently, a male will attack another male which is directing preliminary courtship to a female. The attacker jumps on top of his opponent, grasping his tegmina and/or pronotum and biting him. (2) A male may attack another male which is performing a full wing raising display by showing "aggressive pseudofemale behavior." Before the female has a chance to respond, the aggressive male mounts and feeds upon the exposed abdominal tergites of the displaying male as would a receptive female. However, unlike a receptive female, when his head reaches the region of the first abdominal tergite, he bites the elevated wings or the region of the first tergite of his opponent. This causes the displaying male to run rapidly forward in an attempted escape. (3) Another form of assault occurs in which a male attacks a second male which is performing a full wing raising display. Before the female has an opportunity to respond, the attacking male leaps onto the displaying male's abdomen (this does not resemble the elementary pattern of pseudofemale mounting and feeding), attempting to bite him (particularly his raised wings). Such an action causes the displaying male to run off rapidly. (4) A male may disrupt a copulation sequence in progress by attacking as a female mounts a displaying male. The attacker may break up the sequence by climbing onto the displaying male's abdomen from the side, pushing the female off, and then biting his wings, causing him to run off. Or a male may directly attack the mounting female. (5) Attacks may be directed against copulating pairs. Typically, the attacker jumps upon the copulating animals. Sometimes these attacks are focused at the juncture between the male and female. In two cases in *B. craniifer,* such attacks caused separation of a pair which had just assumed the opposed position. Apparently their genitalia were not as yet securely attached. Attacks on copulating pairs commencing after the initial few seconds following assumption of the opposed position were never observed to cause separation of a copulating pair. The observed forms of male intervention in the courtship of other males are shown for each species in Table 1.

In tests of interspecific sexual interactions in which females were presented with a choice of conspecific and heterospecific males, interspecific pseudofemale behavior was observed in three combinations. In one cross, a male *B. giganteus* mounted a displaying *B. discoidalis* male and bit his wings. Other forms of interspecific male-male aggression were observed between these two species.

In another cross, *B. giganteus* males showed pseudofemale mountings of *B. craniifer* males and vice versa. In at least one case, a mounting *B. craniifer* male launched an attack directed against the wings of a displaying *B. giganteus* male. There was also reciprocal interspecific disruption of copulation sequences by males of these two species.

In an intergeneric combination, *Byrsotria fumigata* males were observed mounting *Blaberus discoidalis* males. It was not observed whether these pseudofemale episodes were aggressive in nature.

Table 1. Forms of male aggression in the courtship situation in the Tribe Blaberini[1]

	Species					
	Blaberus discoidalis	*Blaberus parabolicus*	*Blaberus giganteus*	*Blaberus craniifer*	*Archimandrita tessellata*	*Byrsotria fumigata*
Attacks on males showing preliminary courtship behavior	Present	Present	Present	Present	Present	Present
Attacks on males showing full wing raising display; attack involving pseudofemale behavior			Present[2]	Present	Present	Present
Attacks on males showing full wing raising display; attack not involving pseudofemale behavior	Present	Present	Present			
Attacks during copulation sequence as female mounts and feeds upon displaying male	Present	Present	Present	Present	Present	
Attacks on pairs in copulation		Present		Present		

[1] The omission of one or more forms of behavior in a particular species should not be considered as evidence for the lack of such behavior. Owing to an insufficient number of animals, or because other aspects of behavior commanded greater attention, observations of aggressive behavior were less complete in some species than in others.

[2] In a test of interspecific interactions, a *B. giganteus* male mounted a *B. discoidalis* male and bit his wings.

DISCUSSION

The conditions under which observations were made in the laboratory appear to approximate rather well important conditions found in some natural populations. Gautier (1974) studied a high density population of *Blaberus colosseus* in a Trinidad cave and found that the cockroaches "live in groups including males; females at different phases of their reproductive cycle and older nymphs. These males are not territorial, only very few are observed away from the group." Sexually receptive females were found to travel as much as several meters in a day and this caused modifications in the distribution of males. In cockroaches (e.g., *Blaberus* spp.) with a volatile female sex pheromone, the female sex pheromone acts to attract males but is effective over a distance of a few feet at most (Barth 1968a). In the high density population studied by Gautier (1974), clearly a number of males would come into contact with a sexually receptive female. Gautier (1978) studied another high density cave population of *B. colosseus* in Trinidad. He found that "males are not territorial on sites" which they occupy and that the interindividual relationships of males are of short duration and low intensity. And, significantly, "the presence of a female changes male/male relationships quickly and profoundly by stimulating aggressiveness" in the males. Gautier (1978) also observed a number of cases in which two males were simultaneously in contact with a single female. He concluded that his field observations confirmed his finding in the laboratory that the presence of a female releases aggressive behavior between males.

Sexual selection may lead to the evolution of intense male-male aggression. This appears to have been the case in the genera *Blaberus, Archimandrita,* and *Byrsotria* (Wendelken 1976). In the species reported on here, direct confrontations take place between competing males in the presence of a female. Males aggressively interfere with the courtship of other males, including foiling the female mounting and feeding sequence. It is in this context that we find pseudofemale mounting and feeding with subsequent biting of the displaying male. Aggressive pseudofemale behavior appears to function as one of an array of methods by which a male can discourage the copulation of a receptive female with one of his rivals and thus increase his own chances of copulation. If a male mounts a displaying rival, the female is precluded from doing so. In other words, one way for a male to prevent a receptive female from mounting and feeding upon a displaying rival (and thus copulating) is for the male to do the mounting and feeding himself. When a receptive female responds to a rival's full wing raising display, it is too late for a male to effectively court the female. At this point the only way to preserve the opportunity to direct effective courtship to the female is to first disrupt the ongoing copulation sequence involving the rival male. In a small population of cockroaches of these species, only one or several receptive females will be present at any given time. A male performing pseudofemale behavior prevents an imminent loss of a scarce resource, i.e., the receptive female. The receptive female consequently remains available to respond to subsequent courtship by the pseudofemale performer.

A second aspect of aggressive pseudofemale behavior is related to the fact that a courting male is quite vulnerable to attack when giving a full wing raising display. A male employing pseudofemale mounting and feeding behavior is able to "lure" the displaying male into a still more vulnerable position and then unleash a sudden attack at the very moment the displaying rival is attempting copulation. The result is that the displaying male is driven away and prevented, at least for the moment, from copulating. Such an encounter might also exert a negative influence upon the propensity for subsequent courtship by the victim of the pseudofemale attack. To sum up, the pseudofemale actor engages in behavior that simultaneously increases his fitness and decreases that of his competitor.

A male may engage in pseudofemale behavior as a prelude to an attack or he may attack directly. There appears to be a gradation of responses between these two alternative behavior patterns. Which is chosen may depend upon (a) the level of aggressive tendencies in the attacking male, (b) the temporal proximity to the onset of female mounting, and (c) the relative position of the two males.

In the species reported on here, female sex pheromones are interspecifically effective in releasing male courtship behavior (Barth 1970, Wendelken 1976). Interspecific differences in male sex pheromones play a vital role in reproductive isolation among these species. With the exception of the combination *B. parabolicus* × *B. discoidalis,* females either refuse or are reluctant to mount and feed in response to the displays of heterospecific males (Wendelken 1976). These findings are generally consistent with the results of interspecific mating tests performed by Roth (1970b). That pseudofemale behavior is shown interspecifically suggests that this response is not released by male sex pheromone or that males respond to a wider spectrum of male sex pheromones than do females. In the event that members of two species come into contact, it may be adaptive for a male to be able to disrupt heterospecific courtship if this increases the probability that a conspecific female will be available for copulation with that male.

Thornhill (1979) reports an example of pseudofemale behavior in scorpionflies which functions to allow the pseudofemale performer to steal nuptial prey from rival males and then use the prey for copulation. There is a parallel to the present work in that the objective of prey theft can be accomplished by several means including but not limited to pseudofemale behavior.

Pseudofemale behavior in *Blaberus, Archimandrita,* and *Byrsotria* is an example of a seemingly abnormal behavior turning out on closer inspection to be adaptive. It may be that pseudofemale behavior (whether or not accompanied by an actual attack) serves similar ends in other cockroach species. Future workers should keep in mind that pseudofemale behavior need not lead to an outright attack in order to contribute to the copulatory success of the performing male. In species with an overall lower intensity of male-male aggression, pseudofemale behavior might be exhibited without the overt aggression so prominent in the Tribe Blaberini. Simply occupying a displaying male's abdomen prevents the female from copulating with the rival and buys time for the pseudofemale performer.

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SUMMARY

This paper presents an account of a previously unreported form of pseudofemale behavior in cockroaches and comments on its possible adaptive significance. Females in most species of cockroaches must play an active role in order for copulation to occur. A receptive female "mounts and feeds" upon the exposed dorsal abdominal surface of a male performing the "full wing raising display". This serves to position the female so that the male may achieve genital connection. The appearance in males of the female pattern of mounting and feeding is known as "pseudofemale" behavior. Remarkably intense male-male aggression in courtship situations is found in the neotropical genera *Blaberus, Archimandrita,* and *Byrsotria* of the Tribe Blaberini (Blattaria, Blaberidae, Blaberinae). This can be explained as the result of sexual selection. Courting males frequently disrupt the courtship of rival males. Males may attack at any stage of the courtship of their rivals. In this context, pseudofemale behavior appears to function as part of an array of aggressive tactics males may employ to prevent the scarce receptive females from copulating with their rivals and thus increase their own prospects for achieving copulation. In these genera, pseudofemale behavior operates as follows. First, a male mounting a displaying rival effectively monopolizes that male's abdomen and precludes the receptive female from mounting. Second, after the pseudofemale mounting and feeding sequence has placed the displaying male in a highly vulnerable position, the pseudofemale performer, unlike a receptive female, attacks the displaying male by biting his wings and/or the region of the first abdominal tergite. This causes the displaying male to flee.

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A NEW BRACONID GENUS (HYMENOPTERA) PARASITIZING WEBSPINNERS (EMBIIDINA) IN TRINIDAD

By Scott R. Shaw[1] and Janice S. Edgerly[2]

Early in 1984, while conducting field studies on embiid behavior in the Arima valley of northern Trinidad, the junior author observed a braconid wasp ovipositing into the silk webs of an embiid, *Clothoda urichi* (Saussure) [Clothodidae]. The wasp and a paralyzed embiid were collected, and another wasp was successfully reared from that host. Specimens were sent to the senior author, then stationed at the National Museum of Natural History (USNM), who determined it to be a new braconid genus. A search of the USNM collection yielded no comparable specimens; however, during a subsequent search of the Museum of Comparative Zoology (MCZ) collection a specimen of a different, but related, species was found. Shenefelt (1980) provided a comprehensive index to recorded braconid hosts, which does not include any Embiidina. Callan (1952) mentioned that he collected numerous white cocoons from embiid webs in Trinidad, and he reared a braconid from these which was identified only as "*Apanteles* sp." He suggested that these were parasites of lepidopterous larvae that sometimes live under the silk, not parasites of the webspinners. The establishment of this new genus as a parasite of webspinners therefore provides a totally new host order record for the family Braconidae.

The morphological terminology used in this paper is mostly that of Marsh (1965, 1982) and van Achterberg (1974). Microsculpture terminology is that of Harris (1979). Taxonomic descriptions presented in this paper are solely the work of the senior author, while life history information on the parasite and its host was provided by the junior author.

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Genus **Sericobracon** Shaw, NEW GENUS

Type-species: *Sericobracon arimaensis* Shaw

Head: Subcubical, broader than long; lower clypeal margin truncate; labrum glabrous, slightly concave; mandibles shorter than 1/2 malar space, barely meeting at tips when closed; maxillary palpi 6-segmented; labial palpi 4-segmented; vertex strigate; occipital carina present.

Mesosoma: Mesonotal lobes coriaceous, notauli scrobiculate, meeting posteriorly in a wide rugose area; scutellar disc smooth; scutellar furrow 4–6 foveate; mesopleuron coriaceous, subalar furrow and sternaulus scrobiculate; prepectal carina present; propodeum with basal carina, fork of basal carina, and lateral carinae well developed, basolateral areas smooth (Figs. 2–3); foretibia apparently without stout spines or pegs; hindcoxa with an anteroventral tubercle; forewing (Fig. 1) with two intercubital crossveins, although second intercubitus is mostly desclerotized; first intercubitus desclerotized at lower end; recurrent vein entering first cubital cell; brachial cell open apically; hindwing (Fig. 1) with radiella, cubitella, postnervellus, nervellus, and submediella absent.

Metasoma: Dorsope present (Figs. 4–5); fused terga 2+3 with 2 transverse scrobiculate furrows, the anterior furrow separating terga 2 and 3, the posterior furrow bisecting tergum 3; terga 3–7 smooth and shining; 6 or 7 exposed terga; ovipositor length varying from 0.6 to 1.2× metasoma length (excluding ovipositor).

Etymology: The name is masculine, derived from "sericum" (L.) meaning silk, in reference to the silk webs of the embiid host of the type-species.

Remarks: Based on patterns of body sculpturing we place *Sericobracon* in the subfamily Doryctinae, where it is allied to *Heterospilus* Haliday. Some neotropical *Heterospilus* species are remarkably similar in sculpturing of the mesonotum, propodeum, and metasomal tergites (e.g. Marsh 1982, figs. 7–8). *Sericobracon* also agrees with *Heterospilus* in having the lower end of the first intercubitus desclerotized. *Sericobracon* may be distinguished from other doryctine genera by the absence of stout spines or pegs on the foretibia.

Subfamilial placement of *Sericobracon* is problematic in that recent authors (e.g. Marsh 1965; van Achterberg 1976, 1984) have cited stout foretibial spines or pegs as a defining character of the

Doryctinae. However, according to van Achterberg (pers. comm.) the stout foretibial pegs of Doryctinae are probably related to living in wood or other hard substrates as larvae. Thus, it might be expected that a species not associated with larvae in wood has no distinct pegs (a secondary loss).

Aside from the above mentioned similarities, *Sericobracon* agrees with the Doryctinae in several additional characters. These include: hindcoxa with an anteroventral tubercle, dorsope present, and paralysis of the host prior to egg deposition.

Most Doryctinae are parasites of wood-boring beetle larvae; however, Marsh (1982) notes that *Heterospilus* show an unusually wide range of host associations across three insect orders: Coleoptera, Lepidoptera, and Hymenoptera. In nearly all cases the hosts have cryptic boring habits, usually in plant stems or branches. If *Sericobracon* is closely related to *Heterospilus,* then the host shift to Embiidina may not be so unusual. It is simply a shift to a phylogenetically unrelated host, which occurs in the same microhabitat.

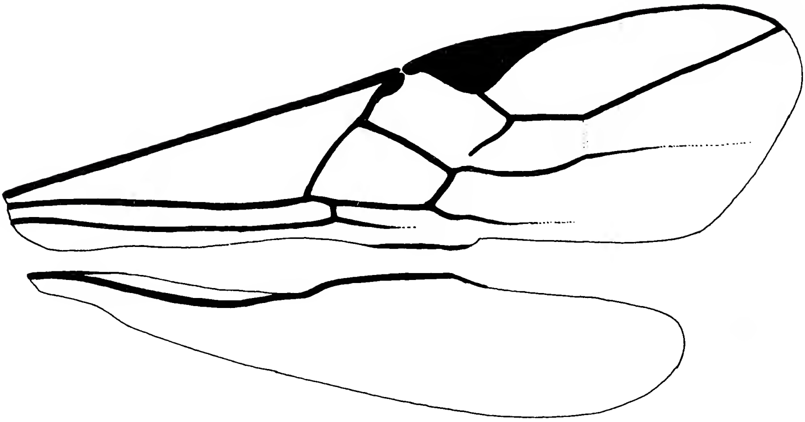
Sericobracon arimaensis, NEW SPECIES
(Figs. 1, 2, 4)

Holotype. Female, Trinidad: Arima valley, northern range, 4 miles north of Arima, Simla Research Station, on silk webs of embiid *Clothoda urichi,* April 1984, (J. S. Edgerly). [Ithaca]

Description of the holotype female: Body length 3.0 mm; flagellum 20-segmented; malar space 1/3 eye height; scutellar furrow 4-foveate; apical area of propodeum (within the areola) rugose (Fig. 2); first tergum 3/4X as long as wide at apex, transversely striate basomedially (Fig. 4); tergum 2 longitudinally striate especially anteriorly; ovipositor length 1.1X metasoma length.

Color: Head golden brown except ocellar triangle black; flagellum beyond F4 dark brown; palpi pale white; mesosoma golden brown except metanotum, metapleuron, and propodeum entirely black; scutellar disc and mesopleuron suffused with black; legs pale yellowish brown; wing venation dark brown; metasoma yellowish brown except tergum 1 and base of tergum 2 entirely black; terga 3–5 mostly suffused with black; ovipositor sheaths dark brown.

Paratype females: Essentially same as holotype except scutellar furrow 6-foveate, tergum 2 more coarsely rugose posteriorly, and tergum 3 sometimes entirely black.



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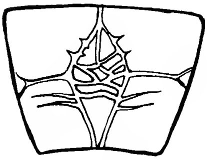

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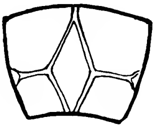

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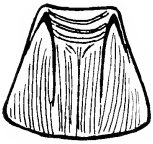

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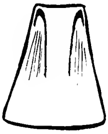

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Figure 1. Wings of *Sericobracon arimaensis.* Figure 2. *Sericobracon arimaensis,* propodeum. Figure 3. *Sericobracon evansi,* propodeum. Figure 4. *Sericobracon arimaensis,* tergum 1. Figure 5. *Sericobracon evansi,* tergum 1.

Male: Unknown.

Paratype data: 1 female, same data as holotype except collected 1 Feb. 1984, ovipositing in web of embiid *Clothoda urichi,* [MCZ]; 1 female, same data as holotype except reared from paralyzed embiid collected 1 Feb., adult wasp emerged 19 Feb. 1984, [MCZ]; 1 female, Trinidad, Lalaja Rd., 23 June 1984, caught on silk of *Clothoda urichi,* (J. S. Edgerly), [USNM].

Remarks: *S. arimaensis* may be distinguished from *S. evansi* by its more coarsely sculptured propodeum and terga 1–2 (figs. 2–5).

Host: Reared from an embiid, *Clothoda urichi* (Saussure). The morphology and biology of this species is discussed by Ross (1944) and Callan (1952).

Life history: *Clothoda urichi* (Saussure), an abundant species in Trinidad, spins silk on vertical objects, generally trees, that support the growth of algae, the food of this embiid. They construct conspicuous silken webs beneath which they live in groups, ranging from one mother with her offspring to 25 or more females with their young. On February 1, 1984 at the Simla Research Station in the Arima Valley, a braconid wasp was observed to penetrate embiid silk with her ovipositor. A paralyzed adult female embiid was found directly beneath the silk under the wasp. She was collected and placed in a petri dish in the laboratory. The female remained paralyzed until February 8 when the endoparasitic wasp larva killed the embiid and emerged to spin a white silken cocoon (.6 cm), within which it pupated. The adult wasp emerged from the cocoon on February 19.

Distribution: Trinidad.

Etymology: The name refers to the Arima valley of Trinidad, the type-locality.

Sericobracon evansi, NEW SPECIES

(Figs. 3, 5)

Holotype. Female, Virgin Islands: St. Croix, E. side of Blue Mt., 14 Feb. 1967, (H. E. Evans). [MCZ]

Description of holotype female: Body length 2.5 mm; flagellum 18-segmented; malar space slightly less than 1/3 eye height; scutellar furrow 6-foveate; apical area of propodeum mostly smooth (Fig. 3); length of tergum 1 equal to width at apex, smooth basomedially (Fig. 5); tergum 2 smooth; ovipositor length 0.6× metasoma length.

Color: Head golden brown except occiput, temples, and vertex suffused with black; flagellum beyond F6 dark brown; palpi white; mesosoma golden brown except metapleuron entirely black; scutellar disc, metanotum, propodeum, mesopleuron, and pronotum suffused with black; legs pale yellowish brown to pale white; wing venation dark brown; metasoma yellowish brown except basal 3/4 of tergum 1 and entire tergum 3 completely black; apical 1/4 of tergum 1 and terga 4–6 suffused with black; ovipositor sheaths black.

Male: Unknown.

Remarks: *S. evansi* may be distinguished from *S. arimaensis* by its smoother propodeum and terga 1–2 (Figs. 2–5).

Host: Unknown.

Distribution: Virgin Islands.

Etymology: Named for Howard Ensign Evans, eminent hymenopterist, gifted natural history writer, and collector of the holotype specimen.

ACKNOWLEDGMENTS

Special thanks to Dr. C. van Achterberg, Rijksmuseum van Natuurlijke Historie, Leiden, who examined a paratype of *Sericobracon arimaensis* and provided his opinion on its phylogenetic placement. Additional thanks are due to Dr. P. M. Marsh, Systematic Entomology Laboratory, U.S. Department of Agriculture, c/o National Museum of Natural History, Washington D.C., and Dr. W. R. M. Mason, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, who reviewed the manuscript and provided their helpful comments. Field work by the junior author was supported by grants from the National Academy of Sciences, Sigma Xi, and the National Science Foundation (NSF Doctoral Dissertation Improvement Grant BSR-8312897).

SUMMARY

Sericobracon Shaw, a new doryctine braconid genus from the Neotropical region, is described and illustrated. Two new species are included in the genus: *S. arimaensis* and *S. evansi.* the type-species, *S. arimaensis,* was reared from *Clothoda urichi* (Saussure), the first record of Braconidae parasitizing Embiidina.

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TRACHYSPHYRUS AND THE NEW GENUS *AELIOPOTES* IN THE COASTAL DESERT OF PERÚ AND NORTH CHILE (HYMENOPTERA: ICHNEUMONIDAE).

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INTRODUCTION

The Study Area

As here considered, the Coastal Desert includes the Peruvian and north Chilean littoral zone and contiguous west Andean slopes between about 5° and 23° South Latitude. Eastward it is bounded by 4–6000 m high Andean peaks, which impose both a rain shadow and a thermic barrier. Westward, the Pacific Ocean with its cold Humboldt Current, creates another rain trap and further exacerbates Coastal Desert aridity. Northward, in Ecuador where the Humboldt Current turns out to sea, the Desert yields abruptly to Thorn Scrub and Tropical Humid Forest. On the far south, below Iquique, Chile, the Andean and Humboldt Current rain shadows intensify and determine a 1000 km stretch of wasteland, which reaches up to 3000 m and is practically unrelieved by rivers.

Consequently, there is little contemporary biotic peregrination between the Coastal Desert and more humid tropical communities on the north or with the Mediterranean Scrub of central Chile on the south. Some high-Andean animals and plants extend across the Peruvian and Bolivian highlands onto the upper west Andean slopes of Perú and Chile, but the Andes are so huge at these latitudes that such interchange is limited to relatively few cold-tolerant species. For this reason, the Coastal Desert possesses many endemic species of flora (Solbrig 1976: 34) and fauna (Porter 1983: 523–47), and plausibly may be recognized as a strongly defined biotic subprovince of the Neotropic Realm.

The mesostenine ichneumonid genus *Trachysphyrus* and its Coastal Desert offshoot, *Aeliopotes*, conform well to the foregoing

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biogeographic pattern. Eight species (*A. paitensis, T. metallicus, T. carrascoi, T. agalma, T. aegla, T. aglaus, T. imperator,* and *T. escomeli*) have not been collected outside the zone and probably constitute endemics. Three additional species are known from the Desert. *Trachysphyrus cleonis* is a high-Andean element that ranges at least as far inland as Cuzco, Perú; *T. venustus* extends widely over the Altiplano and Puna in Perú, adjacent Chile, Bolivia, and northwest Argentina. In contrast, *T. viridis* ranges from southern Perú to Patagonian Argentina, with a preference for Subandean Desert and Chaco habitats. Solbrig (1976: 34–5), notes that many Coastal Desert plants, like the ichneumonid *Trachysphyrus viridis,* show Chaco and Subandean affinities (e.g., *Geoffroea decorticans, Prosopis chilensis, Acacia caven, Bulnesia retama,* and *Larrea divaricata*). Such disjunct geographic patterns probably demonstrate that the Argentine Chaco and the Peruvian-Chilean Coastal Desert were not always so rigorously separated, physically and climatically, as has been the case during the Pleistocene and much of the later Tertiary.

Taxonomy and Relationships

Trachysphyrus and *Aeliopotes* are confined to subequatorial South America. The latter is a Coastal Desert endemic. The former has approximately 20 species distributed from Ecuador to Tierra del Fuego in Andean, subtropical, temperate, and Neantarctic habitats. Of these 20, at least 10 are confined (in Perú, Bolivia, north Chile, and northwest Argentina) to the Andean Puna and Altiplano between 2800 m and more than 4000 m, and 7 of these seem restricted to the western Puna.

The *Trachysphyrus-Aeliopotes* complex includes large mesostenines with uniformly dark wings; no white markings on the mesosoma; a metallic (blue, green, purple, etc.) or black and red ground color; the notauli strong and usually more than half the length of the mesoscutum; the mesoscutal surface punctured but shining; the discocubitus gently arched to a little angled; the mediella straight; the axillus located halfway between the anal margin of the hind wing and the submediella; the propodeal spiracle elongate; the 2nd gastric tergite polished or mat but never strongly punctured; and the ovipositor strong, elongate, moderately compressed, straight to a little upcurved and with a distinct nodus. Other features diagnostic for this group, include the unmodified female flagellum; presence of tyloids on the male flagellum; relatively low (convex to subpyramidal) clypeal profile; usually unmodified apical margin of clypeus; epomia strong in scrobe; stout but never inflated female fore tibia; sharp externo-ventral basal groove on hind coxa; large areolet with intercubiti parallel to moderately convergent above; strongly expanded female postpetiole; and well developed ventro-lateral carina of 1st gastric tergite.

Aeliopotes is a low-altitude (0–2800 m) Coastal Desert relative of *Trachysphyrus.* Its chief distinguishing characters reside in its black and red (not metallic) ground color; dorsally produced and lamellately modified epomia; strong triangular projection laterally at base of petiole (vestigial in small males); and complete lack of a notch at the summit of the nodus on the dorsal valve of the ovipositor tip.

My present concept of *Trachysphyrus* differs from that of other recent authors (Townes 1969, Porter 1967) in that it restricts the genus to those South American species closely allied to the genotype, *T. imperialis* Haliday. I consider both *Trachysphyrus* and *Aeliopotes* to be phyletically proximate to the Sonoran, Floridian, Cuban, and disjunctly South American genus *Compsocryptus. Compsocryptus* particularly resembles *Aeliopotes* in having an expansion at the base of the postpetiole (weak to obsolete in all males). It also has a sympatric Coastal Desert species, *C. fuscofasciatus* (Brullé). *Compsocryptus* easily may be differentiated from related genera by the contrastingly yellow and dark banded fore wing, mat mesoscutum with weak and short notaulus (less than half the mesoscutum), and definitely upcurved ovipositor.

Ecology and Hosts

Information about habit preferences of many species is summarized under the discussion of each taxon.

The only rearing data for this generic group correspond to *T. viridis* (Brullé), which has been associated in Argentina with the saturniid moths *Catocephala lauta* and *Automeris cresus* (Porter 1967: 309). According to Forbes (192: 670), species of *Automeris* construct their cocoons "between leaves on the ground". This habit renders *Automeris* a plausible host for *T. viridis* and other *Trachysphyrus,* whose females most often are found flying just above or crawling among low vegetation and ground litter.

COLLECTIONS EXAMINED

Listed below in alphabetic order are collections which furnished material for this study and/or in which type and voucher specimens are or are to be deposited. I refer to institutional collections by the name of the city where they are located and to individual collections by the surname of the owner. Specimens of *Aeliopotes paitensis, Trachysphyrus carrascoi,* and *T. metallicus* will be distributed to Arica, Cambridge, College Station, Gainesville, Lawrence, Porter, Townes, and Washington.

ARICA. Centro de Investigación y Capacitación Agrícola, Departamento de Agricultura, Universidad de Tarapacá, Arica, Chile.

BUENOS AIRES. Museo Nacional de Ciencias Naturales. Avenida Ángel Gallardo 470, Buenos Aires, Argentina.

CAMBRIDGE. Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

COLLEGE STATION. Department of Entomology, Texas A & M University, College Station, TX 77843.

GAINESVILLE. Florida State Collection of Arthropods, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P.O. Box 1269, 1911 SW 34th Street, Gainesville, FL 32602.

LAWRENCE. Department of Entomology, Snow Entomological Museum, The University of Kansas, Lawrence, KS 66045.

LONDON. Department of Entomology, British Museum (Natural History), London, SW 7 5 BD, England.

PORTER. Collection of Charles C. Porter, 301 North 39th Street, McAllen, TX 78501.

TOWNES. American Entomological Institute, c/o Dr. Virendra Gupta, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P.O. Box 1269, Gainesville, Fl 32602.

TURIN. Museo ed Istituto di Zoologia Sistematica, Via Giolitti 34, Turin, Italy.

WASHINGTON. Department of Entomology, U.S. National Museum, NHB 168, Washington, DC 20560.

Genus **AELIOPOTES** Porter, new genus

Type species: *Amblyteles paitensis* Cockerell.

Fore wing 6.9–12.5 mm long. Coloration black with red gaster, partly red legs, white on flagellum, and wings blackish with metallic reflections. Flagellum moderately long and slender, scarcely flattened below apicad in female, in male with delicate and linear tyloids developed on some segments, its 1st segment 4.6–4.9 as long as deep at apex in females and 3.0–3.7 as long as deep in males. Clypeus weakly to very weakly, more or less symmetrically convex in profile, its apical margin slightly convex. Occipital carina sharp and narrow, joining the moderately elevated hypostomal carina below. Malar space 0.8–1.0 as long as basal width of mandible. Pronotum: submarginal groove broad and usually rather shallow; epomia strong in scrobe and developed above into a broad and sharply differentiated, bluntly triangular or obtuse plate-like structure. Mesoscutum: notauli fine and narrow, reaching 0.7–0.8 the length of mesoscutum; surface shining with uniformly dense moderately small, sharp, adjacent to subadjacent punctures. Mesopleuron with the swollen speculum mostly smooth and shining; surface opposite speculum above along prepectal carina with a shining callous that may be finely and densely punctate or which sometimes is punctured and longitudinally striate throughout or only peripherally invaded by longitudinal wrinkles and whose surface on upper half beyond callous is radiately wrinkled and on lower half is quite uniformly and coarsely puncto-reticulate and wrinkled. Fore tibia stout but not inflated. Hind coxa with a sharp and strong subvertical groove externo-ventrally near base. Wing venation: areolet large, intercubiti rather weakly to strongly convergent above; 2nd abscissa of radius 0.6–0.8 as long as 1st intercubitus; 2nd recurrent a little reclivous, weakly and evenly curved or sometimes comparatively more strongly curved on upper half; discocubitus gently arched, without a ramellus; mediella straight beyond base; axillus far from anal margin of wing, intermediate between anal margin and submediella. Propodeum: spiracle elongate, 2.0–2.5 as long as wide; profile varying from moderately short and high (female) to rather low and elongate (male); basal trans-carina finely traceable throughout or often weak and irregular toward middle; apical trans-carina occasionally fine but sharp throughout, more often faint and irregular to almost absent; basal area usually distinct; median longitudinal carinae sometimes faintly demarking a hexagonal areola; cristae broadly low-cuneate to short subligulate. First gastric tergite: with a strong, bluntly triangular lateral expansion at base of petiole (weak only in dwarf males); postpetiole in female 1.4–1.7 as wide apically as long from spiracle to apex, in male 0.8–1.4 as wide; ventro-lateral carina strong on petiole, variably developed on postpetiole; dorso-lateral carina weak, most distinct toward apex of petiole and on base of postpetiole; dorsal carinae in female visible but not sharp for some distance on petiole and on about basal half of postpetiole, where they define a weak median elevation, absent in male. Second gastric tergite in female smooth and shining to a little dull, with vague to fine but strong micro-reticulation and sparse, medium sized, shallow punctures that emit short, well separated setae and in male similar but with abundant, well separated, rather small and superficial punctures that emit long, considerably overlapping setae. Ovipositor 0.60–0.70 as long as fore wing; straight or slightly upcurved; moderately stout, somewhat compressed; nodus low but distinct and without a notch; tip 0.13–0.18 as high at nodus as long from nodus to apex; ventral valve on tip with fine, well spaced, inclivously oblique ridges.

GENERIC NAME. From the Greek nouns *aëlius,* "sun" and *potes,* "drinker".

1. *Aeliopotes paitensis* (Cockerell)
(Figs. 17, 19–22)

Amblyteles paitensis Cockerell, 1927. Entomologist **60**: 158. Type ♂: Perú, Paita (Washington).

Trachysphyrus paitensis Townes, 1966. Mem. Amer. Ent. Inst. **8**: 72.

Aeliopotes paitensis was redescribed (Porter 1967: 272–75) from 3 females and 6 males (including the holotype) collected throughout most of the Peruvian Coastal Desert between Paita near the Ecuadorian border on the north to Arequipa in the far south. More recent fieldwork has added 2 females and 19 males from much of the same region. This material permits some modification of my original diagnosis.

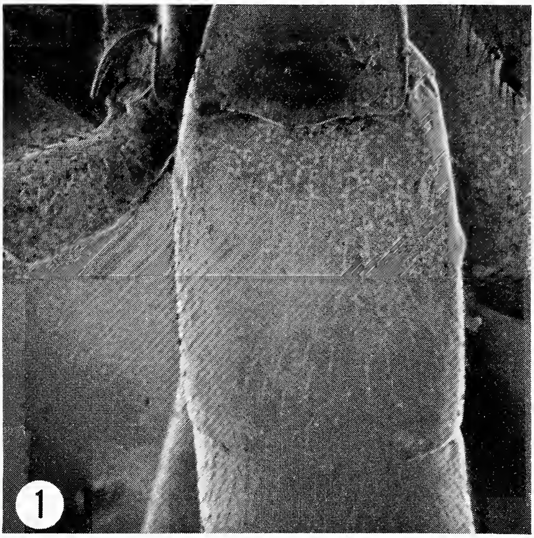


Fig. 1. *Trachysphyrus aegla*, ♂. Paratype. SEM photograph (25×), showing setation of 2nd gastric tergite. Fig. 2. *Trachysphyrus aegla*, ♂. Paratype. SEM photograph (60×), showing mesoscutum with short notauli and sparse punctation.

FEMALE. *Color:* sometimes with a little white at base of 1st flagellomere; white flagellar band sometimes reaching onto 10th flagellomere; fore and mid legs sometimes with only very faint blackish staining, except on fore coxa; gaster sometimes with considerable black staining.

Length of fore wing: 8.5–12.5 mm. *First flagellomere:* 4.6–4.9 as long as deep at apex. *Malar space:* 0.8–1.0 as long as basal width of mandible. *Temple:* 0.3–0.5 as long as eye in dorsal view. *Mesoscutum:* notauli reaching 0.7–0.8 the length of mesoscutum. *Mesopleuron:* swollen area along prepectal carina above opposite speculum sometimes punctured and longitudinally striate throughout. *Wing venation:* radial cell 3.5–4.0 as long as wide. *Propodeum:* spiracle 2.0–2.5 as long as wide; cristae broadly low-cuneate to short subligulate; apical trans-carina occasionally fine but sharp throughout. *First gastric tergite:* postpetiole 1.4–1.7 as wide apically as long from spiracle to apex; ventro-lateral carina often sharp throughout on postpetiole as well as on petiole. *Second gastric tergite:* occasionally rather dull because of unusually well developed but fine microreticulation. *Ovipositor:* sheathed portion 0.6–0.7 as long as fore wing; tip 0.13–0.18 as high at nodus as long from summit of nodus to apex.

MALE. *Color:* gaster sometimes with extensive and conspicuous black staining; wings in small specimens but weakly fuscous and with only faint metallic reflections.

Length of fore wing: 6.9–12.5 mm. *Flagellum:* tyloids all fine and linear; 1st flagellomere 3.0–3.7 as long as deep at apex. *Malar space:* 0.8–0.9 as long as basal width of mandible. *Temple:* 0.6–0.8 as long as eye in dorsal view. *First gastric tergite:* 0.8–1.4 as wide apically as long from spiracle to apex; small males have the baso-lateral expansion only weakly developed, in large males it is as strong as in females.

NEW SPECIMENS EXAMINED. 2♀ and 19♂: PERÚ, Lima Province, Cupiche, 26-VI-1976, C. Porter, C. Calmbacher; La Libertad Province, Samne, 40 km NE Trujillo, ca. 1500 m, 12–17-VII-1975, C. Porter, L. Stange.

VARIATION. *Aeliopotes paitensis* seems widely and perhaps disjunctly endemic to the Coastal Desert at altitudes from 0 to 2800 m. Nonetheless, the variation outlined above appears strictly individual. In spite of this insect's extensive range, it shows no phaenotypically discrete local populations.

FIELD NOTES. My specimens of *A. paitensis* were collected in flight, usually not far off the ground in grassy areas near water. I have not taken the species on *Baccharis.*

Genus TRACHYSPHYRUS

Trachysphyrus Haliday, 1836. Trans. Linnean Soc. London 17: 317. Type: *Trachysphyrus imperialis* Haliday.

Cyanocryptus Cameron, 1903. Entomologist 36: 121. Type: *Cyanocryptus metallicus* Cameron.

Lamprocryptus Cameron, 1910. Trans. Amer. Ent. Soc. 35: 435. Name preoccupied by Schmiedeknect, 1904. Type: (*Cryptus kinbergi* Holmgren) = *viridis* (Brullé)

Mesocryptus Szépligeti, 1916. Ann. Mus. Natl. Hungarici 14: 251. Name preoccupied by Thomson, 1873. Type: *Mesocryptus pulcherrimus* Szépligeti) = *venustus* Myers

Pseudomesocryptus Strand, 1917. Internatl. Ent. Ztschr. 10: 137. New name for *Mesocryptus.*

Fore wing 6.0–16.0 mm long. Coloration metallic green, blue, purple, golden or often varicolored metallic; no pale markings on mesosoma and in only 1 species with white on gaster; wings brownish to black, with a metallic lustre, never contrastingly light and dark banded. Flagellum moderately long and slender, scarcely flattened below toward apex in female, in male with tyloids well developed on some segments and varying from linear to elliptic or ovoid, its 1st segment 3.5–5.5 as long as deep at apex in females and 2.2–3.7 as long as deep in males. Clypeus: in profile almost flat to moderately high convex or, rarely, subpyramidal; its apical margin straight to rather strongly convex, edentate, occasionally a little produced and feebly bilobed on meson. Occipital carina: sharp but not strongly raised; joining the sharp but not much raised hypostomal carina below. Malar space 0.70–1.8 as long as basal width of mandible. Pronotum: submarginal groove broad and variably strong; epomia usually sharp in scrobe but never strongly turned mesad or produced into a plate-like structure above. Mesoscutum: notauli usually strong, extending 0.3–0.9 the length of mesoscutum; surface mostly smooth and shining, sparsely to densely but not grossly punctate, never strongly wrinkled or extensively mat. Mesopleuron with speculum usually smooth and shining but occasionally more or less puncto-reticulate; surface otherwise wholly or in part finely to grossly and usually reticulately wrinkled; no projection or ridge on prepectus below. Fore tibia never inflated. Hind coxa with a sharp and strong subvertical groove externo-ventrally near base.

Wing venation: areolet large to very large, intercubiti almost parallel to moderately convergent above; 2nd abscissa of radius 0.7–1.2 as long as 1st intercubitus; 2nd recurrent practically straight or gently and evenly curved; discocubitus gently and evenly curved, weakly sinuate, or sometimes a little angled, ramellus absent to sometimes very long; mediella straight beyond base; axillus far from anal margin of hind wing, usually about intermediate between hind margin and submediella. Propodeum: spiracle elongate or very elongate; profile varying from short and high to moderately elongate and sloping rearward (especially in males); basal trans-carina, apical trans-carina, and median and lateral longitudinal carinae sometimes all at least weakly detectable or, often, more or less effaced; cristae varying from low and broad subligulate or subcuneate to very strongly projecting ligulate. First gastric tergite: without a lateral expansion at base of petiole; postpetiole in female 1.1–2.3 as wide apically as long from spiracle to apex, in male 0.7–1.7 as wide; ventro-lateral and dorso-lateral longitudinal carinae usually well developed throughout; dorsal carinae varying from obsolete to at least partly sharp. Second gastric tergite smooth and polished or mat and finely granular; in female with widely scattered, inconspicuous, short setae which may be uniformly much shorter to sometimes in part only a little shorter than their interspaces and in male with long, mostly overlapping setae or with short setae as in female; punctures variably abundant, tiny to moderately large, superficial to sharp, but never large, strong, and extensively subadjacent or adjacent. Ovipositor: 0.50–0.90 as long as fore wing; moderately stout, palpably compressed, straight to gently upcurved; nodus more or less distinct; notch weak to large and deep; tip 0.16–0.24 as high at notch as long from notch to apex; ventral valve on tip with fine, sharp, well spaced, inclivously oblique ridges.

KEY TO THE COASTAL DESERT *TRACHYSPHYRUS*

FEMALES

(Females of *T. aegla, T. aglaus,* and *T. imperator* unknown)

1. Head mostly white; gastric tergites 4–7 with broad white apical bands; apical margin of clypeus on median 0.5 gently produced and bilobed .... 10. *T. venustus* Myers

1′. Head at most with narrow white markings; no white on gaster; apical margin of clypeus entire, not or scarcely produced medially 2

2. Second gastric tergite uniformly mat and finely granular; notaulus sharp and narrow, reaching 0.8 or more the length of mesoscutum 3

2′. Second gastric tergite smooth and polished with at most faint micro-reticulation; notaulus 0.3–0.8 as long as mesoscutum, in most species no more than 0.5 as long 4

3. Mesoscutum with very abundant, mostly subadjacent to confluent, medium sized to large punctures; flagellum usually with a white band; head and mesosoma purple with blue reflections; gaster mostly blue or blue-green; no golden sheen on thoracic pleura and propodeum .... 9. *T. viridis* (Brullé)

3′. Mesoscutal punctures strong and dense only anteriorly on central lobe but elsewhere mostly sparse; flagellum dark; body blue or blue and purple, with golden reflections on thoracic pleura and propodeum .... 8. *T. cleonis* Viereck

4. Clypeus subpyramidal in profile; notaulus 0.8 the length of mesoscutum; propodeum with moderately strong reticulate wrinkling; flagellum with white on more or less of segments 4–8 .... 7. *T. escomeli* (Brèthes)

4′. Clypeus low, gently convex to almost flat in profile; notaulus 0.3–0.5 the length of mesoscutum; propodeum with gross reticulate wrinkling; white on flagellar segments 1, 2 or 3–8, 9, or 10 5

5. Areolet asymmetric, apical abscissa of cubitus inserted unusually far dorsad; 1st flagellomere 3.2 as long as deep at apex; mesoscutum with numerous but mostly well separated punctures; propodeal cristae broad and strongly projecting subligulate; sheathed portion of ovipositor 0.60 as long as fore wing, no groove extending forward from notch on dorsal valve of ovipositor .... 3. *T. agalma* n. sp.

5′. Areolet not asymmetric, apical abscissa of cubitus in normal position; 1st flagellomere 3.9–4.2 as long as deep at apex; mesoscutum with punctures, at least on basal 0.5, dense and separated by little more than their diameters; propodeal cristae not broadly projecting, rather inconspicuously subligulate or subcuneate; sheathed portion of ovipositor 0.70–0.90 as long as fore wing; dorsal valve of ovipositor with a deep groove that reaches forward some distance from notch. . . . 6

6. Dorsal valve of ovipositor strongly rippled on tip, profile of dorsal valve between notch and apex slightly concave basad but becoming convex apicad; sheathed portion of ovipositor 0.80–0.90 as long as fore wing . . . . 2. *T. carrascoi* Porter

6′. Dorsal valve of ovipositor smooth or slightly wrinkled on tip, profile of dorsal valve directly declivous between notch and apex; sheathed portion of ovipositor 0.70–0.80 (usually 0.70) as long as fore wing . . . . 1. *T. metallicus* (Cameron)

MALES

(Male of *T. escomeli* lost)

1. Second gastric tergite uniformly mat and granular 2

1′. Second gastric tergite smooth and polished, with more or less distinct micro-reticulation 3

2. Mesoscutum with many, almost uniformly distributed, medium sized to large punctures; flagellum usually with a white band; hind tarsomeres 3–4 usually white; purple with blue or green gaster and no golden on thoracic pleura or propodeum. . . . . 9. *T. viridis* (Brullé)

2′. Mesoscutum with punctures usually dense only toward base of central lobe; no white on flagellum or on hind tarsus; purple or blue and purple with golden reflections on thoracic pleura or propodeum . . . . 8. *T. cleonis* Viereck

3. Head very broadly white; gastric tergites 4–7 with broad white bands; apical margin of clypeus somewhat produced and feebly bilobed on median 0.5 . . . . 10. *T. venustus* Myers

3′. Head not or more narrowly marked with white; no white on gaster; apical margin of clypeus entire 4

4. Temple with grossly tangled and shaggy setae; setae on 2nd gastric tergite well separated; propodeum short and high with apical face sharply discrete and vertically declivous; cristae narrowly ligulate; aggressively projecting; notauli reaching 0.7 length of mesoscutum; malar space 1.0 as long as basal width of mandible; mesosoma golden . . . . 6. *T. imperator* Porter

4′. Temple with setae long but rarely tangled; many species with setae on 2nd gastric tergite long and much overlapping; propodeum more strongly sloping in profile, with apical face less sharply discrete than described above; cristae often conspicuous but not both narrow and greatly projecting; notauli 0.5 or less length of mesoscutum; malar space 0.7–1.0 as long as basal width of mandible; mesosoma purple or purple with a golden sheen 5

5. Mesoscutal punctures mostly separated by considerably more than their diameters, often sparse; propodeal cristae often quite large, bluntly cuneate and prominently projecting; apical trans-carina of propodeum often well developed throughout and narrowly looped forward medially 6

5′. Mesoscutum with punctures largely separated by little more than their diameters; propodeal cristae low to moderately projecting subligulate or subcuneate; apical trans-carina of propodeum largely or entirely absent...................8

6. Setae on 2nd gastric tergite short, much less than the length of their interspaces; temple 1.0 as long as eye in dorsal view.... ....3. *T. agalma* n. sp.

6′. Setae of 2nd gastric tergite long and considerably overlapping; temple 0.8–0.9 as long as eye in dorsal view 7

7. Flagellum black with reddish brown on segments 11–16; thorax and propodeum golden with purple reflections; temple with very long and shaggy setae; areolet exceptionally large, intercubiti parallel, 2nd intercubitus 0.7 as long as 1st intercubitus .... 5. *T. aglaus* Porter

7′. Flagellum with white on some of intermediate segments; thorax and propodeum mainly purple; temple with long but not shaggy setae; areolet large but not as asymmetric as described above, intercubiti quite strongly convergent dorsad .... 4. *T. aegla* n. sp.

8. White flagellar annulus on segments 11 or 12–16, 17, or 18; hind tarsomeres 3–4 white; malar space 0.6–0.8 as long as basal width of mandible; propodeal cristae low, weakly projecting, broadly subcuneate and extended a short distance anteriomesad by a trace of the apical trans-carina .... 2. *T. carrascoi* Porter

8′. White flagellar annulus beginning on any segment from 2–11 and extending as far as 17 or 18; no white on hind tarsus; malar space 0.8–1.0 as long as basal width of mandible; propodeal cristae moderately projecting, subligulate or subcuneate, not prolonged anterio-mesad .... 1. *T. metallicus* (Cameron)

1. *Trachysphyrus metallicus* (Cameron)
(Fig. 4, 5, 16).

Cyanocryptus metallicus Cameron, 1903. Entomologist 36: 122. Type ♂: Ecuador, Andes, outer slopes at 7–8000 ft (London).

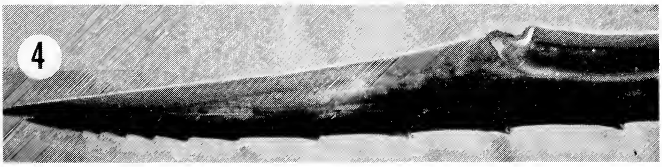
Trachysphyrus phaedimus Porter, 1967. Mem. Amer. Ent. Inst. 10: 281–3. Type ♂: Chile, Tarapacá, Belén, Arica, 17–27-X-1952, L. E. Peña (Cambridge). NEW SYNONYMY

My first redescription of *T. metallicus* (Porter 1967: 277–79) was taken from 1 female and 2 males collected at Huárez and Matucana, Perú. Since then, 12 additional females and 23 more males have accrued, as a result of collecting at Matucana in Perú and in the Tarapacá Province of Chile. This material shows that *T. metallicus* demonstrates conspicuous variation (mainly chromatic) within each local population and also along a north to south cline. The southernmost populations in this cline (Tarapacá, Chile) originally were described as a separate species, *T. phaedimus* Porter (1967: 281–83), which now is synonymized with *T. metallicus.*

The following description redefines *T. metallicus* with special reference to its individual and polytypic variability.

FEMALE. *Color:* white flagellar band present on segments 2 or 3–8 or 9; with or without white line on hind orbit; metallic coloration of scape, head, mesosoma, coxae, trochanters, and gaster varying from deep blue with extensive purplish reflections to mostly bright purple with prominent to inconspicuous blue reflections; legs beyond trochanters varying from black with more or less subdued metallic reflections through mostly deep to bright orange (duller on tarsi).

Length of fore wing: 10.0–15.6 mm. *First flagellomere:* 3.9–4.4 as long as deep at apex. *Malar space:* 1.1–1.3 as long as basal width of mandible. *Temple:* 0.7–0.8 as long as eye in dorsal view; its punctures and setae conspicuous but variably dense. *Mesoscutum:* punctures, especially in Chilean specimens, often separated by as much



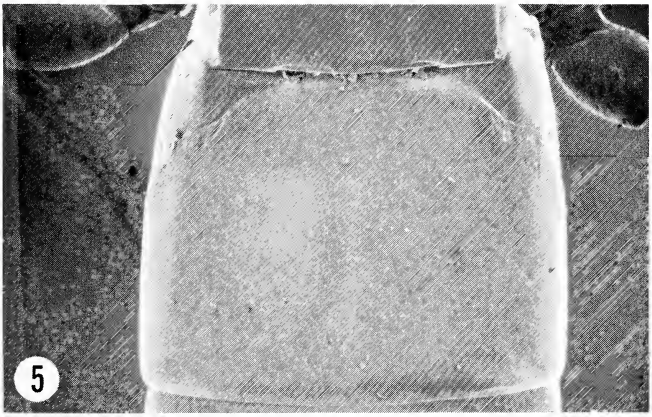


Fig. 3. *Trachysphyrus aegla*, ♂. Paratype. SEM photograph (30×), showing wing venation. Fig. 4. *Trachysphyrus metallicus*, ♀. SEM photograph (85×), showing ovipositor tip in lateral view. Fig. 5. *Trachysphyrus metallicus*, ♀. SEM photograph (25×), showing 2nd gastric tergite in dorsal view (setation very sparse).

as several times their diameter over apical 0.5 of mesoscutum. *Mesopleuron:* swollen area along prepectal carina above opposite speculum often largely smooth and polished with only sparse and tiny punctures. *Wing venation:* ramellus sometimes absent. *Propodeum:* basal and apical faces varying from weakly to (often) sharply discrete; cristae moderately small but well projecting, subligulate to bluntly cuneate. *First gastric tergite:* postpetiole 1.5–1.7 as wide apically as long from spiracle to apex; surface of postpetiole sometimes almost without micro-reticulation. *Second gastric tergite:* often highly polished and with faint to sometimes almost imperceptible micro-shagreening. *Ovipositor:* sheathed portion 0.7–0.8 as long as fore wing; tip 0.20–0.24 as high at notch as long from notch to apex.

MALE. *Color:* white flagellar annulus sometimes on as few as segments 11–17 or as many as 2–18, variable in all populations but averaging most extensive in Chilean specimens; hind orbit with or without a white line; legs beyond trochantelli often extensively orange.

Length of fore wing: 8.8–14.0 mm. *First flagellomere:* 2.6–3.5 as long as deep at apex. *Malar space:* 0.8–1.0 as long as basal width of mandible. *Temple:* 0.9–1.0 as long as eye in dorsal view. *Mesoscutum:* punctures average denser than in female. *Propodeum:* cristae subligulate to subcuneate and strongly projecting; apical transcarina scarcely palpable between cristae. *First gastric tergite: 1.0*–1.3 as wide apically as long from spiracle to apex. *Second gastric tergite:* micro-reticulation varying from faintly detectable to almost absent.

NEW SPECIMENS EXAMINED. 12♀ and 23♂: PERÚ, Lima Province, Matucana, 2389 m, 20–30-VI-1974, C. Porter, L. Stange, 27–30-VI-1976, C. Porter, C. Calmbacher, 15-VI-1979, C. Porter; CHILE, Tarapacá Province, Belén, 3170 m, 18–19-VII-1976, C. Porter, C. Calmbacher, H. Vargas; Chapiquiña, 3370 m, 17–20-VII-1976, C. Porter, C. Calmbacher, 3-VIII-1975, C. Porter, A. Matta; Putre, 3500 m, 8-VII-1977, C. Porter, G. Díaz; Socoroma, 3000 m, 7-VII-1977, Díaz, 19–24-VII-1977, C. Porter, G. Díaz, VII-1977, Malaise Trap, C. Porter, G. Díaz.

RELATIONSHIPS. *Trachysphyrus metallicus* and *T. carrascoi* occur sympatrically and seem to be very intimately related. They may be distinguished in the female by differences of ovipositor tip shape and sculpture and in the male by less conspicuous and stable features of sculpture, proportion, and color.

VARIATION. North Chilean specimens of *T. metallicus* appear superficially very different from Peruvian material, because of their bright purple ground color, largely orange legs, and more extensive white flagellar annulus. Indeed, some individuals from Matucana, Perú have the ground color almost uniformly blue, the legs beyond the trochanters blackish with metallic reflections, and the flagellar annulus relatively brief. However, recent collecting at Matucana, Perú has shown that some specimens in that population have an extensive purple sheen overlaying the blue ground color, as well as largely orange femora and tibiae, and a comparatively broad flagellar annulus.

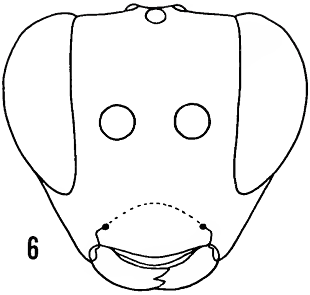
North Chilean populations of *T. metallicus* consequently represent one extreme in what appears to be a gradual cline and do not warrant formal recognition either at the subspecific or specific level.

FIELD NOTES. This species occasionally enters Malaise Traps (1 specimen from Socoroma, Chile), but is more often obtained by hand net on *Baccharis* or in alfalfa and oregano fields. Females consistently are swept from alfalfa patches. Possibly they parasitize some of the introduced noctuid pests, which attack this important forage crop that has been widely planted from the Puna to the coastal river valleys.

2. *Trachysphyrus carrascoi* Porter
(Fig. 12)

Trachysphyrus carrascoi Porter, 1967. Mem. Amer. Ent. Inst. 10: 279–81. Type ♀: Perú, Lima Province, Matucana, 28-V-1920, Cornell University Expedition (Ithaca).

I originally described this species from 2 females collected in Perú. At the same time I also mentioned, but excluded from the type series, 2 males from Putre in Tarapacá Province of north Chile (Porter 1967: 279–81). Recent fieldwork has added 6 females and 2 males of *T. carrascoi.* Study of this new material shows that the species does actually range from Matucana, Perú to north Chile but that the males which I originally associated with *T. carrascoi* probably belong to *T. metallicus.*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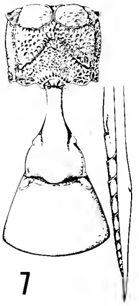
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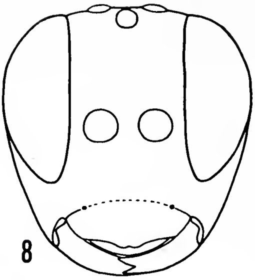
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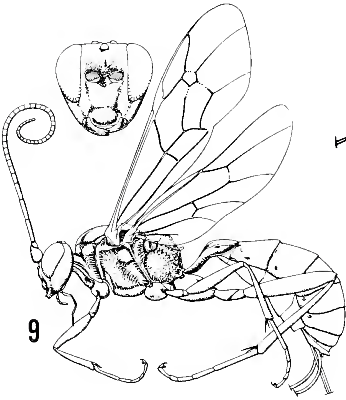
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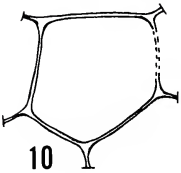
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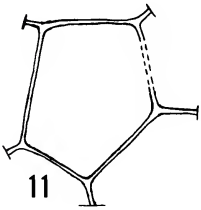
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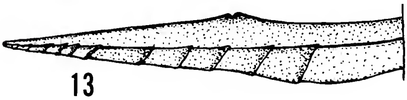
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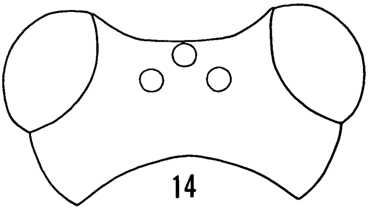
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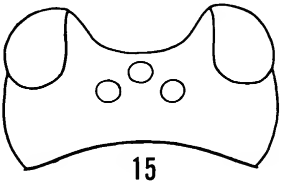
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Fig. 6. *Trachysphyrus viridis,* ♀. Anterior view of head. Fig. 7. *Trachysphyrus cleonis,* ♀. Dorsal view of propodeum and first two gastric tergites, lateral view of ovipositor tip. (From Townes 1969: 432). Fig. 8. *Trachysphyrus venustus,* ♀. Anterior view of head, showing bisinuate apical margin of clypeus. Fig. 9. *Trachysphyrus cleonis,* ♀. Lateral view of entire insect, anterior view of head. (From Townes, 1969: 432). Fig. 10. *Trachysphyrus aglaus,* ♂. Holotype. Areolet. Fig. 11. *Trachysphyrus agalma* ♂. Paratype. Areolet. Fig. 12. *Trachysphyrus carrascoi,* ♀. Ovipositor tip in lateral view. Fig. 13. *Trachysphyrus agalma,* ♀. Holotype. Ovipositor tip in lateral view. Fig. 14. *Trachysphyrus viridis,* ♀. Head in dorsal view. Fig. 15. *Trachysphyrus venustus,* ♂. Head in dorsal view.

Below I give a revised description of *T. carrascoi,* including diagnosis of the previously unknown male.

FEMALE. *Color:* head, mesosoma and gaster metallic purple with more or less conspicuous blue reflections, gaster often almost wholly purple.

First flagellomere: 4.0–4.2 as long as deep at apex. *Clypeus:* almost flat, very low in profile, lower than in *T. metallicus. Mesopleuron:* swollen area above along prepectal carina opposite speculum sometimes much invaded by fine punctures and wrinkles; other wrinkling often extensively irregular. *First gastric tergite:* 1.4–1.7 as wide apically as long from spiracle to apex. *Second gastric tergite:* smooth and shining with micro-shagreening very weak to moderately well developed. *Ovipositor:* sheathed portion 0.8–0.9 as long as fore wing; dorsal valve on tip conspicuously rippled; profile of dorsal valve on tip a little concave over basal 0.5 but with a convex taper toward apex; tip 0.17–0.20 as high at notch as long from notch to apex.

MALE. *Color:* white flagellar annulus on segments 11 or 12 to 16, 17, or 18; head and mesosoma sometimes mostly metallic blue; fore and mid femora orange with purplish metallic staining below and anteriorly; hind femur completely orange; tibiae orange; hind tarsomeres 3 (except near base) and 4 white.

Length of fore wing: 9.6–11.3 mm. *First flagellomere:* 2.5–3.2 as long as deep at apex. *Malar space:* 0.6–0.8 as long as basal width of mandible. *Temple:* 0.9–1.1 as long as eye in dorsal view. *Mesoscutum:* punctures often dense throughout. *Propodeum:* cristae low and weakly projecting, broadly subcuneate; apical trans-carina detectable for a short distance anterio-mesad of cristae. *First gastric tergite:* 1.1–1.3 as wide apically as long from spiracle to apex. *Second gastric tergite:* smooth and highly polished.

NEW SPECIMENS EXAMINED. 6♀ and 2♂: PERÚ, Lima Province, Matucana, 2389 m, 28-30-VI-1974, C. Porter, L. Stange, 4-5-VII-1976, C. Porter, C. Calmbacher; CHILE, Tarapacá Province, Chapiquiña, 3370 m, I-1977, Malaise Trap, C. Porter, G. Díaz.

RELATIONSHIPS. Females of *Trachysphyrus carrascoi* may be distinguished from all other Coastal Desert congeners because of the strongly rippled surface and concave-convex profile of the dorsal ovipositor valve between notch and apex. Otherwise, this species greatly resembles *T. metallicus* and often is hard to recognize from males alone. Male *T. carrascoi* have some white on the hind tarsus (no white in *T. metallicus*) and, in comparison to *T. metallicus,* show lower and weaker propodeal cristae and a shorter malar space.

VARIATION. Some males of *T. carrascoi* have the mesoscutal punctation dense throughout but in others it becomes moderately sparse rearward. The less densely punctate specimens appear to be more common in north Chile, at the southern end of the species' range. As does *T. metallicus,* both sexes of *T. carrascoi* evidence a north-south cline (from blue to purple) in ground color.

FIELD NOTES. This species occurs in the same natural and cultivated high Andean habitats noted for *T. metallicus.* Like *T. metallicus,* it occasionally enters Malaise Traps.

3. **Trachysphyrus agalma** Porter, new species

(Fig. 11, 13)

FEMALE. *Color:* scape, pedicel, and (more dully) part of 1st and 2nd flagellar segments metallic purple; 1st flagellomere white above near apex, 2nd flagellomere white above almost throughout, 3rd flagellomere white with a little brownish below at base; flagellomeres 4–7 almost pure white; 8th flagellomere white above (more narrowly so apicad) and black below; rest of flagellum black; head and mesosoma metallic purple with some dark blue reflections; gaster dark metallic blue with conspicuous purple staining, especially toward base; coxae, trochanters, and trochantelli metallic purple; front femur dull orange with purplish near base and throughout posteriorly; mid femur metallic purple, grading into dull orange on apical 0.3 anteriorly; hind femur metallic purple with orange irregularly on apical 0.5; tibiae orange with some metallic reflections; tarsi mostly dusky to blackish, becoming dull orangish brown basad on 1st segments; wings moderately dark brown with blue reflections.

Length of fore wing: 8.8 mm. *First flagellomere:* 3.2 as long as deep at apex. *Clypeus:* low and gently convex in profile, with highest point near middle; apical margin straight. *Malar space:* 1.0 as long as basal width of mandible. *Temple:* 0.7 as long as eye in dorsal view; weakly and convexly receding. *Mesoscutum:* notauli sharp, not traceable much beyond basal 0.3 of mesoscutum; surface highly polished with numerous but mostly well separated, strong punctures; the punctures largest, densest and somewhat longitudinally slurred on central lobe, especially basad, but elsewhere contrastingly

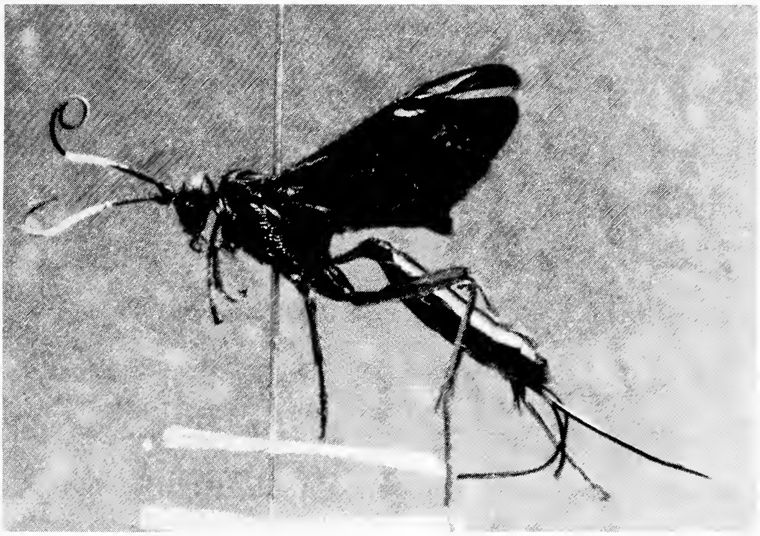


Fig. 16. *Trachysphyrus metallicus*, ♀. Photograph showing entire insect in lateral view.

smaller and sparser. *Mesopleuron:* speculum mostly polished and impunctate; the large anterio-dorsal swelling along prepectus opposite speculum also polished, with small, sharp, scattered punctures; lower 0.5 of mesopleuron anteriad likewise extensively polished and sparsely punctate; surface otherwise with gross but nearly parallel longitudinal wrinkles between speculum and anterior swelling, as well as with much gross wrinkling and foveolation in lower hind quadrant (where there are some intercalated smooth areas) and with strong wrinkles irregularly developed on peripheries of the smooth anterior-dorsal swelling. *Lower metapleuron:* with coarse and almost regular longitudinally oriented wrinkling. *Hind coxa:* dorsum polished and with small, sparse punctures. *Wing venation:* areolet unusually large and high with intercubiti weakly convergent above; 2nd abscissa of radius 0.8 as long as 1st intercubitus; apical abscissa of cubitus originating far dorsad, the 2nd intercubitus only 0.7 as long as ventro-posterior side of areolet; 2nd recurrent inserted a little before middle of areolet, almost straight and nearly vertical; disco-cubitus gently arched; ramellus absent; nervulus interstitial;

upper part of nervellus 1.3 as long as lower. *Propodeum:* moderately short and high, basal face arched and strongly sloping behind, the apical face discrete, nearly vertical, 0.8 as long as basal face; area basalis apically truncate; basal trans-carina moderately strong, highest medially, but comparatively inconspicuous (especially laterad) among the strong surface reticulations; apical trans-carina irregularly detectable, best represented by its large, projecting, broadly subligulate cristae; median longitudinal carinae inconspicuous and irregular, areola hexagonal and a little wider than long; lateral longitudinal carinae obsolete; surface with very coarse wrinkling that is strongest and transversely biased on apical face, grossly reticulate on basal face between the trans-carinae, and contrastingly finer basad of basal trans-carina. *First gastric tergite:* postpetiole 1.8 as wide at apex as long from spiracle to apex; dorsal carinae only faintly suggested in the supra-spiracular region, scarcely delimiting a median elevation; surface of postpetiole smooth and polished with scattered tiny punctures that become most numerous laterad. *Second gastric tergite:* thyridium much broader than long; surface smooth and polished with scarcely a trace of shagreening and with sparse but numerous tiny punctures that emit short, mostly well separated setae (which are densest laterad). *Ovipositor:* sheathed portion 0.56 as long as fore wing; gently upcurved; nodus comparatively prominent, with a conspicuous notch but without a fossa extending forward from the notch; dorsal valve profile strongly and directly tapering between notch and apex; tip 0.26 as high at notch as long from notch to apex.

MALE. Differs from female as follows: *Color:* flagellum black with white above on segments 7 or 8–9, almost wholly white on segments 10–15, and sometimes irregularly white on segment 16; head and mesosoma with a subdued golden sheen in addition to purple and blue reflections; a fine white line on much of hind orbit; femora bright orange; tibiae duller orange; fore tarsus blackish with dull orange, best developed toward base, on 1st segment; mid tarsus blackish, grading into dull orange basad on 1st segment; hind tarsus almost wholly black.

Length of fore wing: 8.0–12.0 mm. *First flagellomere:* 2.8 as long as deep apically. *Clypeus:* gently convex and a little bulging in profile; apical margin weakly convex. *Malar space:* 0.7–0.8 as long as basal width of mandible. *Temple:* 1.0 as long as eye in dorsal view;

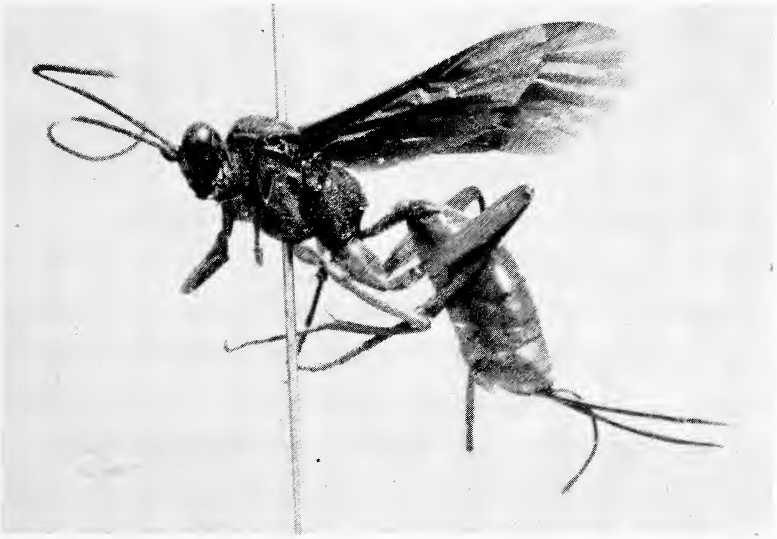


Fig. 17. *Aeliopotes paitensis*, ♀. Photograph showing entire insect in lateral view.

gently receding and convex; surface with small, sharp, numerous punctures that are separated by more than 2X their diameters and which emit long but not shaggy setae. *Mesoscutum:* notauli 0.3–0.5 as long as mesoscutum. *Lower metapleuron:* with coarse wrinkling which is more irregular and reticulate than in female. *Wing venation;* nervellus broken at middle. *Propodeum:* lower and longer than in female; apical face vertical but only 0.6 as long as basal face; basal trans-carina strong and sharp throughout; median longitudinal carinae faint; areola approximately 0.6 as wide as long; cristae bluntly cuneate, broad, rather strongly projecting. *First gastric tergite:* postpetiole 1.2–1.4 as wide apically as long from spiracle to apex; dorsal carinae traceable but not sharp on apex of petiole and basal 0.7 of postpetiole and there defining a broad but inconspicuous median elevation; setae on postpetiole largely shorter than the length of their interspaces. *Second gastric tergite:* thyridium ovoid; surface, much as in female, with minute punctures and short setae that become moderately dense only laterad.

TYPE MATERIAL. Holotype ♀: CHILE, Tarapacá Province, Socoroma, 3000 m, VII-1977, Malaise Trap, C. Porter, G. Díaz.

Paratype: 1 ♂, same data as holotype. Holotype in Florida State Collection of Arthropods. Paratype in Collection of Charles C. Porter.

Relationships. This species belongs to the *Imperialis* species group of *Trachysphyrus* (Porter 1967: 275–6). It shows superficial affinity to *T. escomeli* (Brèthes) and *T. aglaus* Porter.

Trachysphyrus escomeli (Porter 1967: 319–20) is known only from Arequipa on the west Andean slopes of southern Perú and might be expected to overlap the range of *T. agalma* in similar habitats of adjacent north Chile. Females of the 2 species differ because *T. agalma* has the clypeus low in profile (moderately high and bluntly subpyramidal in *T. escomeli*), the temple 0.7 as long as eye in dorsal view and sparsely punctate throughout (less than 0.5 as long as eye and becoming densely punctate above in *T. escomeli*), the notauli impressed for about 0.3 the length of the mesoscutum (0.7–0.8 the length of mesoscutum in *T. escomeli*), the mesopleuron with some areas of coarse wrinkling (with moderately strong reticulate wrinkling in *T. escomeli*), the 2nd gastric tergite scarcely shagreened (with fine micro-reticulation in *T. escomeli*), and the dorsal ovipositor valve tapering directly from notch to apex (a little convexly tapered in *T. escomeli*). Brèthes includes a male in his original diagnosis of *T. escomeli* (1919: 124), but that specimen now appears lost and the author's account of it does not allow comparison with males of related species.

Trachysphyrus aglaus (Porter 1967: 285–86) was described from a single male taken in the west Andean region of central Perú. This species resembles *T. agalma* in its peculiarly shaped areolet and rather strong propodeal cristae, but differs by its shaggy temporal setae, long and overlapping 2nd gastric setae, and shorter temples.

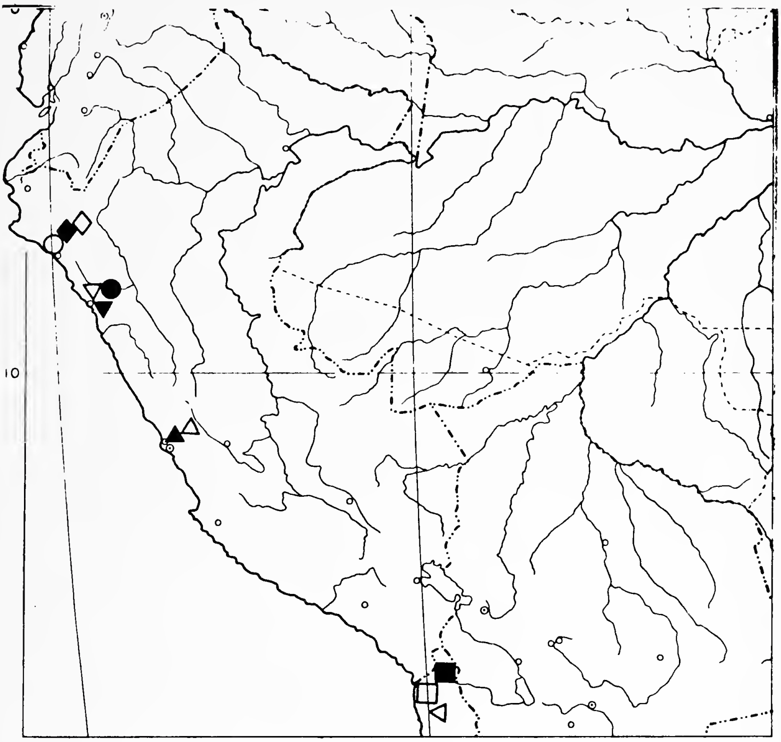
Field Notes. Specimens of *T. agalma* were obtained only by Malaise Trap, although much hand collecting was done at the type locality. The trap was set up across an irrigation ditch bordered by tall bunch grass, oregano fields, and *Eucalyptus* trees.

Specific Name. From the Greek noun *agalma,* "glory, honor, delight."

4. **Trachysphyrus aegla** Porter, new species
(Fig. 1, 2, 3).

Female. Unknown.

Male. *Color:* scape and pedicel mostly metallic purple; flagel-



Peru and north Chile, showing localities where mesostenines were sampled during July 1974 and 1975.

1. 33 kilometers west of Olmos, Peru. ◇
2. Olmos, Peru. ◆
3. Lambayeque, Peru. ○
4. Samne, Peru. ●
5. Simbal, Peru. ▽
6. Laredo, Peru. ▼
7. Matucana, Peru. △
8. Cupiche, Sta. Eulalia, and Palle, Peru. ▲
9. Chapiquiña, Chile. ■
10. Valle de Lluta, Chile. □
11. Codpa, Chile. ◁

Fig. 18. Map showing localities in Peruvian and north Chilean Coastal Desert and adjacent west Andean slopes where *Trachysphyrus, Aeliopotes,* and other mesostenines were collected in July of 1974 and 1975 (most sites were revisted in 1976, 1977, 1979, and 1982).

lum black and white (at least above) on segments 8, 9, or 10–13, 14, or 15; some specimens with a narrow white line on hind orbit; head, mesosoma, coxae, trochanters, fore and mid trochantelli, most of hind trochantellus, fore and mid femora on more than basal 0.5 (at least below), and hind femur faintly (if at all) toward base, all metallic purple with sparse to extensive gold reflections; gaster metallic purple with blue reflections which become prominent beyond 2nd tergite; fore and mid femora orange toward apex or sometimes almost wholly orange above; hind femur mostly orange; tibiae orange; tarsi black with some brownish on 1st metatarsus; wings brownish with purple reflections.

Length of fore wing: 6.4–7.5 mm. *First flagellomere:* 2.6–3.0 as long as deep at apex. *Clypeus:* slightly to gently convex in profile; apical margin broad and gently convex. *Malar space:* 0.8–0.9 as long as basal width of mandible. *Temple:* 0.8–0.9 as long as eye in dorsal view; rounded and gently receding; highly polished with abundant but mostly well separated small, sharp punctures which emit long and, at least dorsad, well overlapping setae. *Mesoscutum:* notauli sharp, traceable about 0.5 the length of mesoscutum; surface highly polished with numerous small to large punctures that are separated mostly by much more than their diameters (the smooth interspaces prominent). *Mesopleuron:* speculum swollen and polished; surface otherwise polished and minutely punctate on much of upper anterior quadrant, on prepectus (sometimes much wrinkled), and on an extensive anterio-ventral area behind prepectal carina, as well as often smooth for some distance below speculum, but otherwise with strong, longitudinally biased wrinkling between speculum and anterior swelling as well as on much of its lower hind quadrant. *Lower metapleuron:* with coarse reticulate wrinkling. *Wing venation:* areolet very large, intercubiti somewhat strongly convergent above, 2nd abscissa of radius 0.8–1.0 as long as 1st intercutitus; 2nd recurrent inserted near middle of areolet; disco-cubitus gently angled, with or without a stump of a ramellus; nervellus broken near middle. *Propodeum:* basal face long, steeply sloping; apical face obliquely reclivous and 0.5–0.6 as long as basal; basal trans-carina fine and sharp nearly throughout, a little weakened on lateral 0.4; apical trans-carina well defined, a little irregular to sharp throughout, narrowly looped far forward in middle, laterad forming moderately prominent and well projecting bluntly cuneate cristae; lateral longitudinal carinae obsolete; surface with strong reticulate wrinkling, the smooth interspaces between the wrinkles rather extensive, and the wrinkling becoming more or less weakened basad of basal trans-carina. *First gastric tergite:* postpetiole 0.9–1.4 as wide apically as long from spiracle to apex; dorsal carinae obsolete; surface

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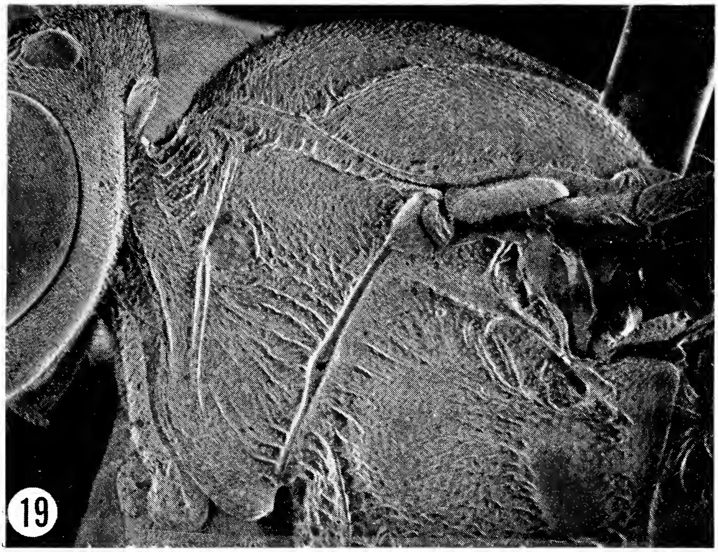

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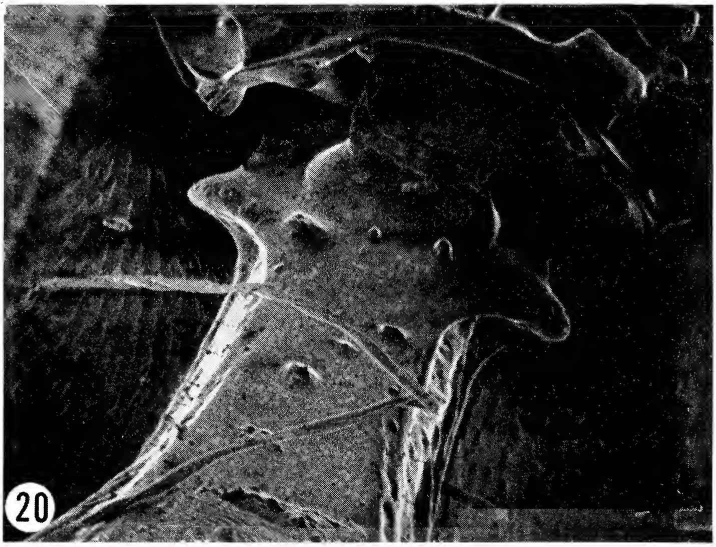

Fig. 19. *Aeliopotes paitensis,* ♀. SEM photograph (32×) of front part of thorax in lateral view (note dorsal contour of epomia). Fig. 20. *Aeliopotes paitensis,* ♀. SEM photograph (120×) showing prominent lateral teeth at base of 1st gastric tergite.

smooth and highly polished, scarcely shagreened, with scattered tiny punctures that emit long, mostly non-overlapping setae (which become longer and overlap apicad). *Second gastric tergite:* smooth and highly polished, sometimes with slight shagreening or micro-reticulation, and with numerous but remotely spaced tiny punctures that emit rather sparse setae which, nonetheless, mostly attain or a little surpass the length of their interspaces.

TYPE MATERIAL. Holotype ♂: CHILE, Tarapacá Province, Belén, 3170 m, 18-19-VII-1976, C. Porter, C. Calmbacher, H. Vargas. Paratypes: 3 ♂, 2 with same data as holotype, 1 ♂, CHILE, Tarapacá Province, Socoroma, 3000 m, 20-VI-1979, C. Porter. Holotype in Florida State Collection of Arthropods. Paratypes in Collection of Charles C. Porter.

RELATIONSHIPS. This high Andean species seems closely related to *Trachysphyrus agalma* Porter and *T. aglaus* Porter. It is best distinguished from the sympatric *T. agalma* by its sparse but very long and overlapping 2nd gastric setae (setae short and not overlapping in *T. agalma*). From the Peruvian *T. aglaus,* it differs in having the flagellum white banded, the temple conspicuously but not shaggily setose, and the areolet comparatively symmetric with dorsally convergent intercubiti.

FIELD NOTES. Specimens of *T. aegla* were obtained in the same type of West Andean Puna habitats already described for *T. carrascoi, T. metallicus,* and *T. agalma.*

SPECIFIC NAME. From the Greek noun *aegla,* "lustre, splendor, glory".

5. *Trachysphyrus aglaus* Porter
(Fig. 10)

Trachysphyrus aglaus Porter, 1967. Mem. Amer. Ent. Inst. **10**: 285–7. Type ♂: Perú, Pachacayo, 28-III-1913, C. H. T. Townsend (Washington). No additional *T. aglaus* have accumulated since my original description.

This species inhabits the Andes of west-central Perú. Among congeners of the Coastal Desert and contiguous highlands, it most resembles *T. agalma* and *T. aegla.*

6. *Trachysphyrus imperator* Porter

Trachysphyrus imperator Porter, 1967. Mem. Amer. Ent. Inst. **10**: 301–2. Type ♂: Perú, Dept. La Libertad, "Jalca of Ramada", 21-VI-1964, R. M. Straw (Washington).

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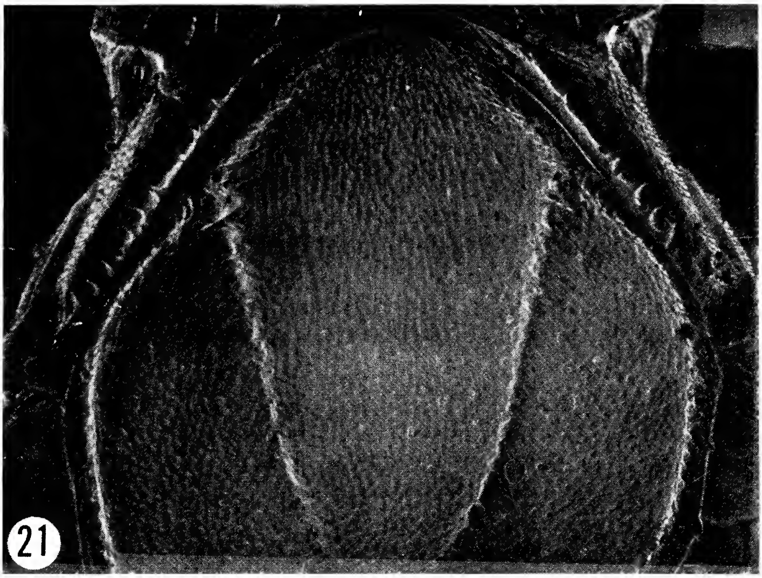

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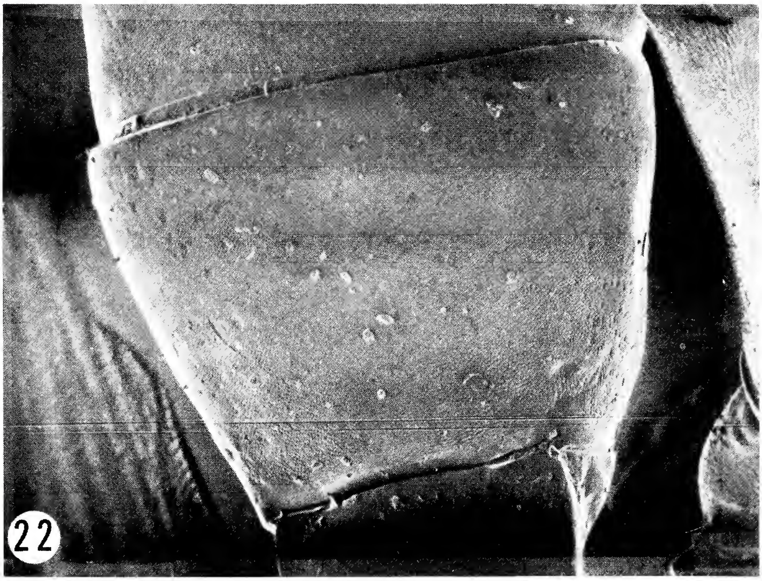

Fig. 21. *Aeliopotes paitensis,* ♀. SEM photograph (60×) of most of mesoscutum in dorsal view (note closed contour of epomia). Fig. 22. *Aeliopotes paitensis,* ♀. SEM photograph (25×) showing 2nd gastric tergite in dorsal view.

Trachysphyrus imperator remains known only from the holotype, obtained in the highlands of northwest Perú. Its closest relatives are *T. imperialis* and *T. peñai* from Neantarctic and Patagonian south Argentina and Chile.

7. *Trachysphyrus escomeli* (Brèthes)

Cryptus Escomeli Brèthes, (1918) 1919. Rev. Chilena Hist. Nat. **22**: 124. Lectotype ♀ (labeled by Porter): Perú, Arequipa (Buenos Aires).

The only known specimen of *T. escomeli* is the lectotype, which I examined in December 1964 at the Museo Nacional in Buenos Aires, Argentina.

Arequipa, the Peruvian type locality for this species, is situated in a vast fertile valley of the Coastal Desert at 2800 m altitude near the main Andean cordillera. Repeated fieldwork from 1975–1982 in nearby north Chile and at Arequipa itself has failed to discovered additional specimens of *T. escomeli.*

As previously mentioned, this species shares some features with *T. agalma* Porter and *T. aglaus* Porter but does not seem closely related to any other *Trachysphyrus.*

8. *Trachysphyrus cleonis* Viereck
(Fig. 7, 9)

Trachysphyrus cleonis Viereck, 1913. Proc. U.S. Natl. Mus. **44**: 470. Type ♀: Perú, Cuzco, 11,500 ft (Washington).

My redescription of *T. cleonis* (Porter 1967: 312–14) was based on 70 females and 69 males from the central and western Andes of southern Perú. Most of this material came from Cuzco and other high inland localities, but several specimens were reported from Oroya, Acolla, and Jauja at elevations approaching 4000 m just above the Coastal Desert on the west Andean slopes.

Western populations of *T. cleonis* have the body metallic blue and the legs blackish. Central Peruvian specimens are purple with orange legs. Such geographic variation suggests past or present discontinuities in the species' distribution, as perhaps determined by Pleistocene to recent climatic instability.

Most of my records for *T. cleonis* span the spring and summer months (September to March). I have not collected the species during June and July fieldwork in Perú between 1974 and 1982. Long-term phaenologic analysis probably will confirm that other sympatric

Trachysphyrus show different but equally consistent patterns of seasonal occurrence.

In this species and the closely related *T. viridis* (Brullé) the second gastric tergite is mat and delicately granular. In all other Coastal Desert *Imperialis* Group *Trachysphyrus* the gastric terga are smooth and polished. *Trachysphyrus cleonis* differs from *T. viridis* by its sparsely punctate mesopleuron, wholly dark flagellum, and gold-stained thoracic pleura and propodeum.

9. *Trachysphyrus viridis* (Brullé)
(Fig. 6, 14).

Joppa viridis Brullé, 1846. *In* Lepeletier: Histoire naturelle des insectes. Hyménoptères **4**: 286. Type ♂: Argentina, Buenos Aires (Turin).

Cryptus Kinbergi Holmgren, 1868. Kongliga svenska fregatten Eugenies resa. .**2**(1): 397. Lectotype ♀ (labeled by Townes): Argentina, Buenos Aires (Stockholm).

This *Trachysphyrus* long has been known as *T. kinbergi* (Holmgren). However, recent examination of Brullé's holotype confirms that *viridis* is the senior available name for the species (Porter 1975: 169)

The only Coastal Desert record for *T. viridis* is of a single female taken at Arequipa, Perú (Porter 1967: 308). Otherwise, *T. viridis* ranges over most of southern South America from Lake Titicaca to the Straight of Magellan, but avoids Chile except at a few localities in the south where Patagonian Desert habitats intrude westward from Argentina. The species prefers semiarid to arid localities between sealevel and 3000 m, being especially characteristic of the Argentine Prepuna, Subandean Desert, Sierras de Córdoba, Chaco, Pampa, and Patagonian Desert.

In accordance with its wide altitudinal and latitudinal range, *T. viridis* varies strikingly in phaenology from population to population. In the south or at high altitudes (1–3000 m), it generally is active during the warmer months of November to April. In the scorchingly subtropical Chaco Thorn Scrub (e.g., at Las Termas De Río Hondo in Santiago del Estero, Argentina), adults emerge mainly during the mild weather of late May to early August.

10. *Trachysphyrus venustus* Myers
(Fig. 8, 15).

Trachysphyrus venustus Myers, 1914. Proc. U.S. Natl. Mus. **45**: 361. Type ♂: Perú, Coropuna at 14,500 ft (Washington).

This is the only *Imperialis* Group *Trachysphyrus* with an apically bisinuate clypeus, mostly white head, and broadly white marked gaster. It occurs in high Andean habitats (Puna and Altiplano) near the snowline and ranges from north Chile through adjoining Perú and south Bolivia to Catamarca Province of northwest Argentina. It flies during the warmest months of the year (late October to January) and even then endures temperatures of at most 8–15°C by day and hard frosts every night.

New Specimens Examined. 1 ♀: CHILE, Tarapacá Province, Putre, 3400 m, "Nov.". This specimen is in the collection of the Centro de Investigación y Capacitación Agrícola (C.I.C.A.) of the Universidad del Norte at Arica, Chile.

ACKNOWLEDGMENTS

This research was supported by my NSF Grants BSR-8313444, DEB-75-2246, and GB-6925. Awards for fieldwork in South America were provided in 1973–1975 and in 1979 and 1981 by the Committee for Research and exploration of the National Geographic Society. Fordham University Faculty Fellowships covering the Spring Semester of 1980 and the Fall Term of 1984 also greatly facilitated museum visits and field studies essential to this project.

In north Chile my activities were supported by the Universidad del Norte (now Universidad de Tarapacá), which furnished laboratory space and allowed unrestricted use of field vehicles. For their incomparable generosity, patience, and kindness, I am indebted to Dr. Raúl Cortés P., Ing. Alfonso Matta V., Ing. Hector Várgas C., Tec. Agr. Nelson Hichins O., and to Aux. Gerardo Díaz P., all of the Departamento de Agricultura of the then Universidad del Norte. Collecting in north Chile also was facilitated by the Chilean National Park Service and by the Chilean National Electric Company (ENDESA), both of which made available fine accommodations at guest houses in remote areas of the Tarapacá highlands.

As a Research Associate of the Florida State Department of Agriculture and Consumer Services, I received much help with this research. I am particularly indebted to Dr. Lionel A. Stange of that institution, who accompanied me on several extended field trips in the Peruvian Desert.

The Scanning Electron Microscope photographs were taken by Mr. Jaime Zung of Fordham University, using a Hitachi S-510 under the supervision of Dr. E. Ruth Witkus.

SUMMARY

The mesostenine genus *Trachysphyrus* occurs from Ecuador to Tierra del Fuego in Andean, temperate, subtropical, and Neantarctic Biomes. It has 7 endemic species in the Coastal Desert, of which *T. aegla* and *T. agalma* are new. *Trachysphyrus* has produced a specialized offshoot in the Coastal Desert (*Amblyteles paitensis* Cockerell). This species now is placed in the new genus *Aeliopotes.*

Trachysphyrus may be recognized by its dark and refulgent wings; lack of white marks on the mesosoma; metallic (blue, green, purple, gold) ground color; strong and usually elongate notauli; shining mesoscutum; at most weakly angled discocubitus; straight mediella; axillus intermediate between anal margin of wing and submediella; long propodeal spiracle; at most finely punctate 2nd gastric tergite; and long, stout, moderately compressed, straight or a little upcurved ovipositor. *Aeliopotes* differs from *Trachysphyrus* especially by its black and red ground color; dorsally lamellate epomia; and baso-laterally toothed 1st gastric tergite.

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INSECTS ASSOCIATED WITH THE FLOWERS OF TWO SPECIES OF *MALACOTHRIX* (ASTERACEAE) ON SAN MIGUEL ISLAND, CALIFORNIA

By Scott E. Miller[1] and W. S. Davis[2]

The insects associated with *Malacothrix incana* (Nutt.) T. & G. and *M. implicata* Eastwood on San Miguel Island were sampled as part of a general analysis of hybridization between the two species on the island (Davis and Philbrick, 1986). On San Miguel Island, *M. incana* is widely distributed on unstabilized and stabilized sand dunes on slopes near the ocean or on sandy substrate on the upper surfaces of the island including the slopes of San Miguel Peak and Green Mountain. In contrast, *M. implicata* is generally restricted to the slopes near the ocean or the walls of canyons above the ocean. Hybrid plants were found only where *M. incana* and *M. implicata* were growing in a common area and constituted less than 1% of the total number of the three forms in these areas. Hybrid plants were most frequent on the slopes above Cuyler Harbor and above Tyler Bight.

Plants of *M. implicata* are spreading or erect perennials with large heads containing up to 80 florets. The ligules are white and have a purple stripe on the abaxial surface. Plants of *M. incana* are perennial and become mound-shaped after several years of growth. The large heads contain up to 100 florets with yellow ligules. The hybrid is also perennial and has large heads with pale yellow florets whose ligules often bear a reddish stripe on the abaxial surface.

During our visit to San Miguel Island in May, 1984 a majority of the plants of *M. incana, M. implicata* and the hybrid were in full bloom. Numerous open heads were present on plants of both species and one plant of *M. incana* had over 200 open heads. Herbarium label data indicate that the blooming period of *M. incana* generally coincides with that of *M. implicata* on other Channel Islands as well as on San Miguel Island and that flowering of both species reaches a maximum in the months of May and June.

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In cultivation, plants of *M. incana* have been found to be self-compatible and all have had a chromosome number of 2n = 14 while plants of *M. implicata* have all been self-incompatible and have had a chromosome number of 2n = 18. The one hybrid plant propagated from wild fruit was sterile and 16 univalents were found in meiosis. Tests using long and short wave UV light (366nm and 245nm) on flower heads of plants in cultivation indicate that the reflective pattern of *M. incana* is quite different from that of *M. implicata,* and that the hybrid has the same pattern as in *M. incana.*

Because of the differences between *M. incana* and *M. implicata* in flower color, breeding system, and UV reflectance it was clear that a study of the pollinators of the two species would contribute to a general study of the causes of interspecific hybridization.

The only mention in the literature of insects on *Malacothrix* on San Miguel Island are the records of six native bee species at flowers of *M. implicata* by Cockerell (1937), the recent synonomy of one of these bees by Rust (1984), and there were no data on pollinator choice among the three flower types (Miller and Menke, 1981; Miller, 1985b).

METHODS

The present preliminary report is based on collections made on San Miguel Island, 24–27 May 1984, and data from Cockerell (1937), supplemented by earlier observations on this and other of the California Islands. On the May, 1984 trip most of the island was surveyed, with concentrated efforts on the slopes above Cuyler Harbor and Tyler Bight. Insect specimens are deposited in Santa Barbara Museum of Natural History, Natural History Museum of Los Angeles County, U.S. National Museum of Natural History, and California Department of Food and Agriculture collections. Our collecting emphasized sampling the diversity of insects present; time did not allow detailed observation of the abundance and activities of each species. Although our data are only preliminary, we feel that they are adequate to infer general patterns and suggest directions for future research, which should address seasonal and diurnal activity patterns of the insects, insect-flower interactions, and flower constancy of the insects (e.g. Hurd and Linsley, 1975; Hurd et al., 1980).

RESULTS

In general, *Malacothrix incana, M. implicata,* and the interspecific hybrids are visited by the same suite of generalist bees and a few flies, as well as small beetles and true bugs (Table 1). Many of these species were seen on many other flowers in a variety of families including Convolvulaceae (*Calystegia macrostegia* subsp. *macrostegia* [Greene] Brummit) and Crassulaceae (*Dudleya greenei* Rose), in the Cuyler Harbor area. Because bees carry large pollen loads and move actively between flowers, they are probably the major pollinators of *Malacothrix,* although flies and beetles (as well as wasps which were not seen on flowers of *Malacothrix* on San Miguel Island) probably have some role in pollination.

It is probable that the most important pollinator is the native bee *Agapostemon texanus* Cresson, the relatively large metallic green females of which are abundant and active, especially in the early morning when the flowers of both species of San Miguel Island *Malacothrix* are open and receptive for pollination. Individuals of *A. texanus* were, in general, the most commonly observed bees on *Malacothrix* (although they were more obvious due to size and color than many of the small halictids), and were observed flying between *Malacothrix* flowers of the same and different colors. However, the relatively constant wind on the island made following individual bees for long periods impossible, so we have no data on flower preference or constancy. Pollen from the hind legs of eleven *A. texanus* females collected on *Malacothrix* was stained with cotton blue lactophenol and compared under a phase contrast light microscope with pollen of *M. implicata* and *M. incana.* The majority of the pollen grains from the bees were comparable to the pollen of *Malacothrix* in size, external wall structure, and other morphological characters although it was not possible to distinguish the pollen of *M. incana* from that of *M. implicata.* These observations are consistent with the biology of *A. texanus* in the laboratory (Roberts, 1969).

The insects found on flowers of *Malacothrix* on San Miguel Island in May, 1984 are listed in Table 1, which also includes records from Cockerell (1937). All of the taxa identified to species, except *Lopidea nigridea hirta* and the Hymenoptera, are San Miguel Island records first published here. All these species were

Table 1. Pollinating and herbivorous insects known from flowers of *Malacothrix* on San Miguel Island (X = observed in May, 1984; Ckll = observed by Cockerell in July, 1937).

	inc.	impl.	hyb.
Thysanoptera			
Undetermined	X		
Thripidae			
Frankliniella occidentalis (Pergande)		X	X
Thrips tabaci Lindeman			X
Hemiptera			
Anthocoridae			
Orius harpocrates Herring	X		X
Miridae			
Lopidea nigridea hirta Van Duzee	X		X
Coleoptera			
Chrysomelidae			
Diachus auratus (Fabricius)	X	X	X
Melyridae			
Trichochrous (s. l.) sp. A	X	X	X
Trichochrous (s. l.) sp. B		X	
Staphylinidae			
Tachyporus sp.		X	
Bruchidae			
Acanthoscelides napensis Johnson		X	
Coccinellidae			
Scymnus nebulosus LeConte		X	
Lepidoptera			
Tortricidae			
Argyrotaenia franciscana insulana Powell (larvae)			X
Diptera			
Syrphidae			
Allograpta exotica (Wiedeman)			X
Carposcalis sp.		X	
Copestylum mexicana (Macquart)	X		
Sphaerophoria contiqua Macquart	X	X	
Bombyliidae			
Lepidanthrax borius Hall	X		
Hymenoptera			
Anthophoridae			
Epeolus minimus (Robertson) = *E. eastwoodae* Cockerell		Ckll	
Hypochrotaenia suavis (Cresson)		X	

Table 1. (continued) Pollinating and herbivorous insects known from flowers of *Malacothrix* on San Miguel Island (X = observed in May, 1984; Ckll = observed by Cockerell in July, 1937).

	inc.	impl.	hyb.
Apidae			
Xeromelecta californica (Cresson)		X	
Bethylidae			
Goniozus sp.		X	
Braconidae			
Apanteles (s. l.) sp.	X		
Colletidae			
Colletes hyalinus gaudalis Cockerell	X		
Halictidae			
Agapostemon texanus Cresson = *A. californicus psammobius* Cockerell	X	X, Ckll	
Lasioglossum pavonotum (Cockerell)	X	X, Ckll	X
Lasioglosum titusi (Crawford)		X	
Dialictus megastictum (Cockerell)	X	X, Ckll	
Dialictus pilosicaudus (Cockerell)		Ckll	
Dialictus cabrilli (Cockerell)		Ckll	
Dialictus miguelensis (Cockerell)	X		
Dialictus perichlarus (Cockerell)	X	X	
Ichneumonidae			
undetermined		X	
Megachilidae			
Anthidium palliventre Cresson			X
Pteromalidae			
undetermined		X	

collected on flowers, but some of them spend more time on leaves and stems than on flowers. The interspecific hybrid is somewhat more poorly represented with respect to its insects because fewer plants were seen. *Lopidea nigridea hirta* was described as a San Miguel Island endemic (Van Duzee, 1921), but the status of *hirta* (as species, subspecies or synonym of a more widespread species) is unclear without revision of the very large genus *Lopidea*. Two tortricid moth larvae were reared from the flowers of the hybrid *Malacothrix* (SEM lot 84E1A, B), yielding adult females of *Argyrotaenia*, probably *franciscana insulana;* the various island populations once lumped under *insulana* are quite variable and need review. *Lepidanthrax borius* is here first recorded from San Miguel and San Nicolas Islands; Cockerell's (1940: 292) San Nicolas record of *L. angulus* Osten Sacken might be a misidentification of this. The five species of *Dialictus* were described by Cockerell (1937, in the genus *Halictus*) from San Miguel island. *Dialictus cabrilli* is still considered a San Miguel Island endemic (Rust, in Miller, 1985a), but this may be due to the poor taxonomic condition of this difficult genus. Observations on other islands (Miller, unpubl.) and, specifically, from San Nicolas Island (Table 2) suggest that a similar suite of general pollinators is active on *M. incana* on other islands. Pollinator collections made on San Nicolas Island in May, 1984 were superficial compared to those on San Miguel Island, but consist of the same dominant elements.

Other parts of plants of *Malacothrix* were examined as well as flowers, and three families of Homoptera were found on stems and roots. The western aster root aphid, *Aphis armoraceae* Cowen (Aphididae) on the stem of a hybrid plant on the slopes above Cuyler Harbor, was associated with the introduced ant *Lasius niger* L. (Hymenoptera: Formicidae). The black scale, *Saissetia oleae* (Olivier) (Coccidae) was taken on stems of *M. incana* near Cabrillo Monument, Cuyler Harbor, in May, 1977 (by SEM) and on the slopes above Cuyler Harbor in May, 1984. An unidentified mealybug (Pseudococcidae) was taken from the root of a plant of *M. implicata* at Cuyler Harbor, but the specimen was lost in the mail during attempts to obtain an identification.

CONCLUSIONS

All the forms of *Malacothrix* on San Miguel Island are apparently visited by the same suite of generalist bees and a few flies, as

Table 2. Associates of flowers of *Malacothrix incana* on San Nicolas Island (collected 11 and 31 May, 1984 by S. Junak from plants on stabilized sand dunes east of Corral Harbor, elevation about 20m).

- Coleoptera
  - Melyridae
    - *Trichochrous* (s. l.) sp.
- Diptera
  - Bombyliidae
    - *Lepidanthrax borius* Hall
- Hymenoptera
  - Sphecidae
    - *Bembix americana nicolae* Cockerell
    - *Podalonia mexicana* (Saussure)
  - Eumenidae
    - **Stenodynerus* sp.
  - Anthophoridae
    - *Hypochrotaenia formula* (Viereck)
  - Halictidae
    - **Agapostemon texanus* Cresson
    - **Dialictus megastictum* (Cockerell)
    - **Evylaeus kincaidii* (Cockerell)

*Also collected on the hybrid *Malacothrix incana* × *M. polycephala* (ined.)

well as small beetles and true bugs. Circumstantial evidence suggests that the bee *Agapostemon texanus* is probably the most important pollinator. Future research should examine the specific nature of the insect-flower interactions. The simplified nature (fewer species of both plants and pollinators compared to similar mainland sites) of insect-plant interaction systems on the California Islands presents excellent opportunities for testing hypotheses of insect-plant interaction and evolution (e.g. Cruden, 1972; Thorp, 1979).

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We thank the National Park Service for permitting the research and for their assistance during the visit to San Miguel Island. Ralph N. Philbrick and Steve Junak, Santa Barbara Botanic Garden, enthusiastically assisted in fieldwork. We thank the following systematists for identifications: N. Evenhuis, Bishop Museum (Bombyliidae); R. J. Gill, California Department of Food and Agriculture (Coccidae); T. J. Henry, Systematic Entomology Laboratory, U.S.D.A. (Hemiptera); J. M. Kingsolver, SEL (Bruchidae and Melyridae); T. Kono, CDFA (Thysanoptera and Aphididae); A. S. Menke, SEL (Sphecidae); D. R. Miller, SEL (Coccidae); J. A. Powell, University of California, Berkeley (Tortricidae); T. N. Seeno, CDFA (Chrysomelidae); R. R. Snelling, Los Angeles County Museum (Apoidea); and F. C. Thompson, SEL (Syrphidae). R. J. McGinley, A. S. Menke, R. W. Rust, and R. R. Snelling reviewed the manuscript.

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CAMPONOTUS (*KARAVAIEVIA*) *TEXENS* SP. N. AND *C.* (*K.*) *GOMBAKI* SP. N. FROM MALAYSIA IN COMPARISON WITH THE OTHER *KARAVAIEVIA* SPECIES (FORMICIDAE: FORMICINAE)*

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Introduction

Two weaving species of *Camponotus,* collected in a rain forest in Malaysia in 1984 (Maschwitz, 1985), have turned out to be new species of the subgenus *Karavaievia.* These are described below as *Camponotus* (*Karavaievia*) *texens* and *C.* (*K.*) *gombaki* and are compared with the other species of the subgenus *Karavaievia* Emery (1925).

Materials and Methods

The two colonies of *Camponotus texens* were found by U. Maschwitz: one of the Gombak Valley, about 27 km north of Kuala Lumpur, and the other one in the region of Kuantan, on the east coast of Malaysia. Of *C. gombaki,* only one colony was discovered in the Gombak Valley. Twenty workers of each of the colonies were used for the descriptions that follow. The description of the sexuals for *C. texens* was based on 5 males from the colony of Kuantan and 5 females from the Gombak Valley. Only 5 females, but no males, were available for *C. gombaki.*

One worker of *Camponotus* (*Karavaievia*) *overbecki* was made available to the author by Dr. Baroni Urbani from the Santschi Collection in Basel (Switzerland). Three workers of this species were used for classifiction from the Forel Collection in Geneva (Switzerland) along with three workers and two deälate females of *Camponotus* (*Karavaievia*) *exsectus* from the Emery Collection in Genoa (Italy). However, specimens of *C.* (*Karavaievia*) *dolichoderoides* were not available from either the Forel or Emery Collections.

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The examinations of *C. texens, C. gombaki* and *C. overbecki* were made with the aid of a binocular microscope; the measurements of the animals were made at a magnification of 65×. Scanning electron micrographs of *C. texens* and *C. gombaki,* presented as part of this article, were taken by a Hitachi S 500.

The following abbreviations are used below (measurements as in Bolton, 1977):

TL: total length. The total outstretched length of the individual from the mandibular apex to the gastral apex.

HL: head length. The straight-line distance between the anterior clypeal margin and the mid-point of the occipital margin in full-face view.

CI: cephalic index = (HW × 100)/HL

SL: scapus length. The straight-line length of the antennal scape excluding the radicle.

SI: scapus index = (HW × 100)/SL

PW: pronotal width. The maximum width of the pronotum in dorsal view.

OD: ocular diameter. The maximum width of the eyes.

All measurements are expressed in millimeters.

The critical reading of the manuscript by Dr. C. Baroni Urbani and Dr. P. van Voris is gratefully acknowledged.

RESULTS AND DISCUSSION

Characteristics of the Subgenus *Karavaievia* Emery 1925

The description of the subgenus *Karavaievia* follows that of Emery (1925). This description is mainly a listing of characters which are partly superficial but which serve to distinguish this subgenus from all the others (Emery, 1925). A thorough diagnosis of '*Karavaievia*' would require a revision of the whole genus *Camponotus,* which is urgently needed but which is not the intention of this paper. Thus, the subgenus *Karavaievia* is in a preliminary state like the classification of the genus *Camponotus* itself.

According to Emery (1925) *Karavaievia* is closely related to the subgenera *Myrmamblys, Myrmoteras,* and *Myrmoplatys.* The most important difference between these subgenera and *Karavaievia* is the nearly complete absence of any dimorphism in the worker caste of the *Karavaievia* species. Specific for *Myrmoplatys* is the scapal insertion near the midlength of the frontal carinae, the depression of the anterior part of the head and the relatively short flagellar segments. *Myrmotarsus* includes massive and large species with depressed tibiae. Workers of *Myrmamblys* have heads that are longer than wide with parallel sides. The characteristics of *Karavaievia* are as follows:

Workers

Apart from minimal variability, all workers are monomorphic and about 5.5 mm long. Head trapezoidal, with rounded occipital corners. Head sides convex, occipital margin more or less concave, and anterior margin mostly straight. The eyes are situated behind the midlength of the sides of the head. Length of head subequal to its width (i.e. CI $\sim$ 100). Clypeus narrow, convex, and without median carina. Its anterior margin almost straight, and in the middle third slightly concave. Frontal carinae relatively short and subparallel to moderately divergent. Mandibles short, with lateral borders strongly curved and 5 teeth on each masticatory border. Antennal scapes projecting beyond the occipital margin by about one third of their length. Pedicel longer than the following flagellar segments; apical flagellar segments slightly thickened. Alitrunk with a deep impression (metanotum) between promesonotum and propodeum, and two raised stigmata at the deepest point of the impression. Petiolar scale tapers to a transverse ridge.

Females

Total length about 11 mm. Head about twice as wide as that of the workers, and with less convex sides. Anterior clypeal margin with a median semicircular excision. Apical flagellar segments not thickened.

Males

Anterior clypeal margin straight. Mandibles with only one strong, apical tooth. Total outstretched length about 6.5 mm.

Camponotus texens sp. n.

Derivatio nominis: The species name is derived from the Latin word 'texere' = weave.

A. Holotype ☿: TL 5.4, HL 1.26, HW 1.29, CI 103, SL 1.51, SI 85, PW 0.77, OD 0.31.

Frontal carinae extend to about midlength of head. Apart from a slight projection behind the scapal insertion, they are straight and slightly divergent (Fig. 1a). Anterior clypeal margin almost straight, but in the middle third weakly concave, with slightly indented edges. Eyes are situated behind the midlength of the sides of the head; their maximum diameter is 0.31 mm, or about 0.24 HW.

Head and alitrunk dark brown; gaster and petiole dirty yellow. Antennae and legs, including tibiae, dark brown, while apical flagellar segments, tarsi and front of head are dirty yellow like the gaster. Surface of head, alitrunk and gaster weakly shining. Accordingly, cuticular punctures and reticulated sculpture (SEM) are weak (Fig. 1a, c). Gaster with an imbricate sculpture (Fig. 3b), which is much more pronounced in gaster of males (Fig. 3c). Yellowish white, decumbent pubescence on the whole body, including scapes and legs. Longer erect, yellowish white hair especially on clypeus, but also on rest of head, alitrunk and gaster. Propodeum, seen in profile, broadly rounded and slightly higher than promesonotum. Dorsal part of the propodeum convex, descending part straight. In the lower fifth, the declivity is slightly concave.

Paratype ☿☿ : TL 5.1–5.8, HL 1.26–1.38, HW 1.29–1.48, CI 98–106, SL 1.43–1.57, SI 85–100, PW 0.77–0.92, OD 0.31–0.39 or 0.24–0.31 HW (20 measured).

Holotype ☿, Western Malaysia: Pahang, near Kuantan, 20.2.1984 (Naturhistorisches Museum, Basel).

Paratypes: 20 ☿☿ with the same data as holotype (2 in British Museum (Natural History), London; 2 in Museum of Comparative Zoology at Harvard University; 2 in National Museum of Malaysia, Kuala Lumpur; 2 in Museo Civico di Storia Naturale, Genova; 12 in collection of the author).

B. Gynetype (♀): TL 11.3, HL 2.33, HW 2.24, CI 96, SL 2.16, SI 104, PW 1.76, OD 0.69.

Frontal carinae extend about to midlength of the head. Apart from a lateral projection beyond the scapal insertion, they are almost straight and only slightly divergent. Clypeus wider than that of worker (0.67 mm as against 0.50 mm). Its anterior margin shows a median semicircular excision, with indented edges (Fig. 1b).

Mandibles strong, distinctly rounded on outside and with 5 subequal teeth on inside. Frontal area not clearly delimited and hardly more shining than surroundings. Head and alitrunk black, tergites

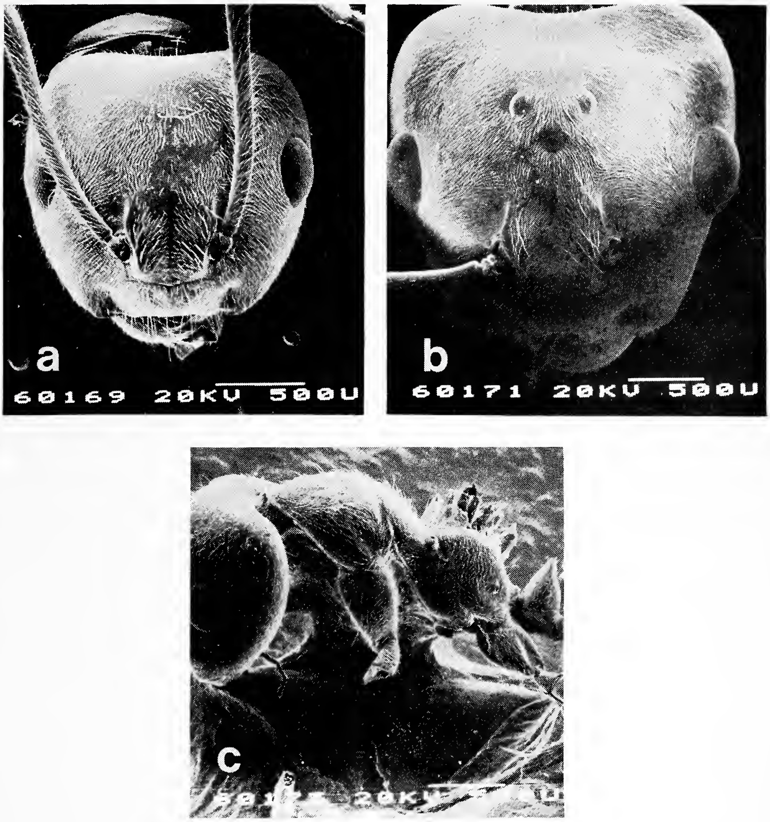

Fig. 1. Scanning micrograph of *Camponotus texens:* a, head of worker; b, head of female; c, alitrunk of worker in profile.

of gaster dark brown; sternites lighter brown; front of head, distal antennal flagellum and legs yellow brown. Wings yellowish, veins yellow brown.

Head, alitrunk and gaster covered with fine, light yellow, decumbent pubescence. Longer erect hairs distributed over the whole body. Eyes distinctly larger than those of workers and situated behind the midlength of the sides of the head. OD 0.69 mm, or about 0.30 HW. Petiole with a broad base, tapering toward the apex into a narrow ridge, seen from the side.

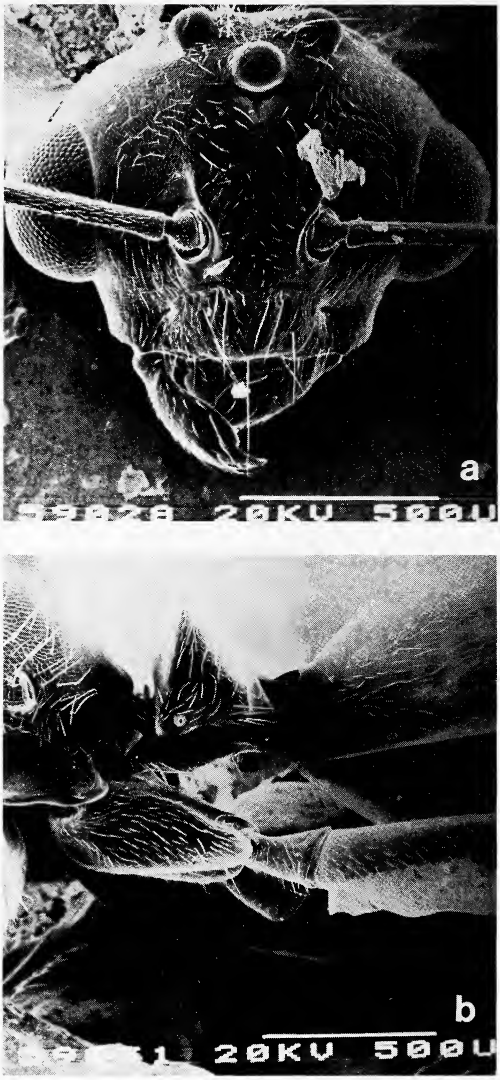

Fig. 2. Scanning electron micrograph of *Camponotus texens* male: a, head; b, petiole of alitrunk and gaster in profile.

Paratype ♀♀: TL 10.8–11.3, HL 2.29–2.46, HW 2.20–2.40, CI 95–98, SL 2.12–2.19, SI 101–107, PW 1.72–1.92, OD 0.69, OD/HW 0.28–0.31 (4 measured).

Gynetype, Western Malaysia: Gombak Valley, ca. 25 km north of Kuala Lumpur, 31.12.1982, U. Maschwitz leg. (Naturhistorisches Museum, Basel).

Paratypes: 4 ♀♀ with the same data as gynetype (collection of the author).

C. Allotype (♂): TL 6.7, HL 1.0, HW 1.02, CI 102, SL 1.00, SI 102, PW 1.32, OD 0.46.

The trapezoidal head nearly as wide as long (CI 102), with prominent convex eyes, extending to the upper end of the head sides. Occipital margin strongly convex with protruding ocelli (Fig. 2a); clypeus narrow (width about 0.17 mm) with straight anterior margin. Short frontal carinae sinuate, reaching back to midlength of head. Eyes very large; maximum diameter 0.46 mm, or about 0.45 HW. Scapes long, projecting beyond occipital margin of the head by more than half their length. Pedicel expanded at its distal end and thicker than following flagellar segments.

Head and alitrunk dark brown like scapes and legs; petiole and gaster lighter brown; antennal flagellum yellow brown. Wings yellowish with lighter brown veins. Decumbent pubescence on head and alitrunk thin, but denser on gaster; in addition, body covered with longer, erect hairs. Cuticular sculpture of head, alitrunk and petiole reticulated, that of gaster imbricated (Fig. 3c). Propodeal profile rounded, with weakly convex dorsal and weakly concave descending part. Petiolar scale triangular in profile, with a broad base tapering to a ridge (Fig. 2b). Ridge with slight median excision. Paratype ♂♂: TL 6.5–6.7, HL 0.86–0.92, HW 0.93–0.99, CI 96–108, SL 1.00, SI 93–99, PW 1.16–1.24, OD 0.43–0.46 (4 measured). Allotype, Western Malaysia: Gombak Valley, ca. 25 km north of Kuala Lumpur, 31.12.1982, U. Maschwitz leg. (Naturhistorisches Musaeum, Basel).

Paratypes: 4 males with same data as allotype (collection of the author).

Camponotus gombaki sp. n.

Derivatio nominis: The name is derived from the Gombak Valley, in which the first and only colony of this species was found, and in honor of the 'Gombak Field Station of the University of Malaya,' where we worked during our research stay.

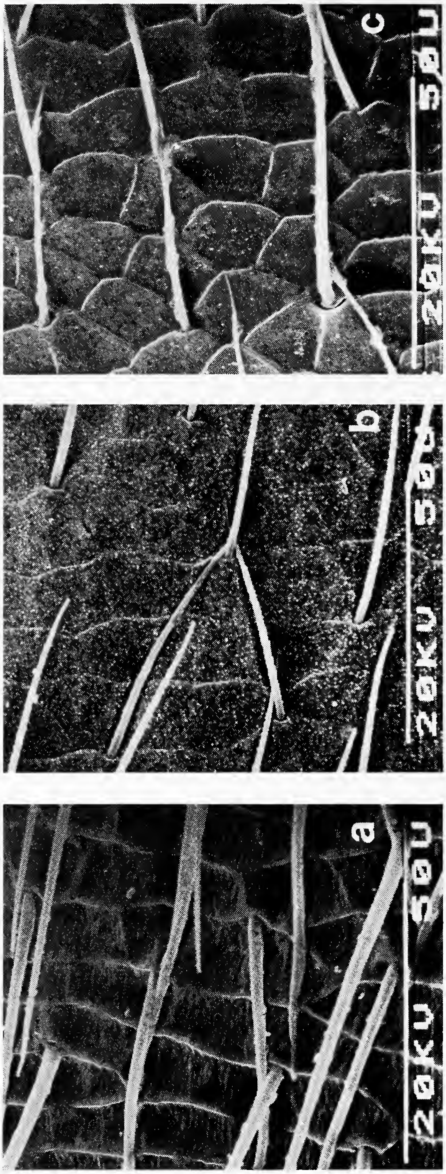

Fig. 3. Scanning electron micrograph of the cuticular structure of the gaster: a, *Camponotus gombaki* worker; b, *C. texens* female; and c, *C. texens* male.

A. Holotype ☿: TL 6.1, HL 1.46, HW 1.49, CI 102, SL 1.56, SI 96, PW 0.93, OD 0.34.

Frontal carinae slightly sinuate, reaching back to midlength of the head (Fig. 4a). Anterior clypeal margin almost straight, but in the middle third weakly concave. Eyes situated behind the midlength of the sides of the head, with maximum diameter of 0.34 mm or about 0.23 HW.

Head and alitrunk reddish brown, gaster dark brown, almost black. Petiole reddish brown at base, but dark brown in upper half. Legs and antennae, like head and alitrunk, reddish brown to top. Surface of head, alitrunk and gaster opaque, with very dense punctures, which appear elongated on the gaster. Cuticular structure under SEM regular reticulated on head and irregular reticulated on alitrunk; cuticular sculpture of gaster is shown on Fig. 3a. Yellowish white, decumbent pubescence less dense than in *C. texens* workers; yellowish white, erect, longer hairs occur mainly on forehead and vertex, less dense on alitrunk and gaster. Propodeum in profile broadly rounded (Fig. 4c, d) and lower than promesonotal dorsum. Dorsal part of propodeum convex, descending part slightly flatter. In the lower sixth, the declivity is slightly concave.

Paratype ☿☿: TL 5.6–6.4, HL 1.40–1.62, HW 1.44–1.72, CI 97–105, SL 1.56–1.62, SI 86–104, PW 0.92–1.04, OD 0.34–0.40, or 0.22–0.26 HW (20 measured).

Holotype ☿, Western Malaysia: Gombak Valley, ca. 25 km north of Kuala Lumpur, 15.2.1984 (Naturhistorisches Museum, Basel).

Paratypes: 20 ☿☿ with same data as holotype (2 in British Museum (Natural History), London; 2 in Museum of Comparative Zoology at Harvard University; 2 in Malaysia, National Museum of Malaysia, Kuala Lumpur; 12 in collection of the author).

B. Gynetype (♀): TL 11.4, HL 2.18, HW 2.24, CI 103, SL 2.38, SI 94.1, PW 1.92, OD 0.54.

Frontal carinae extend about to midlength of head. Apart from a lateral projection behind the scapal insertion, they are almost straight and hardly divergent. Width of clypeus subequal to that of *C. texens.* Anterior clypeal margin with semicircular excision (Fig. 4b). Mandibles strong, distinctly rounded on outside, and with 5 subequal teeth on inside. Frontal area clearly delimited and more shining than neighboring head parts.

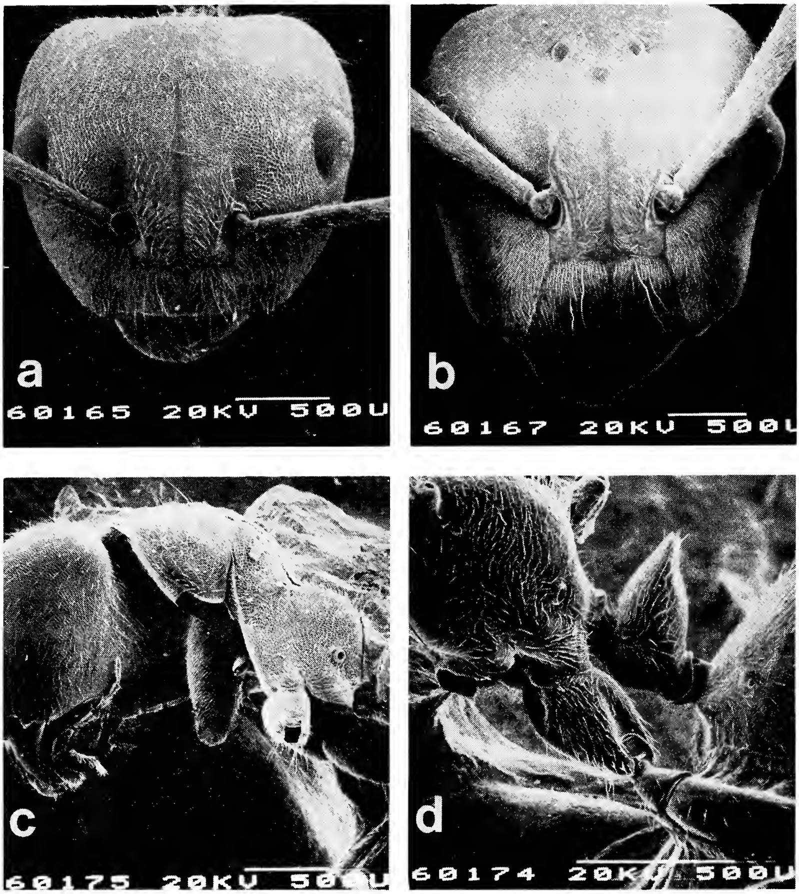

Fig. 4. Scanning electron micrograph of *Camponotus gombaki;* a, head of worker; b, head of female; c, alitrunk of worker in profile; d, petiole of worker, with parts of alitrunk and gaster in profile.

Head, alitrunk, petiole and legs reddish brown; gaster, antennae and mandibles dark brown. Wings yellowish, veins yellow brown. Body covered with short, yellowish white, decumbent pubescence; longer, erect, yellowish white hair is particularly dense on clypeus, but also on rest of body, including scapes and legs. Longer hair on alitrunk is less dense than in *C. texens* female. Eyes are situated behind the midlength of the sides of the head and markedly larger than those of workers, but smaller than those of *C. texens* females; maximum diameter 0.54 mm, which is about 0.24 HW. Petiolar profile with broad base, which tapers to a transverse ridge and into a point, as seen from above.

Paratype ♀♀: TL 11.4, HL 2.21–2.23, HW 2.24–2.29, CI 103–104, SL 2.3–2.4, SI 94–98, PW 1.92–1.99, OD 0.58–0.62, OD/HW 0.24–0.25 (4 measured).

Gynetype, Western Malaysia: Gombak Valley, ca. 25 km north of Kuala Lumpur, 15.2.1984 (Naturhistorisches Museum, Basel).

Paratypes: 4 ♀♀ with same data as gynetype (collection of the author).

Camponotus overbecki Viehmeyer stat. n.

Camponotus dolichoderoides var. *overbecki* Viehmeyer 1915: 162.

Material examined: 1 syntype worker from the Santschi Collection (Naturhistorisches Museum, Basel) leg. Overbeck: Singapore. TL 5.8, HL 1.43, HW 1.56, CI 109, SL 1.61, SI 97, PW 0.88, OD 0.39.

Frontal carinae extend to about midlength of the sides of the head; as in *C. texens,* they are slightly divergent and—apart from a lateral projection behind the scapal insertion—straight. Anterior clypeal margin almost straight, but slightly concave in the middle third. Eyes are situated behind the midlength of the sides of the head; maximum diameter 0.39, which is about 0.39 HW.

Head and alitrunk reddish brown, gaster blackish brown with lighter anterior segment boundaries. Petiole, legs, tarsi, and apical antennal flagellum yellow. Head, alitrunk and gaster shining, less punctured than in *C. texens* and in particular in *C. gombaki.* Whole body covered with fine, yellowish white, decumbent pubescence; longer erect denser than in *C. texens* and in particular in *C. gombaki.* Propodeum in profile broadly rounded and slightly higher than promesonotal dorsum. Dorsal part of propodum weakly convex, descending part slightly flatter. In the lower fourth, the declivity is slightly concave.

On the whole, the differences between *C. gombaki* and *C. texens* are not exceeding those between *C. overbecki* and *C. dolichoderoides.* As *C. texens* and *C. gombaki* certainly belong to different species because of the differences in their behavior (Maschwitz et al., 1985), there is no sufficient reason to continue designating *C. overbecki* as a variety of *C. dolichoderoides.* It is therefore made a species on its own. The female of *C. overbecki* is described by Viehmeyer (1915) from an isolated specimen as follows: head narrower and more elongated than that of worker; eyes larger and more convex than those of workers and situated in front of the midlength of the sides of the head. Clypeus slightly emarginate anteriad. Dispersed, decumbent pubescence on the whole body. Female dealate and 6.5 mm long.

Body length of 6.5 mm is far smaller than that of any other known *Karavaievia* females. Head deviates markedly in shape and size, and eyes are situated in front of the midlength of the sides of the head and more convex than those of workers. This was not found in any other *Karavaievia* female. In contrast to all other *Karavaievia* females, clypeus slightly carinated and emarginated. These basic differences from all known *Karavaievia* females suggest that the female described by Viehmeyer is not a female of *C. overbecki.*

Males of *C. overbecki* as described by Viehmeyer (1915): Head with strongly convex eyes slightly broader than long, occipital margin strongly convex, anterior clypeal margin straight, mandibles with a large apical tooth. Propodeal profile with weakly convex dorsal and concave descending face; dorsal face with shallow, median, longitudinal furrow. Petiolar scale lower and slightly thicker than that of worker, tapering to a transverse ridge, which is slightly excised in the middle. Densely reticulated, front part of the body more opaque than gaster. Dirty yellow brown, gaster with indistinct narrow, dark bands in front of the posterior segment borders, femora and tibiae slightly darkened; wings yellowish with yellow brown veins. 6 mm in length.

Camponotus dolichoderoides Forel

Camponotus dolichoderoides Forel, 1911: 51. (Types not found, presumed lost.)

Description is translation of Forel (1911): workers 6 mm in length; strong, curved, shining mandibles, with 5 teeth and widely separated punctures. Clypeus without carina, anterior margin straight, and not or only weakly protruding. Frontal carinae little sinuate and hardly divergent. Scapal insertion close to the posterior clypeal margin. Head trapezoidal, with strongly convex sides, and nearly as broad as long with maximum diameter in the posterior third. Occipital margin moderately concave; eyes situated close beyond the midlength of the sides of the head. Scapes project behind the occipital margin by about one third of their length. Apical antennal flagellum slightly thickened. Promesonotal dorsum broadly rounded with deep promesonotal suture. Deep impression between promesonotum and propodeum, with two raised stigmata on the ground. Dorsal propodeum in profile slightly convex, forming almost a right angle with declivity which is almost straight. Petiolar scale in profile cone shaped. Gaster oval, tibiae cylindrical, not thickened and without spines. Cuticular surface weakly reticulated and slightly opaque, covered with punctures which are particularly dense and elongated on gaster. Decumbent pubescence very fine, yellowish, distributed over the whole body, including tibiae and scapes, especially dense on gaster. Uniformly dirty yellow brown; tarsi, apical antennal flagellum and front head reddish to yellow red. Hayvep, Borneo.

Camponotus exsectus Emery

Camponotus exsectus Emery, 1901: 53. Syntype ☿☿ and ♀♀: Museo Civico di Storia Naturale, Genova (examined).

Original description (Emery, 1901): workers dirty yellow, shining, front head and gaster lighter, segment borders brownish, decumbent pubescence denser on head and alitrunk than on gaster. Body, including scapes and legs, covered with longer, whitish, erect hairs. Weak cuticular punctures on the whole body, those of the gaster elongated. Head rounded and convex. Clypeus weakly convex and not carinated; anterior clypeal margin with wide excision in the middle third, and indented edges. Mandibles strongly curved on outside and 5 teeth on inside. Frontal carinae almost straight, linea frontalis weak, but clearly visible. Scapes project beyond occipital margin by about one third of their length. Viewed in profile, pro- and mesonotum form a curved line which is connected to the propodeal outline by an obtuse angle. Propodeal profile broadly rounded. Scale biconvex, tapering into a sharp transverse ridge. Length: 4-3/4 to 5-1/2 mm.

According to my own examination, workers are more shining than those of *C. texens,* but not as much as those of *C. gombaki.*

Erect hairs more numerous than in *C. texens.* Propodeal dorsum clearly higher than dorsum of promesonotum, and in profile more inclined than in *C. texens, C. gombaki,* and *C. overbecki.* Dorsal part of propodeal profile convex, descending part nearly straight. Frontal area clearly delimited.

Original description of female (Emery, 1901): darker than workers; sides, scutellum, propodeal dorsum, legs, and major part of gaster brown. Head and mesonotum opaque; pubescence very dense, in particular on gaster. Head trapezoidal, mandibles similar to those of workers; clypeus narrow with deep semicircular excision in the middle of the anterior margin, limited by protruding acute angles. Antennae strong, petiole similar to that of workers. Punctures on gaster weak and not elongated. Length 11 mm. Mentawei, Sipora.

According to my own examination, *C. exsectus* females are larger than females of *C. gombaki* and *C. texens.* HW 2.5, HL 2.5, PW 2.3. Frontal carinae less divergent than those of *C. texens* and *C. gombaki* females. Frontal area indistinctly delimited; mandibles reddish brown with black teeth; gaster shining.

Comparison of *Karavaievia* Species

The subgenus is characterized by morphological traits and possibly by behavioral characters, too. The common morphological traits include the subuniform size of workers, females and males, the shape of the head, the position of the eyes, the characteristic shape of frontal carinae, clypeus, mandibles, antennae and alitrunk. All known *Karavaievia* species originate from the Indo-Malayan area, in particular from Malaysia and Singapore. A possibly common behavior of all *Karavaievia* species is the weaving of silk nests on the undersides of leaves which, however, has only been investigated for *C. texens* and *C. gombaki* (Maschwitz et al., 1985). For *C. overbecki,* there is only the statement of Viehmeyer (1915) that Overbeck found workers and males in 'carton nests' on the underside of leaves. Nothing has become known so far, however, on the nest-building of *C. dolichoderoides* and *C. exsectus.*

My examination of two workers and a male of *C. texens* and of two workers of *C. gombaki* showed no openings of metapleural glands. This is in accordance with the observations in all weaver ants studied by Hölldobler and Engel-Siegel (1984).

The two species described by Forel (1911) as *C. horrens* and *C. moeschi,* found on the Philippines, were assigned by Forel (1911) to the same group as *C. dolichoderoides,* and also Chapman and Capco (1951) classified *C. horrens* in the subgenus *Karavaievia.* Emery (1925), on the other hand, classified *C. moeschi* in the subgenus *Myrmamblys* and *C. horrens* in the subgenus *Colobopsis;* in the latter case, however, Emery was not quite sure, because neither soldiers nor females of this species had been found. *C. horrens* and *C. moeschi* definitely do not belong to the subgenus *Karavaievia.* This is supported in the case of *C. horrens* by the carinated and twice-excised anterior clypeal margin of the workers, the strongly divergent frontal carinae and the position of the eyes in the posterior fourth of the head. Features against *C. moeschi* as a member of the subgenus *Karavaievia* are the notched clypeus, lobed in the anterior part; the elongated head, convex in the occipital part; position of the eyes at the posterior third of the head, and the weakly impressed metanotal groove.

The differences between workers of the *Karavaievia* species are in coloration, sculpture and pubescence, slight differences in the shape of the frontal carinae, differences in size of head and eyes, and in shape and size of propodeum. A broader comparison of the *Karavaievia* sexuals, however, is not yet possible, because females of only 3 species and males of 2 species are known. *Karavaievia* workers are dirty yellow and brown, from reddish brown to blackish brown; in most cases, the front of the head, the apical flagellar segments and the tarsi are of a uniform color, which differs from the color of the rest of the body.

Key to the species of *Karavaievia*

Workers

1. Head and alitrunk shining and covered with erect hairs.......2
   Head and alitrunk opaque and only sparsely covered with erect hairs..3
2. Uniformly dirty yellow, anterior parts of head and gaster lighter. Gaster with darker segment borders. Frontal carinae straight and diverging.................................. *C. exsectus*
   Head, alitrunk and legs reddish brown, gaster blackish brown with lighter brown segment borders. Apical antennal flagellum

and front of head yellow. Frontal carinae weakly sinuate .... *C. overbecki*

3. Propodeal profile arched, dorsal and descending parts almost straight, forming an angle of about 90°. Uniformly dirty yellowish brown; tarsi, apical antennal flagellum and front of head reddish................................ *C. dolichoderoides*
Propodeal profile rounded 4
4. Propodeum higher than promesonotum. HW 1.35–1.51, HL 1.31–1.47, OD 0.24–0.28 HW. Head, alitrunk, scapes and legs dark brown; gaster, petiole, apical antennal flagellum and front of head dirty yellow............................ *C. texens*
Propodeum lower than promesonotum. HW 1.44–1.72, HL 1.40–1.62, OD 0.22–0.26 HW. Head and alitrunk reddish brown at base, and darker brown in upper half. Head and alitrunk opaque and densely punctured.................. *C. gombaki*

Females

1. Petiolar scale blunt in dorsal view................ *C. exsectus*
Petiolar scale acute in dorsal view..........................2
2. Head, alitrunk, petiole and legs reddish brown, gaster, antennae and mandibles dark brown. Frontal area clearly delimited and more shining than the surroundings. Gaster opaque. OD 0.54–0.62, or 0.24–0.25 HW .... *C. gombaki*
Head and alitrunk black, tergites of gaster dark brown, sternites brown. Frontal area clearly delimited. Gaster shining. OD 0.69 or 0.28–0.31 HW.............................. *C. texens*

Males

1. Color on the whole dirty yellowish brown with indistinct narrow bands in front of the posterior segment borders .... *C. overbecki*
Head and alitrunk dark brown like scapes and legs; petiole and gaster lighter. Antennal flagellum yellowish brown .... *C. gombaki*

SUMMARY

Two new silk nest weaving species, *Camponotus texens* and *Camponotus gombaki,* are described as members of the subgenus *Karavaievia* Emery 1925. The subgenus now consists of five species, which are probably all weaver ants. Additionally, a key to the species of *Karavaievia* is presented.

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SUBSTITUTE NAMES FOR SOME EXTINCT GENERA OF FOSSIL INSECTS*

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During the preparation of the hexapod volume of the Treatise on Invertebrate Paleontology, now in press†, several junior homonyms were noted among the extinct genera. This seems to be an appropriate occasion to propose substitute names for these homonyms. In those instances in which the authors are still living, I have already called their attention to the homonymy, with the suggestion that they propose names of their own choice. In some other cases replacement names are already available, through synonymy, and these are being proposed in the hexapod volume of the Treatise. Most of the homonyms, however, require new names, and since the current editorial policy of the Treatise excludes the proposal of new names of taxa in that work, the present article is intended to meet that need. It consists of proposals of new generic names to replace certain names that are not being taken care of elsewhere. The gender of each new name is the same as that of the original one. The names proposed here are in the orders Palaeodictyoptera, Odonata, Diptera, Hymenoptera, Coleoptera, and Lepidoptera.

ORDER PALAEODICTYOPTERA

Family uncertain

Boltonocosta, *nomen novum pro* ORTHOCOSTA Bolton, 1912, p. 310, *non* Fritsch, 1879, p. 28. Type-species: *Orthocosta splendens* Bolton, 1912, original designation, becomes *Boltonocosta splendens* (Bolton), new combination. The genus is known only from the Upper Carboniferous of England.

Eurydictyella, *nomen novum pro* EURYDICTYA Guthörl, 1934, p. 49, *non* Ulrich, 1889, p. 301. Type-species: *Eurydictya*

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richteri Guthörl, 1934, original designation, becomes *Eurydictyella richteri* (Guthörl), new combination. The genus is known only from the Upper Carboniferous of Germany.

ORDER ODONATA

Family Aeshnidae

Neoligaeschna, *nomen novum pro* OLIGOAESCHNA Piton & Theobald, 1939, p. 6, *non* Selys, 1889, p. 160. Type-species: *Oligoaeschna jungi* Piton & Theobald, 1939, original designation, becomes *Neoligaeschna jungi* (Piton & Theobald), new combination. The genus is known only from the Oligocene of France.

ORDER DIPTERA

Family Architipulidae

Leptotipuloides, *nomen nudum pro* LEPTOTIPULA Bode, 1953, p. 312, *non* Alexander, 1917, p. 160. Type species: *Leptotipula fastigata* Bode 1953, original designation, becomes *Leptotipuloides fastigata* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Family Bibionidae

Lithosomyia, *nomen novum pro* MESOMYIA Pongracz, 1928, p. 174, *non* Macquart, 1849, p. 341. Type-species: *Bibio brevis* Heer, 1849, p. 225, SD Carpenter, herein, becomes *Lithosomyia brevis* (Heer), new combination. The genus is known by several species from the Miocene of Croatia.

Family Rachiceridae

Trecela, *nomen novum pro* ELECTRA Loew, 1850, p. 38, *non* Stevens, 1831, p. 278. Type-species: *Electra formosa* Loew, 1850, original designation, becomes *Trecela formosa* (Loew), new combination. The genus is known only from the Lower Oligocene of the Baltic amber, The name *Trecela* is an anagram of *Electra* and is considered feminine.

ORDER HYMENOPTERA

Family Eumenidae

Eunortonia, *nomen novum pro* PSEUDONORTONIA Timon-David, 1944, p. 41, *non* Soika, 1936, p. 168. Type-species: *Pseudonortonia sepulta* Timon-David, 1944, original designation, becomes *Eunortonia sepulta* (Timon-David), new combination. The genus is known only from the Oligocene of France.

Family Chrysididae

Protochrysidis, *nomen novum pro* PROTOCHRYSIS Bischoff, 1917, p. 139, *non* Pascher, 1911, p. 191. Type-species: *Protochrysis succinalis* Bischoff, 1917, original designation, becomes *Protochrysidis succinalis* (Bischoff), new combination. The genus is known only from the Lower Oligocene of the Baltic amber.

ORDER COLEOPTERA

Family Curculionidae

Oligocryptus, *nomen novum pro* EUCRYPTUS Scudder, 1893, p. 63, *non* Haldeman, 1842, p. 191. Type-species: *Eucryptus sectus* Scudder, 1893, original designation, becomes *Oligocryptus sectus* (Scudder), new combination. The genus is known only from the *Oligocene* of Colorado.

Sitonitellus, *nomen novum pro* SITONITES Haupt, 1956, p. 80, *non* Heer, 1865, p. 90. Type-species: *Sitonites egregius* Haupt, 1956, original designation, becomes *Sitonitellus egregius* (Haupt), new combination. The genus is known only from the Eocene of Germany.

Family unknown

Aptilotitus, *nomen novum pro* APTILOTUS Bode, 1953, p. 237, non Mik, 1898, p. 206. Type-species: *Aptilotus capitecarens* Bode, 1953, original designation, becomes *Aptilotitus capitecarens* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Auchenophorites, *nomen novum pro* AUCHENOPHORUS Bode, 1953, p. 229, *non* Turner, 1907, p. 270. Type-species: *Auchenophorus sculpturatus* Bode, 1953, original designation, becomes *Auchenophorites sculpturatus* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Barocephalus, *nomen novum pro* BARYCEPHALUS Bode, 1953, p. 228, *non* Guenther, 1860, p. 149. Type-species: *Barycephalus nudatus* Bode, 1953, original designation, becomes *Barocephalus nudatus* (Bode). The genus is known only from the Jurassic of Germany.

Clinomerus, *nomen novum pro* CATOMERUS Handlirsch, 1939, p. 67, *non* Pilsbry, 1916, p. 395. Type-species: *Catomerus laticollis* Handlirsch, 1939, original designation, becomes

Clinomerus laticollis (Handlirsch), new combination. The genus is known only from the Jurassic of Germany.

Critoderma, *nomen novum pro* CYCLODERMA Heer, 1865, p. 89, *non* Peters, 1854, p. 216. Type-species: *Cycloderma deplanatum* Heer, 1865, original designation, becomes *Critoderma deplanatum* (Heer), new combination. The genus is known only from the Jurassic of Switzerland.

Critotrachelus, *nomen novum pro* CYCLOTRACHELUS Bode, 1953, p. 222, *non* De Chaudoir, 1838, p. 27. Type-species: *Cyclotrachelus exsecatus* Bode, 1953, original designation, becomes *Critotrachelus exsecatus* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Dicyphelus, *nomen novum pro* DICYPHUS Bode, 1953, p. 234, *non* Fieber, 1858, p. 327. Type-species: *Dicyphus concameratus* Bode, 1953, original designation, becomes *Dicyphelus concameratus* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Eurynotellus, *nomen novum pro* EURYNOTUS Bode, 1953, p. 207, *non* Kirby, 1819, p. 418. Type-species: *Eurynotus brevicollis* Bode, 1953, original designation, becomes *Eurynotellus brevicollis* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Heeriaopsis, *nomen novum pro* HEERIELLA Handlirsch, 1906, p. 401, *non* Meunier, 1904, p. 86. Type-species: *Elytridium laevigatum* Heer, 1878, p. 196, original designation, becomes *Heeriaopsis laevigatum* (Handlirsch), new combination. The genus is known only from the Triassic of Sweden.

Mesolobites, *nomen novum pro* LOBITES Dunstan, 1923, p. 53, *non* Mojsisovics, 1873, p. 155. Type species: *Lobites tuberculatus* Dunstan, 1923, original designation, becomes *Mesolobites tuberculatus* (Dunstan), new combination. The genus is known only from the Triassic of Australia.

Mesoncus, *nomen novum pro* LOXONCUS Bode, 1953, p. 218, *non* Schmidt-Goebel, 1846, p. 4. Type-species: *Loxoncus procerus* Bode, 1953, original designation, becomes *Mesoncus procerus* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Oligovarus, *nomen novum pro* VARUS Schlechtendahl, 1894, p. 209 *non* Stål, 1865, p. 141. Type-species: *Varus ignotus* Schlechtendahl, 1894, original designation, becomes *Oligo-*

varus ignotus (Schlechtendahl), new combination. The genus is known only from the Oligocene of Germany.

Ooidellus, *nomen novum pro* OOIDES Bode, 1953, p. 234, *non* Agassiz, 1846 (Index, p. 260). Type-species: *Ooides denudatus* Bode, 1953, original designation, becomes *Ooidellus denudatus* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Parnosoma, *nomen novum pro* PEDINOSOMA Bode, 1953, p. 235, *non* Reibisch, 1893, p. 252. Type-species: *Pedinosoma detectum* Bode, 1953, original designation, becomes *Parnosoma dectectum* (Bode), new combination. The genus is known only from the Jurassic of Germany.

Peridosoma, *nomen novum pro* PEROSOMA Bode, 1953, p. 217, *non* Bronn, 1862, p. 135. Type-species: *Perosoma praecisum* Bode, 1953, original designation, becomes *Peridosoma praecism* (Bode), new combination. The genus is known only from the Jurassic of Germany.

ORDER LEPIDOPTERA

Family Nymphalidae

Jupitellia, *nomen novum pro* JUPITERIA Scudder, 1889, p. 488, *non* Bellardi, 1875, p. 20. Type-species: *Jupiteria charon* Scudder, 1889, original designation, becomes *Jupitellia charon* (Scudder), new combination. The genus is known only from the Oligocene of Colorado, U.S.A.

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