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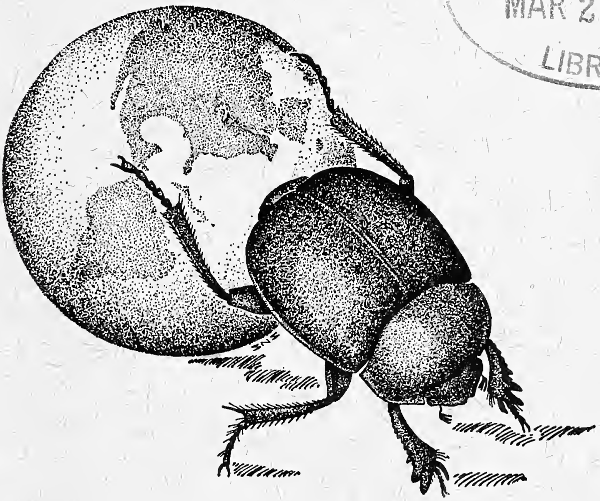

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NOTE ON GALL INHABITANTS OF *ASPHONDYLIA HELIANTHIGLOBULUS* OSTEN SACKEN (DIPTERA: CECIDOMYIIDAE) IN WESTERN PENNSYLVANIA

John D. Plakidas

Abstract.—The insects associated with the gall of *Asphondylia helianthiglobulus* Osten Sacken (Diptera: Cecidomyiidae) were reared during the summer and winter of 1979–1980. Only those galls formed on the flower disc of *Rudbeckia laciniata* L. (Compositae) were investigated. From the gall cells of *A. helianthiglobulus* three hymenopterous species were reared: *Rileya americana* Girault (Eurytomidae), *Torymus advenus* O.S., and *Torymus* sp. (Torymidae). Dipterous larvae associated with the gall were represented by the families Agromyzidae, Cecidomyiidae, Chloropidae, and Drosophilidae.

Introduction

The gall midge, *Asphondylia helianthiglobulus* Osten Sacken (Diptera: Cecidomyiidae) (for synonymy see Rogers et al. 1979) forms an apple like gall on the flower disc of the coneflower, *Rudbeckia laciniata* L. (Compositae). The gall is composed of individual cells surrounded by plant tissue. One host larva develops per cell. Externally there is no evidence of seed formation, however petals and sepals do develop on the gall.

From field studies it was observed that female midges oviposited into immature flower discs as early as July 8, with gall formation being visible by July 15. Adult emergence began the third week in August.

Materials and Methods

In 1979 gall collections began the first week of August and continued on a weekly basis through the last week of September. In addition, gall collections were made once monthly from October 1979 through January 1980 to determine which species utilized the gall as an overwintering reservoir. Two locations for gall collections were used: stream beds in the Linesville, Pennsylvania area, Crawford County; and McCandless Township, Allegheny County, Pittsburgh, Pennsylvania.

Galls sampled during August and September 1979 were dissected in the lab. Larvae and pupae recovered from the gall cells of *A. helianthiglobulus* were placed on moist paper towels in plastic petri dishes. From both summer and winter collections dipterous larvae and puparia recovered from the plant tissue adjacent to the gall cells were reared in the same manner described above.

Reared adult specimens were sent to the Insect Identification and Beneficial Insects Introduction Institute, Beltsville, Maryland, for identification.

Results

The following is a list of species reared from the gall cells of *Asphondylia helianthiglobulus*. None of these species including *A. helianthiglobulus* were found to overwinter in the gall.

Eurytomidae (Hymenoptera).

1. *Rileya americana* Girault. Adults were reared from August 23 through September 11.

Torymidae (Hymenoptera).

2. *Torymus advenus* (O.S.). Adults emerged from August 21 through October 15.
3. *Torymus* sp. Adult emergence was recorded from August 20 through September 24.

Dipterans associated with the gall were all recovered from the plant tissue adjacent to the gall cells. Those adults reared are presented below.

Agromyzidae.

1. *Melanagromyza matricarioides* Spencer. Adult emergence was recorded from August 26 through October 3.

Cecidomyiidae.

2. *Neolasioptera rudbeckiae* (Felt). Adults were reared from both summer and winter collections. *Amblyaspis* sp. (Hymenoptera: Platygastridae), a primary endoparasite, was reared from larvae of *N. rudbeckiae*.
3. *Mycodiplosis* sp. A single adult was reared February 15, 1980 from McCandless.

Chloropidae.

4. *Chaetochlorops inquilinus* (Coq.). The puparia of this fly are found overwintering in the gall.

Drosophilidae.

5. *Drosophila quinaria* Loew. A single adult was reared October 2 from McCandless.

Unless otherwise noted, all of the species listed above were present in both the Linesville and McCandless collections.

Acknowledgments

My grateful thanks to the following for identifications: Drs. C. W. Sabrosky—Chloropidae, E. E. Grissell—Eurytomidae and Torymidae, G.

Steyskal—Agromyzidae, P. M. Marsh—Platygastridae, R. J. Gagné—Cecidomyiidae, and W. N. Mathis—Drosophilidae.

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8506 Forest Avenue, Pittsburgh, Pennsylvania 15237.

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XC(1), 1982, pp. 5–7

DESCRIPTION OF THE MALE GENITALIA OF *HOLCOSTETHUS HIRTUS* (VAN DUZEE) WITH A REVISED KEY TO NORTH AMERICAN SPECIES (HEMIPTERA: PENTATOMIDAE)

F. J. D. McDonald

Abstract.—A description of the male genitalia of *Holcostethus hirtus* is given and an emended key to the species of the genus is provided.

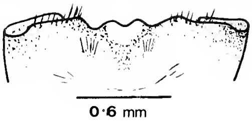
At the time McDonald (1974) revised the genus *Holcostethus* in North America, the male of *H. hirtus* was unknown. This paper provides a description of the male genitalia of *H. hirtus* and an emended key. Specimens of this species that have lost their long, grey, dorsal setae do not run to the correct name in the original key.

Holcostethus hirtus (Van Duzee, 1937)

Ventral border of pygophore (Fig. 1) sinuous with very shallow notches. A pair of small triangular flap-like pseudoclaspers (Fig. 3), one on each side, within dorsal surface of pygophore. Proctiger box-like (Fig. 2) with vertical sides, distal margin produced into a distinct lip. Claspers L-shaped (Fig. 4) with a basal thumb-like tubercle; inner surface of apex finely serrate; a number of stout setae on outer margin. Theca small, cylindrical with a pair of small tubercles one on each side at base. Conjunctival appendages membraneous (Fig. 5), bilobed, bluntly rounded, fused basally onto a thecal shield. Median penial lobes (Fig. 6) plate-like, apically acute, centrally fused together by a stout cross bar. Ejaculatory duct sinuous, projecting beyond median penial lobes.

Key to the Species of *Holcostethus* in N. America

1. Ventral surface of abdomen dark chocolate brown, sometimes mottled, margins may be outlined in yellow 2
– Ventral surface of either yellow, buff or reddish brown with or without black markings 5
2. Anterolateral margins of pronotum straight or only very slightly concave; scutellum with a distinct yellow tip; male theca lacking apical tubercles *piceus* (Dallas)
– Anterolateral margins of pronotum distinctly convex; scutellum concolorous or at most with a very faint white tip; male theca with apical tubercles 3



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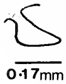

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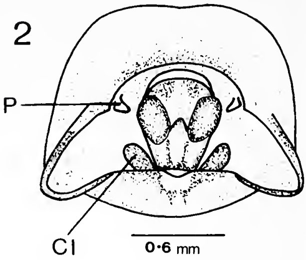

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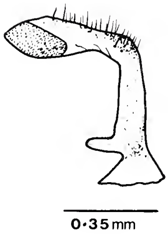

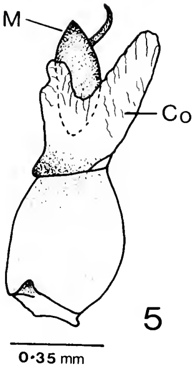

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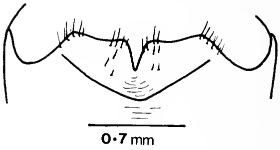

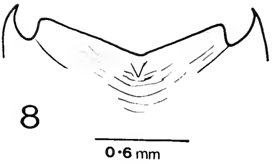

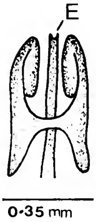

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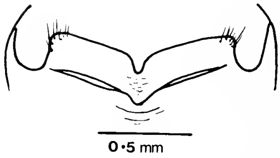

Fig. 1–6. *Holcostethus hirtus*. 1. pygophore ventral border; 2. pygophore, dorsal; 3. left pseudoclasper; 4. left clasper, ental; 5. aedeagus, lateral, co-conjunctival appendage, M—median penial lobe; 6. median penial lobes, E—ejaculatory duct.

Fig. 7–9. Pygophore, ventral border; 7. *H. tristis*; 8. *H. abbreviatus*; 9. *H. limbolarius*.

3. Connexiva fuscous with continuous narrow yellow border; long grey setae usually present on dorsum especially pronotum; male ventral border of pygophore as in Fig. 1 *hirtus* (Van Duzee)

– Connexiva checked black and yellow; dorsum without long grey setae; male pygophore with a distinct V-shaped notch centrally (Fig. 7) 4

4. Small species, not more than 7.5 mm long (apex of head to tip of membrane) and 4.00 mm wide (between lateral angles of pronotum);

male ventral border of pygophore with a small protuberance below median notch *ruckesi* McDonald

– Larger species, over 7.5 mm long and 4.00 mm wide; male ventral border of pygophore without protuberance *tristis* (Van Duzee)

5. Reddish brown species with distinctive zig-zag black markings on abdominal sterna; jugae not meeting in front of tylus; restricted to E. States *fulvipes* (Ruckes)

– Brown colored species without distinctive markings on abdomen 6

6. Dark punctation on pronotal dorsum continuing irregularly to edge of anterolateral margins; latter submarginally impressed; connexiva with distinct checked pattern of yellow and black; male ventral border of pygophore as in Fig. 8; dorsal border bearing a large pair of spines *abbreviatus* Uhler

– Anterolateral margins of pronotum calloused and without dark punctures, lacking submarginal impressions; connexival margin yellow; male ventral border of pygophore as in Fig. 9; dorsal border without spines *limbolarius* (Stal)

Acknowledgments

I should like to thank Mr. W. R. Dolling of the British Museum for the loan of material. I am grateful to Professor L. H. Rolston, Entomology Department, Louisiana Sate University, for pointing out the problems he encountered with my original key.

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Department of Plant Pathology and Agricultural Entomology, University of Sydney, N.S.W. Australia.

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STERNAL GLANDS IN THREE SPECIES OF MALE SOCIAL WASPS OF THE GENUS *MISCHOCYTTARUS* (HYMENOPTERA: VESPIDAE)

David C. Post and Robert L. Jeanne

Abstract.—Males of *Mischocyttarus flavitarsis* and *M. drewseni* possess a large mass of ducted exocrine gland cells on each of the fifth, sixth, and seventh (terminal) gastral sternites. The epidermal cells in the region of these glands are elongated, suggesting that they also have a secretory function. Males of a third species, *M. mexicanus,* have relatively few ducted gland cells on the fifth and sixth sternites and none on the seventh sternite. In *M. flavitarsis* (but not in *M. drewseni* or *M. mexicanus*), the gland cell ducts of sternites five and six open into a dense brush of long hairs.

Mischocyttarus, even though it is strictly New World in distribution, is the largest genus of social wasps (Richards 1978). Recent studies of four species reveal a diversity of male mate-locating behavior within the genus. Males of *Mischocyttarus labiatus* (F.) in Colombia, *M. mexicanus* (de Saussure) in Florida, and *M. drewseni* de Saussure in Brazil patrol routes in areas where females converge to feed or to nest (Litte 1981; personal communication; Jeanne and Castellón Bermúdez 1980). The males of *M. flavitarsis* (de Saussure) in Arizona pursue two different strategies, depending on the season: during the summer nesting season they patrol routes in female foraging areas, but in the fall, during dissolution of the colonies prior to hibernation, they defend small territories near hibernation sites (Litte 1979). Males of *M. labiatus* and *M. flavitarsis* drag and rub the gaster on perch sites, as though scent-marking (Litte 1981, 1979), while *M. mexicanus* and *M. drewseni* evidently lack this behavior (Litte, personal communication; Jeanne and Castellón Bermúdez 1980). Landolt and Akre (1979) reported that a *M. flavitarsis* male from Washington State possessed large glandular masses on the sixth and seventh (terminal) gastral sternites. The glands are probably the source of a secretion which the male applies to his perch (Litte 1979). However, the roles of this behavior and of any pheromone that may be deposited remain to be determined.

These behavioral observations suggest differences in the occurrence of sternal glands among these species. The purpose of this paper is to determine the presence of these glands and to describe their morphology in males of three of the species: *M. flavitarsis, M. drewseni,* and *M. mexicanus.* This is the first study of the histology of exocrine glands in male social wasps.

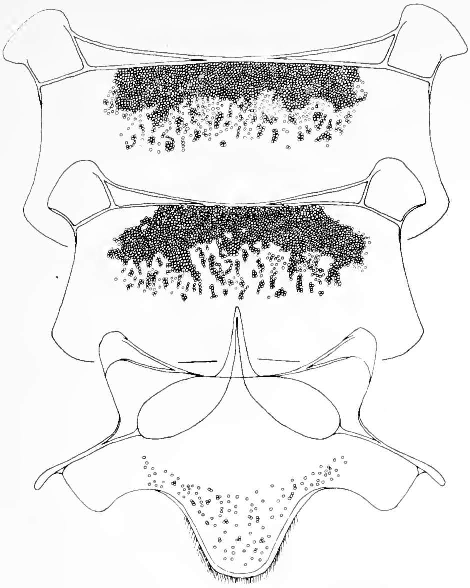


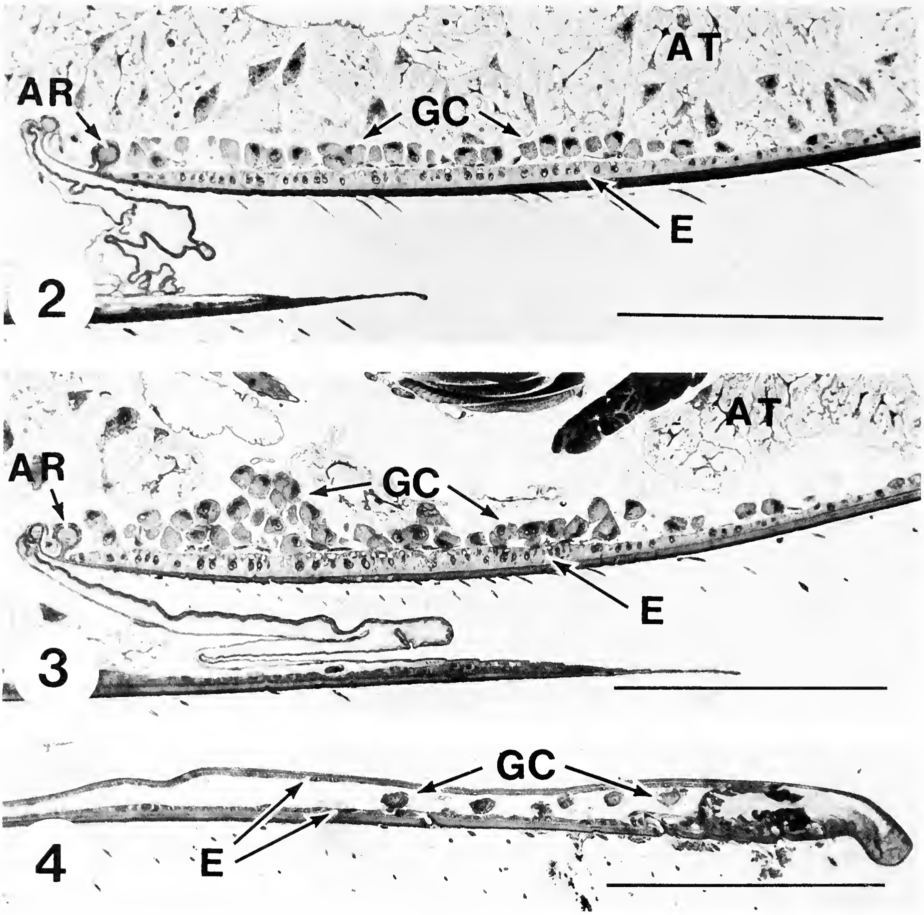
Fig. 1. Location of the class 3 gland cells on the fifth, sixth, and seventh gastral sternites of the male of *M. drewseni*.

Methods

Adult males of each species were collected from the localities of the behavioral studies cited above, as follows. *M. flavitarsis navajo* Bequaert: near the Southwestern Research Station, Portal, Arizona (fall of 1959 and 1978); *M. mexicanus* (de Saussure): Archbold Biological Station, Lake Placid, Florida (early spring of 1980); *M. drewseni* de Saussure: Fazenda Taperinha, Santarém, Pará, Brazil (November, 1978). *M. f. flavitarsis* (de Saussure) from Turlock, California, was examined with SEM for comparison with *M. f. navajo*.

Specimens were fixed in Kahle's solution, embedded in Spurr Low-Viscosity embedding media (Polysciences), and sectioned 2 μ thick for examination with a light microscope (Post and Jeanne 1980). Specimens were prepared for scanning electron microscopy as described by Post and Jeanne (1980) and examined with a JELCO JSM-U3 scanning electron microscope.

The glands of each species differ from one another only in relative size. For this reason we illustrate the fifth (antepenultimate), sixth (penultimate), and seventh (terminal) gastral sternites of *M. drewseni* and discuss the other species in relation to it.



Figs. 2–4. Longitudinal section (2 μ thick) through the glandular area of the fifth, sixth, and seventh gastral sternites of *M. drewseni*. 2. Fifth sternite. 3. Sixth sternite. 4. Seventh sternite. Anterior to left. AR = anterior ridge; AT = adipose tissue; E = epidermal cells; GC = glandular cells; Scale = 0.25 mm.

Results

Internal Anatomy

A broad, dense mat of individually ducted gland cells (''class 3 cells'' of Noirot and Quennedey 1974) underlies the anterior margin of each of sternites 5 and 6 in *M. drewseni* (Figs. 1–4). The duct of each cell passes through the integument to open onto the surface of the sternite (Fig. 5). The gland cell mass on the fifth sternite measures 1.9 mm wide by 0.6 mm front to rear

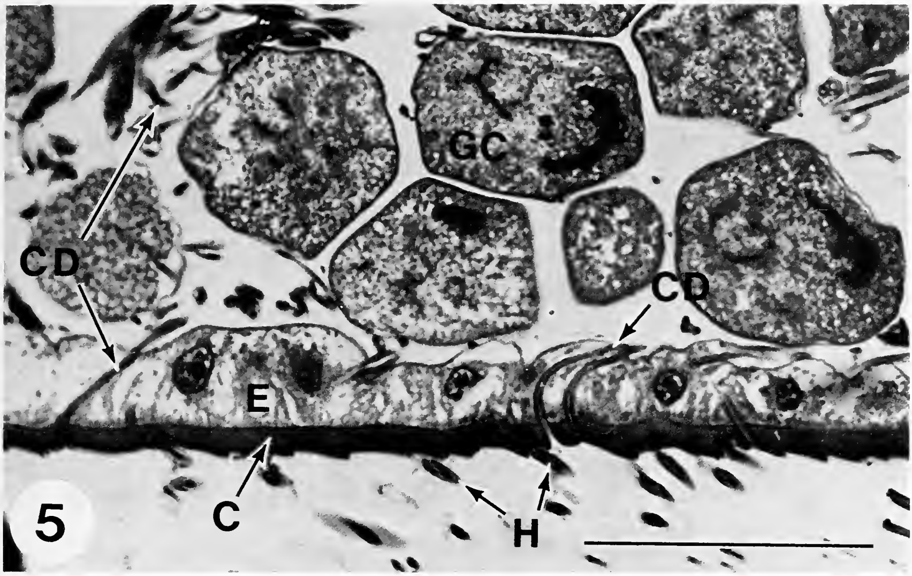


Fig. 5. Longitudinal section (2 μ thick) through the glandular area of the sixth gastral sternite of *M. flavitarsis navajo.* C = cuticle; CD = glandular cell ducts; E = epidermal cells; GC = glandular cells; H = hairs of the sternal brush. Scale = 0.05 mm.

and is a single cell layer thick (ca. 0.025 mm) (Fig. 2). In contrast the mass on the sixth sternite is 1–3 cells thick (Fig. 3) and greater in extent (2.0 mm by 0.7 mm). The seventh sternite has only scattered class 3 cells underlying its posterior half (Figs. 1, 4). In one specimen there were 115 cells.

The location of class 3 cells on each sternite is the same in *M. flavitarsis navajo* as in *M. drewseni,* but the cells are more numerous. The masses of cells extend the full width of sternites 5 and 6 (2.8 and 2.6 mm, respectively) and are somewhat bilobed, measuring, respectively 0.8 mm and 0.9 mm along the midline and 1.0 mm and 1.1 mm on the sides. Both masses of cells are also thicker than in *M. drewseni*: that on the fifth is 2–4 cells thick, while that on the sixth is 2–8 cells thick (both glands are thinner at the edges). The class 3 cells on the seventh sternite form a dense mat, one cell thick, comprising about 300 cells in one specimen.

In contrast, *M. mexicanus* has only a few scattered class 3 cells on the anterior margins of sternites 5 and 6. In one specimen there were 73 and 48 cells on the two sternites, respectively. The seventh sternite lacks class 3 cells.

In all three species the epidermal layer is thickened in the region of the class 3 cells, suggesting that these cells are actively secreting (“class 1 cells” of Noirot and Quennedey 1974) (Figs. 2–4). The layer is much thicker

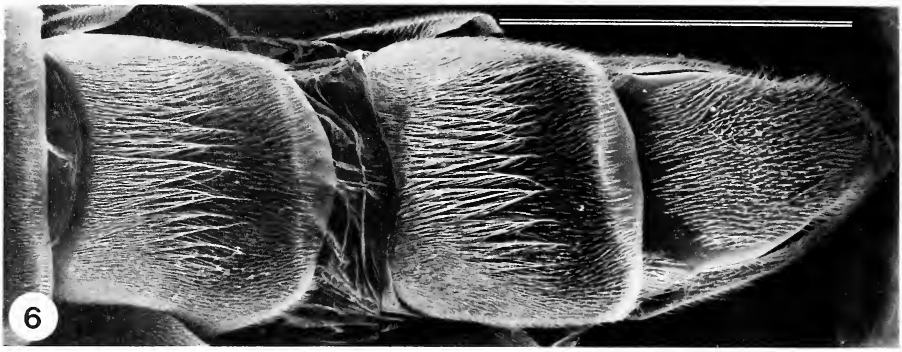


Fig. 6. SEM photograph of the fifth, sixth, and seventh (terminal) gastral sternites of *M. f. navajo.* Sternites are pulled apart to expose their anterior margins. Scale = 2.0 mm.

in *M. drewseni* ($\bar{x}$ = 27.0 μ; SD = 9.5 and $\bar{x}$ = 33.9 μ; SD = 16.1 on the fifth and sixth sternites, respectively; 3 specimens) than in *M. f. navajo* ($\bar{x}$ = 20.6 μ; SD = 4.2 and $\bar{x}$ = 21.9 μ; SD = 6.4 on the fifth and sixth sternites, respectively; 3 specimens). The epidermal cells of *M. mexicanus* are not highly modified on these two sternites (6.7 μ thick; 1 specimen). On the seventh sternite the elongation is greater in *M. f. navajo* ($\bar{x}$ = 24.9 μ; SD = 3.4; 3 specimens) than in *M. mexicanus* (15.5 μ; 1 specimen) and *M. drewseni* ($\bar{x}$ = 11.1 μ; SD = 0.3; 2 specimens).

External Morphology

The anterior regions of both the fifth and sixth gastral sternites of *M. flavitarsis navajo* (6 specimens) and *M. f. flavitarsis* (2 specimens) males are densely covered with long, brush-like hairs, while the seventh sternite lacks these (Fig. 6). All three sternites of *M. drewseni* (3 specimens) and *M. mexicanus* (3 specimens) lack these hairs, and resemble the seventh sternite of *M. flavitarsis.*

Glandular duct openings are located between the long hairs of *M. f. navajo* (Figs. 5, 7) and between the body hairs of *M. drewseni* (Fig. 8) and *M. mexicanus.*

Discussion

Landolt and Akre (1979) report sternal bushes and ducted, globular gland cells on the sixth and seventh gastral (seventh and eighth abdominal) ster-

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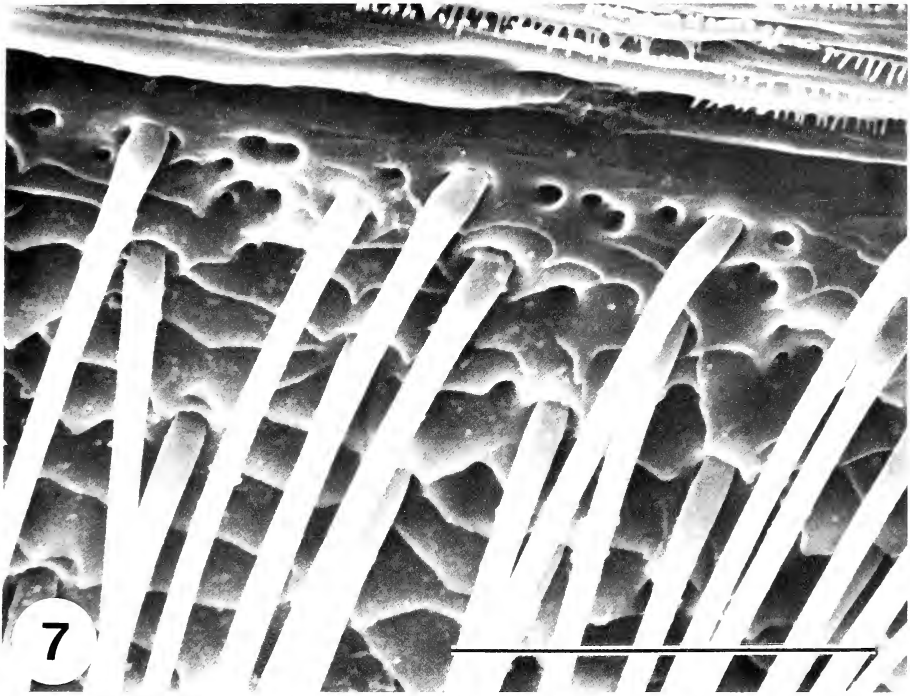
Figs. 7–8. SEM photograph of the glandular cell duct openings (seen as pores) near the base of the fifth gastral sternite. 7. *M. f. navajo.* 8. *M. drewseni.* Scale = 0.05 mm.



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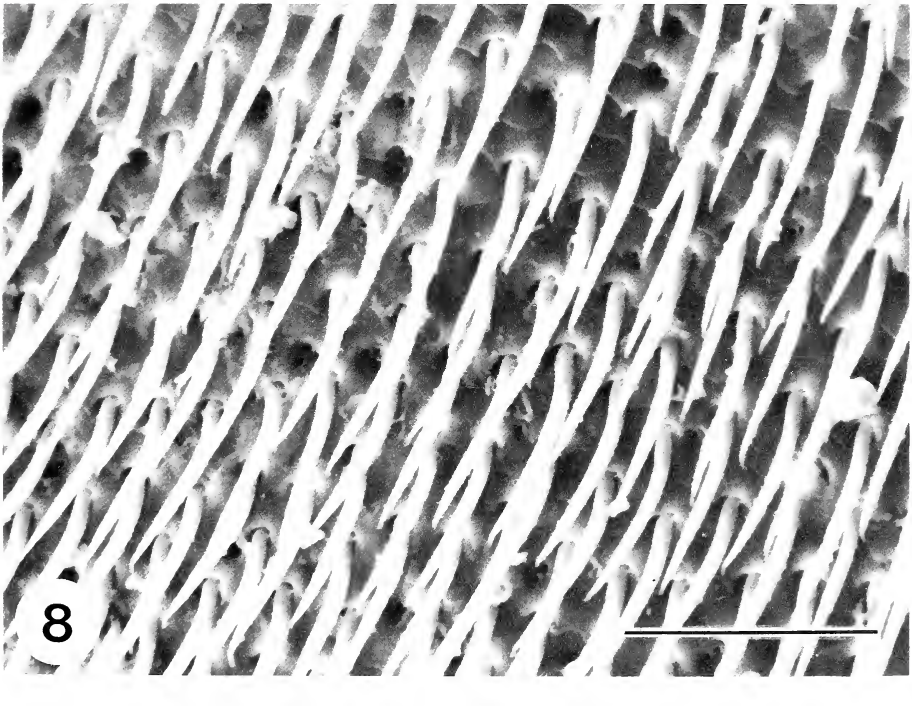

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nites of a male of *M. flavitarsis* from Washington State (probably *M. f. idahoensis* Bequaert). Our specimens of *M. f. navajo* from Arizona and *M. f. flavitarsis* from California clearly have these structures on gastral sternites 5 and 6. Either Landolt and Akre were in error or the subspecific difference is real. We were unable to obtain specimens of *M. flavitarsis* from Washington State, so we cannot resolve the question.

Since the number of gland cells is fixed in the adult stage, the observed differences in the number of class 3 gland cells are species differences and cannot be attributed to developmental differences. Of the three species we examined, *M. flavitarsis navajo* has the greatest number of class 3 gland cells on all three sternites and is the only species with sternal brushes. It also appears to be the only one of the three whose males rub these sternites on the substrate (Litte 1979; personal communication; Jeanne and Castellón Bermúdez 1980). A sternal brush appears to be a common structure in species of aculeate wasps known to rub a secretion onto a substrate, for example males of *Eucerceris* spp. and *Philanthus* spp. (Alcock 1975; Gwynne 1978; O'Neill 1979), and females of *Polistes* spp. (Hermann and Dirks 1974; Turillazzi 1979; Post and Jeanne 1980) and *Mischocyttarus* spp. (Jeanne 1970). These facts suggest the possibility that the 5th and 6th sternal glands serve different functions in *M. drewseni* and *M. mexicanus* than in *M. flavitarsis*. The location of the class 3 gland cells on the posterior half of sternite 7 in *M. flavitarsis* and *M. drewseni* suggests that their role is different from that of the cells on the preceding two segments.

The differences in height of the thickened epidermal cells may reflect only developmental differences. Since we had no information about age or activity of the specimens we sampled, all we can say is that in all three species these cells appear to be glandular in function.

This study reveals that species in the genus *Mischocyttarus* are not uniform with respect to the occurrence and size of male sternal glands. It is likely that further diversity will be found among the remaining 199 species. Our results, combined with the behavioral studies already completed, strongly suggest interspecific differences in the importance of chemical signals in the behavior of males, either on the natal nest, in a reproductive context, or both.

Acknowledgments

Marcia Litte kindly collected and fixed *Mischocyttarus mexicanus* and *M. flavitarsis navajo* specimens. Roy Snelling provided specimens of *M. f. flavitarsis* and *M. f. navajo*. Martin Garment provided technical assistance with the SEM. We thank Donas Erica and Violeta Hagmann for their hospitality during our stay in Brazil. Research supported in part by the College of Agriculture and Life Sciences and The Graduate School, University of

Wisconsin, Madison, and by National Science Foundation grant BNS 77-04081.

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THE TEMPORAL DISTRIBUTION OF *CHIRONOMUS DECORUS* (CHIRONOMIDAE) IN NORTHERN NEW JERSEY, 1979[1]

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Abstract.—The temporal distribution of *Chironomus decorus,* inhabiting a shallow, brackish pond, was determined over the course of one season. Data on larval abundance and adult flight activity were collected at regular intervals to study population trends. Initial population levels, following thaw of the winter ice cover, were relatively low. As temperatures rose throughout the spring and early summer, midge abundance gradually increased. Larval density peaked in mid-summer, averaging 700 third and fourth instar larvae per 0.02 m^2 of substrate. Population numbers decreased rapidly in late summer, prior to the onset of colder temperatures and winter weather conditions. Fluctuations in water level, salinity, and dissolved oxygen levels, are discussed in terms of their limiting affect on the aquatic environment and its inhabitants. Temperature appears to fill the primary role in regulating the population of *C. decorus* in the study area. Peaks in adult emergence and larval abundance suggest 5–6 generations were completed during 1979.

Introduction

Residents living adjacent to the Hackensack Meadowlands of New Jersey are plagued each spring and summer by tremendous swarms of the midge, *Chironomus decorus* Johannsen. The aquatic larvae develop in an area that was once salt marsh meadow, but is now a brackish, muck-bottomed pond. The habitat is subjected to daily tidal fluctuations, to a depth of one foot or less at ebb tide, and up to three feet at flood tide. Access roads and gas pipelines prevent a significant amount of water exchange, and organic materials are steadily introduced through garbage dump runoff and disposal plant effluents. The implementation of effective control measures for this chironomid is hampered by a relative lack of knowledge concerning the biology and habits of the species in this environment. Field investigations

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were undertaken to examine the temporal distribution of *C. decorus* during 1979, as measured by larval abundance and adult flight activity.

Materials and Methods

A quantitative survey of the larval populations was initiated in March of 1979, immediately following thaw of the winter ice cover. Three aquatic sampling stations were established along a transect running parallel to the southern shore of the study area (Fig. 1), and were permanently tagged with buoys. An airboat was used for transportation through the shallow water, to avoid disturbance of the upper 5 cm of bottom substrate, where 95% of the vertical distribution of chironomid larvae has been found to occur (Carter 1976; Mundie 1957). An Ekman dredge was employed as a sampling device to obtain 0.02 m^2 sections of mud, to an approximate depth of 7 cm. At each of the three stations, five samples were obtained, one from a central position at the buoy, and one taken 4–5 m from the buoy at each of the four cardinal directions. The sampling procedure consisted of first raising the sample from the bottom and immediately releasing the contents of the dredge into a bucket. The combined mud and water yield of each dredge sample was approximately four liters. The mud and water were whipped to a slurry, and a portion of the mixture funneled into a half-liter plastic container. The aliquots were transported to the laboratory for subsequent examination.

Larval sampling was conducted from early March through November. Collections were made on a semi-monthly basis in the spring and fall, and at weekly intervals during the summer. Environmental factors were monitored on each sampling date, including benthic mud and surface water temperatures, dissolved oxygen content, pH, and salinity of the water. Temperature measurements were taken with a mercury thermometer, and dissolved oxygen was determined in the field with a Hach kit.[3] A refractometer was used to ascertain salinity levels in ppt, and pH was periodically determined with commercially prepared indicator papers.[4] Daily sampling times were selected according to published tide tables, when water levels accommodated boat usage.

The larvae were separated from the mud slurry in the laboratory by rinsing each aliquot through a series of U.S. Standard Sieves, with screening ranging from 20 to 50 mesh. Head capsule width measurements were taken to determine the instar of the larvae (Ford 1959). Preliminary trial separations indicated that the first and second instars were often lost in the rinse water. Their recovery by flotation methods was inconsistent and hampered by

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[3] Model OX-10, Hach Chemical Co., Ames, Iowa.

[4] pHydrion Midget, Ward's, Rochester, New York.

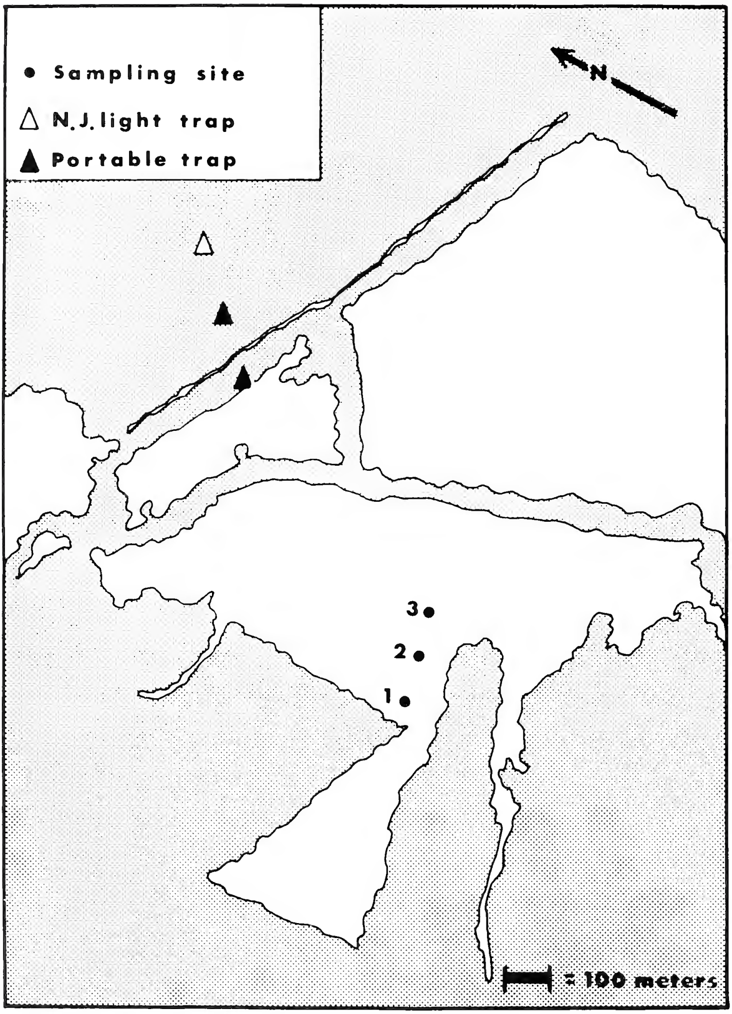

Fig. 1. Study site in the Hackensack Meadowlands, Bergen County, New Jersey, with locations of larval sampling stations and of adult traps (shaded, land; clear, water).

small detritus. Therefore, only third and fourth instar larval counts were used to assess population levels.

Light trap data gave an indication of seasonal adult emergence patterns. One New Jersey light trap, permanently established 600 m from the shore, was operated once weekly for a 24 hr period, from April to November. Two CDC portable traps were positioned closer to the shore, at 425 and 275 m distances. The portable traps were operated one evening a week, between 8:30 pm and 10:30 pm, from May to November. The time selected was based

Table 1. Head capsule width measurements for the four larval instars of *Chironomus decorus*, collected in the Hackensack Meadowlands, Bergen County, New Jersey.

	Head capsule width (mm)	
Instar	Range	Mean + C.I.
First	0.07–0.13	0.10 ± .0039
Second	0.14–0.20	0.17 ± .0029
Third	0.25–0.33	0.29 ± .0037
Fourth	0.40–0.61	0.50 ± .0108

upon a study (Ping 1917) reporting that peak flight activity of *C. decorus* occurs just after sunset. The weekly trap collections were synchronized with larval sampling dates, and the numbers of male and female adults were recorded.

Results

The range of head capsule width measurements for *C. decorus* was uniform for each instar (Table 1). As there was no overlapping of sizes, head capsule measurements were confirmed as a reliable means of determining the instar of field-collected larvae. The mean numbers of third and fourth instar larvae collected per 0.02 m^2 are presented on a weekly basis in Figure 2. The samples taken in early March contained only low levels of fourth instar larvae, and no individuals were detected in April. Third and fourth instar larvae suddenly appeared in May, and numbers increased as the summer progressed. A maximum density of 700 larvae per 0.02 m^2 was recorded in mid July. The population then declined in early August, and stabilized at comparatively low levels for the duration of the fall season.

Mean larval abundance per sample was different at the three stations (Site 1 = 208.6 ± 56.99; Site 2 = 180.5 ± 47.80; Site 3 = 141.4 ± 38.16), while the numbers of larvae collected from the five locations at any one station were statistically the same (5% level of significance). Duncan's multiple comparison test revealed that adjacent stations (1 and 2, 2 and 3) were the same, while larval numbers at stations 1 and 3 were significantly different. This indicates that a density gradient existed, with highest concentrations of larvae at station 1, and density decreasing toward station 3. The larval density gradient was accompanied by changes in substrate composition. Fine silt and ooze predominated at station 1, and shifted to a coarser mixture of muck and broken vegetation at station 3. Sublette (1957) and Whitsel et al. (1963) have also reported that *C. decorus* prefers to inhabit finer substrates.

Changes in the recorded environmental data reflected the seasonal time span of the investigation (Figure 3). Water temperatures gradually increased

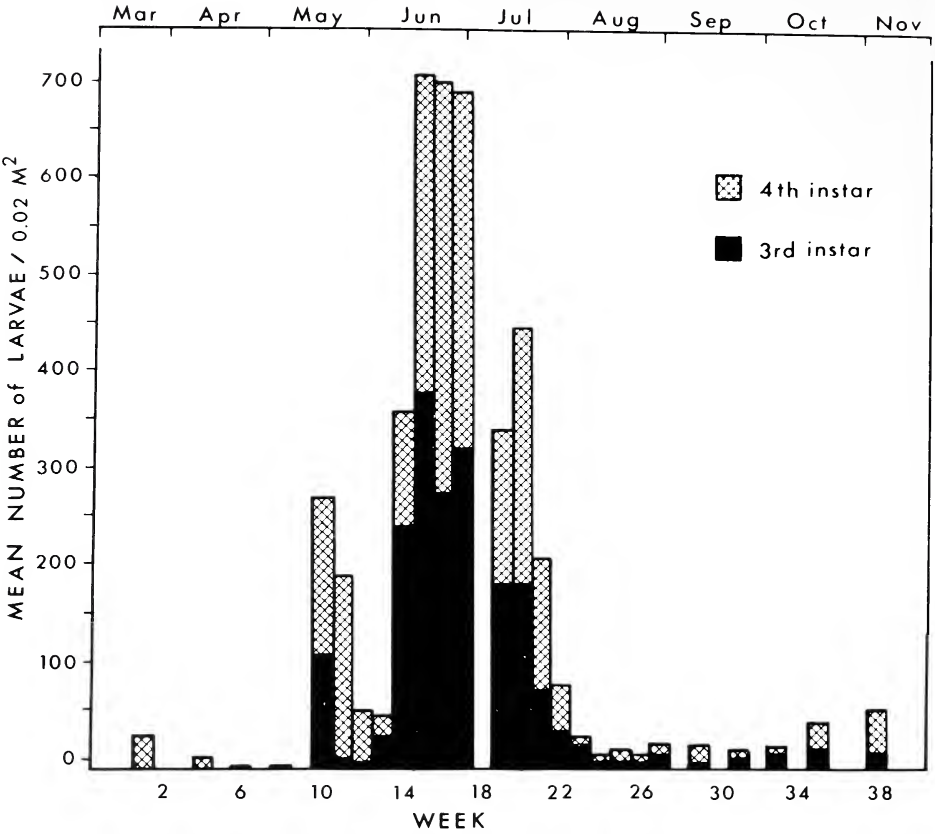

Fig. 2. Average number of third and fourth instar larvae of *C. decorus*, collected in the Hackensack Meadowlands, Bergen County, New Jersey, 1979.

from 6.5°C in early March, when larval numbers were lowest, to 24°C in May, when the larval population increased significantly. Throughout the summer months, temperatures oscillated from week to week, but exhibited an overall rising trend. A maximum of 33.5°C was attained in early August, when larval numbers began declining. Temperatures remained above freezing until late October. The dissolved oxygen content of the water was highest in early spring, when monitoring was initiated (12 ppm), and fell to relatively low levels (3–5 ppm) for the summer and fall seasons. The pH of the water was constant, between 6.8–7.0, throughout the study. The salinity of the water, during the spring precipitation period, was zero ppt. Salinity increased with the onset of dryer, warmer conditions, attaining a maximum of 13 ppt in August. Salinity readings averaged 9 ppt during the remainder of the season.

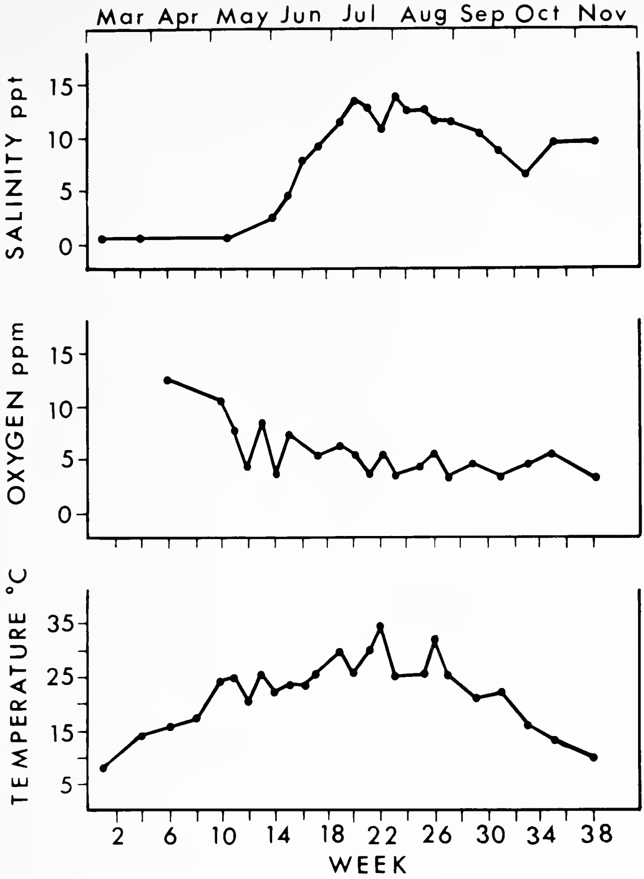

Fig. 3. Temperature, oxygen, and salinity levels recorded in the aquatic habitat of *C. decorus*, Hackensack Meadowlands, Bergen County, New Jersey, 1979.

The warm summer temperatures were accompanied by a proliferation of submergent vegetation, particularly the green algae *Cladophora* sp. and *Enteromorpha* sp. A vegetative mat had formed over the water surface by mid July. In late July the plant life rapidly diminished, and had nearly disappeared by mid August.

The numbers of adults collected from the N.J. light trap and the two portable traps are plotted on a logarithmic scale in Figure 4. The pattern of adult flight activity closely resembles the larval population trends. Adults were less active in the early spring and fall when lower temperatures prevailed, with emergence occurring primarily during June and July.

The use of different trap types prohibited averaging of data from the three trap locations, and limited statistical analysis. However, the overall fluc-

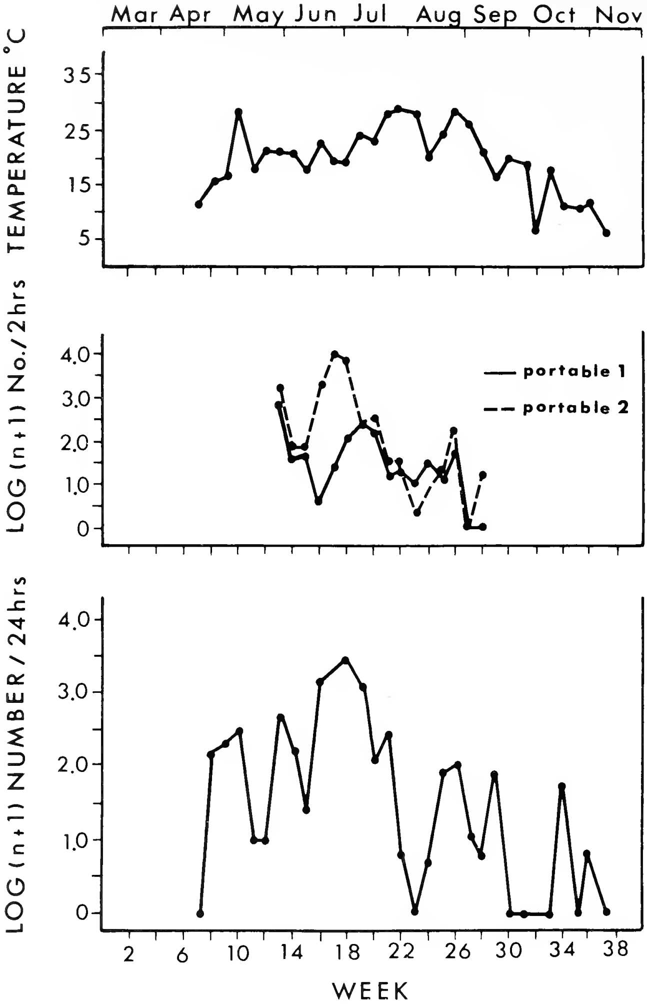

Fig. 4. Air temperatures and numbers of adult *C. decorus* collected in one N.J. light trap and two portable CDC traps, Hackensack Meadowlands, Bergen County, New Jersey, 1979.

tuations in abundance appeared similar among the three sets of data. The N.J. light trap and portable 2 exhibited the strongest correlation (Table 2), while the centrally located trap, portable 1, was weakly correlated with the other two traps. Males dominated the trap counts at portable 2, but the sex ratio became more equal with increasing distance from the shore.

Discussion

The population trend of *C. decorus* typifies that of an insect inhabiting a temperate region, where temperature is the dominant regulator of insect

Table 2. Adult *Chironomus decorus* collected during a 15 week period from three light traps located in the Hackensack Meadowlands, Bergen County, New Jersey.

Light trap	Distance from shore (meters)	Total adults	Sex ratio (M:F)	Correlation coefficient (R) with N.J. trap
New Jersey	600	8,324	1.8:1	
Portable 1	425	1,542	4.4:1	0.48
Portable 2	275	10,339	26.0:1	0.85

activity and population growth (Corbet 1964). A resumption of larval growth and development following thaw of the winter ice cover is considered a facultative developmental response to warmer temperatures (Oliver 1971). The disappearance of third and fourth instar larvae during April, and their reappearance in May, suggest a generation of individuals developing in synchrony. A more sensitive sampling technique might have detected the presence of first and second instar larvae during April. This generation was probably a consequence of an early initial spring emergence of the overwintering population (Oliver 1971).

The gradual rise in spring temperatures was accompanied by increases in the midge population. A sigmoid relationship between temperature and development has been demonstrated in some chironomid species (Biever 1967). A faster developmental time and shorter life cycle, in the presence of higher temperatures, appears likely for *C. decorus*.

The sudden decline in larval abundance, and accompanying drop in vegetative growth, occurred during a period in August when temperatures reached their highest levels. The temperature fluctuations within the habitat were probably more extreme on a daily basis than is indicated by the recorded data. Local wind and tidal effects reduced the water level at ebb tide to a few centimeters or less, exposing a great deal of the benthic mud surface. On a hot day, with ebb tide occurring at midday, the maximum daily temperatures attained would have been greater than those recorded during the high tide sampling situation. Temperature may have surpassed the tolerance levels of *C. decorus* and the aquatic life (Brauner 1979), and directly influenced survival.

Dense growths of algae and vegetation, such as were present in the study site, have been attributed with causing mid summer declines in chironomid populations (Bay and Anderson 1965). Plant respiration, and decomposition of an organic aggregate derived from the death of a large algal bloom, can reduce oxygen tension in the water (Cole 1975). Therefore, vegetation as well as temperature could have produced an oxygen deficit, detrimental to the larvae.

The variability in the number of adults collected by the three light traps was partially due to the use of different types of trap, and the length of the sampling interval for each type. Undefined differences in light trap efficiency, and local environmental factors, could have caused the weak correlation observed between the centrally located trap and the other two traps. The distance between the traps and the source would also be expected to affect the number of adults trapped. The decreasing male sex ratio in traps located further from the shore indicates that distance did influence light trap reliability to some extent. The male swarming behavior, in which assemblages form over stationary points (Downes 1969) may have limited dispersal of males. A differential flight ability between the sexes, where the female is the stronger flyer, would also result in fewer males reaching points further from the source.

The overwintering status of the study population in New Jersey was not clearly defined by the data collected. However, it was presumed that population growth of *C. decorus* was minimal after November, when larval sampling and adult trapping were discontinued. Previous research has indicated that populations of chironomids, located in temperate regions, generally overwinter as larvae in a state of suspended growth and development (Oliver 1971). Laboratory reared larvae, of a species closely related to *C. decorus,* ceased feeding and became inactive at temperatures of 50°F (10°C) or lower (Biever 1967). Adults become lethargic at 5°C or lower (Ping 1917).

The number of generations completed by *C. decorus* can be estimated by counting the number of apparent peaks in larval abundance and adult flight activity. Highest levels were attained at points in mid May, June, July, August, September, and late October. As the season progressed, and generations began overlapping, the peaks were less distinct and more difficult to distinguish. Five to six generations may have been completed by *C. decorus* in northern New Jersey, during the 1979 reproductive season. This finding is similar to that of Ping (1917) for a source located in Ithaca, New York.

Summary and Conclusions

Data obtained from larval sampling and trapping of adults indicated that the highest levels of *C. decorus* were attained in midsummer, 1979. Abundance during the spring and fall seasons was relatively low, apparently being regulated by environmental factors. The initial rise in spring temperatures resulted in a resumption of larval growth and development, and emergence of overwintering individuals. Population accrual continued to accompany rising temperatures throughout the summer, with the highest numbers occurring in July. A sudden drop in larval abundance in late summer may have been a result of extreme temperatures. In terms of nuisance potential, emergent adults reached peak levels during a limited interval of the reproductive season. Larval and adult data indicated that *C. decorus* can complete 5–6 generations in this habitat in a single year.

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PIT CONSTRUCTION BY ANTLION LARVAE: INFLUENCES OF SOIL ILLUMINATION AND SOIL TEMPERATURE

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Abstract.—Pits constructed by antlion larvae are most frequently found in areas which are darker and cooler than areas exposed to the sun. Soil illumination and soil temperature, therefore, are two factors which may play a role in determining the probability of pit construction. The influence of these factors upon the probability of pit construction by *M. immaculatus* larvae was examined. Soil illumination and soil temperature were independently varied in the laboratory. Soil temperature was found to have a significant effect upon pit construction, whereas soil illumination was found to have no such significant effect. This supports the view that the construction of pits in shaded areas is a response to temperature rather than to light.

Antlions of the genus *Myrmeleon* are best known for the ability of their larvae to construct inverted conical pits in dry, loose, fine grained soil. These pits provide the antlion larva with an effective means of capturing prey (Topoff 1977; Turner 1915). It has been frequently observed that antlion larvae begin constructing pits at, or immediately following sundown (Haub 1942; Topoff 1977; Wheeler 1930; Youthed and Moran 1969b). It has also been observed that antlion pits are usually found in shaded areas such as under ledges of rock, under logs which do not touch the ground at all points or under man made sources of shade (Green 1955; Haub 1942; Topoff 1977; Turner 1915). Shaded areas differ from areas exposed to the sun in two obvious respects; they are darker and they are cooler. These two characteristics also apply to any given area at or after sundown, when it is compared to the same area during the day. It therefore appears that soil illumination and soil temperature are two physical properties of the environment which may play a role in determining the probability of pit construction by antlion larvae.

In a series of laboratory experiments using larvae of *Myrmeleon immaculatus* (De Geer), Haub (1942) demonstrated that soil temperature does indeed influence the probability of pit construction. A similar result was demonstrated by Youthed and Moran (1969a) for larvae of *M. obscurus*

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(Rambur). Haub (1942) concluded that, "the building of pits after sundown is due to a temperature factor rather than light" (p. 116). However, he did not provide evidence to warrant the exclusion of light as a factor controlling the probability of pit building.

Antlion larvae appear to be well equipped to respond to light. Wheeler (1930) noted that the larvae possess seven eyes on each side of the head which appear to be transitional between ocelli and compound eyes. These eyes point in all directions except backwards. Behavioral responsiveness of antlion larvae to light has been reported. For example, Turner (1915) has demonstrated negative phototaxis in *M. immaculatus* and Comes (1909) found a similar result for *M. formicarius*.

Given the ability of antlion larvae to respond to light, the experiment discussed below attempts to determine whether the level of soil illumination influences the probability of pit construction by *M. immaculatus* larvae. In short, the study tests the validity of Haub's (1942) contention regarding the lack of control of light over pit construction. The study also attempts to replicate the findings of Haub (1942) and Youthed and Moran (1969b) regarding the influence of soil temperature upon probability of pit construction.

Materials and Methods

Forty-seven *M. immaculatus* larvae were used. All larvae were collected from the bank of a creek near the Southwestern Research Station of the American Museum of Natural History in southeastern Arizona. Only larvae found at the bottom of pits were used in the study. This insured that all antlion larvae used were capable of building pits under normal field conditions.

The experiment proper was carried out in an International Radiant Co. humidity chamber (Model H15) in which temperature and relative humidity could be independently regulated and thermostatically controlled. The chamber window was covered with cardboard to prevent ambient light from entering. Within the chamber, larvae were placed in one of two white plastic containers filled with 6 cm of dry silt. Each container was divided into two 11 × 16 cm compartments by a piece of cardboard and only one larva was placed in a compartment. Therefore, 4 larvae could be tested in each experimental session. A 75 W light bulb was used to illuminate the chamber in the high illuminance condition of the experiment and a 15 W bulb covered by a red translucent piece of plastic was used in the low illuminance condition. A Gossin Lumasix light meter was used to measure the illuminance at the silt surfaces within the chamber. Petri dishes containing 0.5 cm of dry silt were used to store the larvae between the time of collection and the time of testing.

The 4 larvae and the silt in which they were to be tested were collected 3 h prior to each session. This was the approximate amount of time needed for the silt to reach its desired temperature after being placed in the environmental chamber. During this 3 h period, the larvae were stored in a shaded area of the laboratory. The experiment was run as a 2 × 2 factorial design with 2 temperature levels (hot and cool) and 2 illumination levels (light and dark). Therefore, 4 different experimental conditions were used: (1) hot-light, (2) hot-dark, (3) cool-light and (4) cool-dark. Each experimental condition was run 3 times, making a total of 12 test sessions, and each session lasted 3 h. All testing was done between 1200 and 2200 h (MST). Each time a condition was repeated, it was run at one of 3 different times during the day: early afternoon, late afternoon or evening. These periods often overlapped by as much as 1 h. A total of 12 larvae were tested under each experimental condition, except that due to the death of one larva, only 11 were tested under the hot-light condition. The silt temperature was checked at the beginning and the end of each test session. Silt temperatures in the hot conditions ranged from 38–47°C whereas temperatures in the cool conditions ranged from 20–24°C. The measured silt surface illuminance was 1,076 lx in the light conditions and 86 lx in the dark conditions. At the beginning of each test session, one larva was placed on the surface of each silt compartment within the environmental chamber. Three hours later, each compartment was checked for pit construction. A larva was scored positive for pit construction if: (1) a pit existed in its compartment, or (2) the larva was in the process of pit construction and had dug out more than one concentric circle. Larvae which were not scored positive for pit construction were placed in a box of silt and checked for pit construction 24 h later. All these larvae built pits and this ruled out physical damage during the experiment as a reason for lack of pit construction.

Results

The mean percentage of larvae constructing pits, per session, was determined for each condition of the experiment. The greatest amount of pit construction occurred in the cool-dark condition (58.3%), followed in descending order by the cool-light condition (41.7%), the hot-light condition (11.0%) and the hot-dark condition (8.3%). The mean percentage of larvae constructing pits was 9.7% per session under the hot temperature level as compared with 50.0% per session under the cool temperature level. Under the light illumination level, the mean percentage of larvae constructing pits was 26.3% per session as compared with 33.3% per session under the dark illumination level. A two-way ANOVA in conjunction with the arcsine transformation for percentage data revealed a significant difference between the two temperature levels ($F = 9.16$, df = 1,8, $P < 0.025$). No significant difference was found between the two illumination levels (F = 0.30, df = 1,8, $P > 0.05$) nor was any significant interaction found between temperature and illumination (F = 0.48, df = 1,8, $P > 0.05$).

The overlap of the early afternoon, late afternoon and evening replicates within each condition prevented the inclusion of time of day as a separate factor in the design. However, since the early afternoon and evening time periods never overlapped, differences in pit building activity during these two time periods were examined. The mean percentage of larvae constructing pits was 12.5% per session during the early afternoon time period (1230 to 1530 h) and 39.5% per session during the evening time period (1835 to 2200 h). A single classification ANOVA in conjunction with the arcsine transformation for percentage data revealed a significant difference between the two time periods (F = 6.34, df = 1,6, $P < 0.05$).

Discussion

The finding that the greatest amount of pit building took place under the cool-dark condition is consistent with field observations that antlion larvae frequently build pits in areas that are darker and cooler than nearby areas exposed to the sun (Green 1955; Haub 1942; Turner 1915). The significant difference in pit building behavior between the two temperature levels (hot and cool) supports the finding of Haub (1942) that soil temperature can influence the probability of pit construction in *M. immaculatus* larvae. It is interesting to note that Haub found no pit construction above 28°C and 100% mortality above 38°C. This did not appear to be the case in the present study since pit construction occurred at temperatures as high as 44°C and only one out of 24 larvae died within a temperature range of 38–47°C. It seems that larvae in the present study were better able to withstand and function at high temperatures than the larvae used by Haub. Although both studies employ *M. immaculatus* larvae, those used in the present study were collected in Arizona whereas those used by Haub were collected in Ohio. A comparison of summer soil temperatures measured in the field suggests that this seemingly greater tolerance for high temperatures by Arizona *M. immaculatus* larvae may represent a regional adaptation to higher temperature extremes than those encountered by Ohio *M. immaculatus* larvae.

The absence of a significant difference in pit building behavior between the two illumination levels (light and dark) supports the view that the construction of pits after sundown or in shaded areas is a response to temperature rather than to light. In other words, frequent construction of pits in cool, dark areas is probably a response to coolness as opposed to darkness. The absence of an influence of illumination level upon pit building probability was most likely not due to an inability of the larvae to discriminate between the illumination levels used since Youthed and Moran (1969b) found that antlion larvae (*M. obscurus*) can discriminate between illumination levels similar to those used in the present study.

The significant difference in pit building activity found between the early afternoon and evening time periods seems to indicate endogenous temporal variation in pit building since external conditions were the same during both periods. This would be in agreement with findings of Youthed and Moran (1969b) who demonstrated an endogenous circadian pit building rhythm in *M. obscurus* larvae. Pit building in *M. immaculatus* larvae therefore appears to be under the control of internal as well as external factors.

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SUSCEPTIBILITY OF KENTUCKY BLUEGRASS CULTIVARS AND SELECTIONS TO INFESTATIONS OF AND INJURY BY THE BLUEGRASS BILLBUG (COLEOPTERA: CURCULIONIDAE)

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Abstract.—Nine cultivars and selections of the Kentucky bluegrass, *Poa pratensis* L., were examined for susceptibility to a natural infestation of the larvae of the bluegrass billbug, *Sphenophorus parvulus* Gyllenhal. There was a significant correlation ($r = 0.767$, $df = 7$, $P < 0.05$) between larval infestations and percent damage to the bluegrasses. 'Kenblue' was among the least damaged entries and had minimal infestation. This established cultivar is characterized by narrow leaves, an upright (taller) posture, and high susceptibility to the leaf spot and melting-out disease incited by *Drechslera poae* (Baudys) Shoem. The other cultivars and selections had broader leaves, lower growth, and showed less disease damage. Possibly, these characteristics render these other bluegrasses more apparent than Kenblue and, thereby, are preferred over Kenblue for oviposition by the adult billbugs.

Introduction

The bluegrass billbug, *Sphenophorus parvulus* Gyllenhal, often causes damage to Kentucky bluegrass, *Poa pratensis* L., which is widely used as a turf and pasture grass in the northcentral and northeastern U.S. The damage caused by this pest is particularly severe in Nebraska (Kindler and Kinbacher 1975). In 1978, a natural infestation of bluegrass billbugs in the turfgrass plots at the N.J. Agric. Exp. Stn. Res. Ctr. at Adelphia, N.J., provided an opportunity to assess the relative susceptibility of 9 Kentucky bluegrass cultivars and selections. The data provided a partial test for the earlier observations of Kindler and Kinbacher (1975), and 1979 observations of Lindgren et al. (1981) that suggested differential reaction of Kentucky bluegrass cultivars to the bluegrass billbug.

Methods

The various cultivars and experimental selections of Kentucky bluegrass were seeded in a replicated test at Adelphia, during September 1974. The test site was on a loamy sand. Plot size was 1.22 × 1.83 m with a 0.15 m unplanted border between each plot. The grass was mowed at 3.8 cm during the fall of establishment but lowered to 1.9 cm thereafter. Weeds were controlled, as needed, with DCPA, dicamba, and 2,4-D. Soil was limed to maintain a pH of 6.0. The test was irrigated as needed for rapid establishment, and later, to prevent severe drought stress. Two nitrogen fertilizer levels (1.7 and 3.2 kg/92.94 m^2) were established on each plot during the 1974–78 period. The fertility level appeared to have little, if any, effect on bluegrass damage.

During the 2nd week of July 1978, there was evidence of differential damage to the various cultivar plots, and an initial observation showed that the damage to the Kentucky bluegrass was primarily due to the larvae of the bluegrass billbug. Populations of other coleopterous pests such as the Japanese beetle, *Popillia japonica* Newman, northern masked chafer *Cyclocephala borealis* Arrow, European chafer *Rhizotrogus majalis* (Razoumowsky), and black turfgrass ataenius *Ataenius spretulus* (Hald.) that are also serious pests of turfgrasses in northeastern region (Tashiro 1973), were not present in the turfgrass plots at levels that would cause significant damage. During the 3rd week of July, the plots were examined for billbug infestations and extent of injury.

The infestations were quantified by two separate determinations, each with two replicates, and each sample covering 0.09 m^2 of turfgrass in each cultivar plot. The larvae were examined and counted by laying back the sod with sharp knife and removing and examining the sod and soil to a depth of 4 cm. The damage to cultivars was visually assessed twice on the basis of percent damage (0, 10, 20, . . . , 100); the observations were repeated 2 more times, providing 6 determinations for each cultivar and selection. Each observation of injury was carried out by a different observer to minimize potential error inherent in this procedure if left entirely to the judgement of a single individual.

The data on larval counts (4 determinations), and percent injury to cultivars (6 determinations) were pooled to obtain mean values and for statistical analysis to establish significant differences among the sample means. The data also were analyzed for correlation between larval counts and damage to bluegrass cultivars and selections.

Results and Discussion

Table 1 presents data on damage to Kentucky bluegrass cultivars and selections and mean numbers (per 0.09 m^2) of billbug larvae responsible for the damage. The counts of billbug larvae ranged from a low of 1.3/0.09 m^2 for 'Kenblue' to a high of 60.3/0.09 m^2, for 'Nugget.' Low damage, ca. 25 to 27%, was recorded on Kenblue, 'F 1757,' and 'F 353.' The entries showing high damage, over 80%, were Nugget, 'Cheri,' and 'K3-182.'

A significant correlation coefficient ($r = 0.767$, $df = 7$, $P < 0.05$) was found between the larval counts and the damage to the bluegrasses. Since one selection, K3-182, was exceptional in that despite low larval counts (18.5/0.09 m^2) it was most severely damaged (87%), it was of interest to

Table 1. Susceptibility of Kentucky bluegrass cultivars to damage by the bluegrass billbug in turfgrass trials during September 1978 at Adelphia, N.J.

Bluegrass cultivar or selection	$\bar{x}$ percent turfgrass damage[1]	$\bar{x}$ number of billbug larvae per 0.09 m^2[2]
Kenblue	27.4 a	1.3 a
F 1757	24.7 a	12.3 b
F 353	26.7 a	13.0 b
Princeton 104	39.1 a	14.8 b
Baron	67.8 b	51.0 c
Merion	76.0 b	57.8 c
Nugget	82.4 b	60.3 c
Cheri	83.5 b	45.3 c
K3-182	87.0 b	18.5 b

[1] Assessment based on 3 separate observations, each with 2 replicates; N = 6. Means not followed by the same letter are significantly different at 5% level by Duncan's multiple range test.

[2] Based on 2 separate observations, each with 2 replicates; N = 4. Area of each sample (replicate) = 0.09 m^2. Means not followed by the same letter are significantly different at 5% level by Duncan's multiple range test.

evaluate the correlation coefficient by deleting this selection from data analysis. Analyzed in this way the correlation coefficient was even more highly significant ($r = 0.950$, $df = 6$, $P < 0.01$). Although we have no explanation to account for the extensive damage of K3-182, inasmuch as the data analysis with or without inclusion of this cultivar provided a significant correlation coefficient, the observations of Kindler and Kinbacher (1975) and Lindgren et al. (1981) were reaffirmed. Moreover, in the study of the differential reaction of Kentucky bluegrass cultivars to the bluegrass billbug by Kindler and Kinbacher (1975), the relationship was established with 15 cultivars; we had 9 entries in the present study, with 'Merion' and Nugget being common to both studies. Lindgren et al. (1981) in their 1979 study had included 38 cultivars, only 3 cultivars, Merion, Nugget, and 'Baron' being common to the present study.

The cause(s) for the differential larval density and susceptibility of the Kentucky bluegrass cultivars to the billbugs is a matter of speculation at this time. Of all the entries in the test, Kenblue is an established cultivar characterized as upright (taller) and narrow-leafed. Moreover, this variety is highly susceptible to leaf spot and melting-out disease (caused by *Drechslera poae*). The main purpose of the other entries, was to select Kentucky bluegrass for resistance to this disease. This selection however generally resulted in broader leaves and lower growth, relative to Kenblue. It may well be that these qualities render these selections more apparent and, also, as more suitable substrates for oviposition by the adult bluegrass billbugs.

More research is clearly necessary to determine the nature of resistance and the underlying mechanisms. Potentially this kind of information would be valuable for developing improved billbug resistant cultivars.

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NOTES ON THE NATURAL HISTORY OF *MORPHO GRANADENSIS POLYBAPTUS* BUTLER (LEPIDOPTERA: NYMPHALIDAE: MORPHINAE), AND ITS RELATION TO THAT OF *MORPHO PELEIDES LIMPIDA* BUTLER

Allen M. Young

Abstract.—Various aspects of the natural history of the Neotropical butterfly *Morpho granadensis polybaptus* Butler (Lepidoptera: Nymphalidae: Morphinae) in a zone of geographical overlap with *M. peleides limpida* Butler in Costa Rica are reported for the first time. The work reported is part of a long-range study on the comparative natural history of Central American *Morpho,* represented in Costa Rica by at least five valid species. Of particular interest is the comparison of *M. granadensis* with *M. peleides* since both species are closely related forms in the South American *achilles* "superspecies" complex. *Morpho granadensis* is exceedingly rare in museum collections and the type specimen is from Costa Rica. The species is narrowly restricted in Costa Rica to a band of tropical rain forest within about 100 to 600 meters elevation along the Caribbean watershed of the Cordillera Central and adjacent highlands. The early stages are strikingly similar to those of *M. peleides,* including various aspects of caterpillar behavior. Oviposition is single. Although the caterpillars are legume-feeders, either the scope of food plant suitability is narrower or different between this species and *M. peleides,* since the former cannot survive on at least one common food plant (*Mucuna urens*) of the latter. *Morpho peleides* has a much wider geographical range that *M. granadensis,* and probably utilizes a greater range of food plants. The species is also sympatric with *M. amathonte* Deyrolle; baiting studies indicate that *M. granadensis* is about half as abundant as the other two species. A model for further comparative study of the two species is presented.

Introduction

Some of the seminal papers on the life cycles and natural history of various species of *Morpho* butterflies (Lepidoptera: Nymphalidae: Morphinae) in Central America have appeared recently on the pages of this journal (e.g., Young 1972a; Young and Muyshondt 1972a) and elsewhere (Young 1971a, b, 1972b, 1973, 1974, 1975a, b, 1978b, 1979, 1980a; Young and Muyshondt 1972b, 1973; Young and Thomason 1974). As part of a long-range goal of studying the biology of all Central American species of this widespread

Neotropical genus, field studies were conducted on *Morpho granadensis polybaptus* Butler in northeastern Costa Rica, in a region where this species and another one of the *achilles* "superspecies," *Morpho peleides limpida* Butler, are sympatric. Of particular interest is the study of *M. granadensis polybaptus* in Costa Rica, the site of the type specimen for this species (Seitz 1924). This paper reports the first description of the early stages and larval food plant association for this species, and compares these attributes and others with previously reported data on *M. peleides* from Costa Rica (Young and Muyshondt 1973; Young 1972a, b, 1978b; and other papers). Because adults of both species are very similar (Fig. 1), and one species (*peleides*) is far more abundant than the other in zones of geographical overlap, studies on the comparative natural history of these forms is of particular interest, in the context of recent discussions of ecological mechanisms of environmental exploitation among closely related sympatric species (e.g., see MacArthur 1972).

The major findings of this paper are the following: (1) the early stages of *M. granadensis* are strikingly similar morphologically and behaviorally to those of *M. peleides,* (2) one larval food plant of *M. granadensis,* the woody vine *Machaerium seemannii* (Leguminosae) is also one of several leguminous larval food plants of *M. peleides* in this region (Young and Muyshondt 1973) but caterpillars of *M. granadensis* die in early instars when reared on several of these other plant species, suggesting a narrower range of food plants in *M. granadensis,* (3) the egg-to-adult developmental times are very similar in both species, (4) overall average egg production is probably much lower in *M. granadensis* as captive females are less prone to oviposit and lay fewer eggs when they do, and (5) *M. granadensis* has a relatively restricted distribution within a narrow band of Caribbean watershed tropical rain forest within about 100 to 600 meters elevation, while *M. peleides* is far more catholic in its distribution throughout the whole country. Furthermore, *M. granadensis,* although very similar in habitat association and natural history to *M. peleides,* is probably not as abundant locally as the latter. Along with *M. amathonte* Deyrolle, both species readily come to bait (rotten bananas) although sex ratios are invariably skewed towards males (see also Young 1974, 1975a; Young and Thomason 1974; Young 1972a). Based on this study and several previous ones (as cited above), a general model for ecological segregation in zones of sympatry among the five species of *Morpho* in Costa Rica is presented as a testable set of hypotheses for further study.

Methods

Morpho granadensis was studied at "Finca La Tigra," a locality within the premontane tropical wet forest zone of northeastern Costa Rica, and

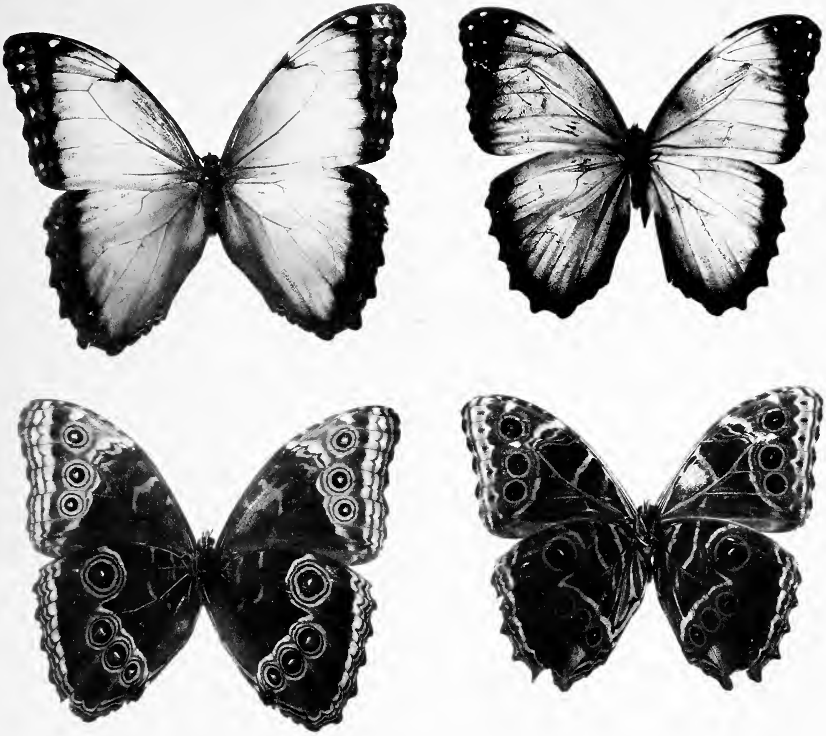

Fig. 1. Dorsal and ventral aspects of *Morpho peleides limpida* (left column) and *M. granadensis polybaptus* from northeastern Costa Rica. Specimens part of reared and wild-caught series in the collections of the Milwaukee Public Museum.

about 10 km east of La Virgen (10°23′N, 84°07′W; about 220 m elev.), Heredia Province. This locality is about 15 km west of the site where I originally found *M. granadensis* (Young 1972a), the first known collection of this species since its original discovery in Costa Rica in 1904 (specimen in the Allyn Museum, a male, collected by A. Hall, at "Castillo"). This original locality is probably Castilla (10°43′N, 85°25′W). Through baiting (with rotten bananas) within the mixed primary-secondary tropical rain forest at La Tigra (Fig. 2), it was possible to obtain a new series of specimens and mated females. Collecting of new material was kept to an absolute minimum. Periodically between 1977 and 1981, I baited *M. granadensis,* along with *M. peleides* and *M. amathonte* within an approximately 2,000 square-meter plot of forest, placing three piles of rotting bananas at scat-

Fig. 2. View through the light-gap associated with the plot of mixed primary and secondary premontane tropical rain forest at "Finca La Tigra" in northeastern Costa Rica where *Morpho* butterflies were baited with rotten bananas over several years. Adults of at least three species (see text) occur in this habitat. It borders on a cacao plantation created largely by "tunnelling" of advanced secondary forest to allow room for cacao trees.

tered places along two different foot paths within this area. Baits were always placed at the same places as I was interested in estimating the relative abundance of the three species in various months at this somewhat seasonal (although very irregular) locality (Fig. 3). The baiting also provided fecundated females from which to obtain fertile ova for rearing studies. I did not attempt to make a thorough study of abundance and temporal distribution on a daily basis (e.g., Young 1972a), but rather only collected or observed butterflies at baits whenever possible.

I used the bagging method described earlier (Young 1978b; Young and Muyshondt 1973) to rear caterpillars. Generally I obtained fertile ova by confining a freshly-caught female in a large clear plastic bag containing fresh cuttings of various suspected leguminous food plants (candidates taken from the list generated in Young and Muyshondt 1973 for *M. peleides*) and keeping each bag tightly closed. In this manner butterflies were kept for one to three weeks, during which each was fed daily outside the bag with rotten bananas. The cuttings were replaced as needed, fresh ones sprayed with water, and eggs removed at regular intervals. With *Morpho,* this technique is very successful. I deliberately tested samples of first instar larvae within

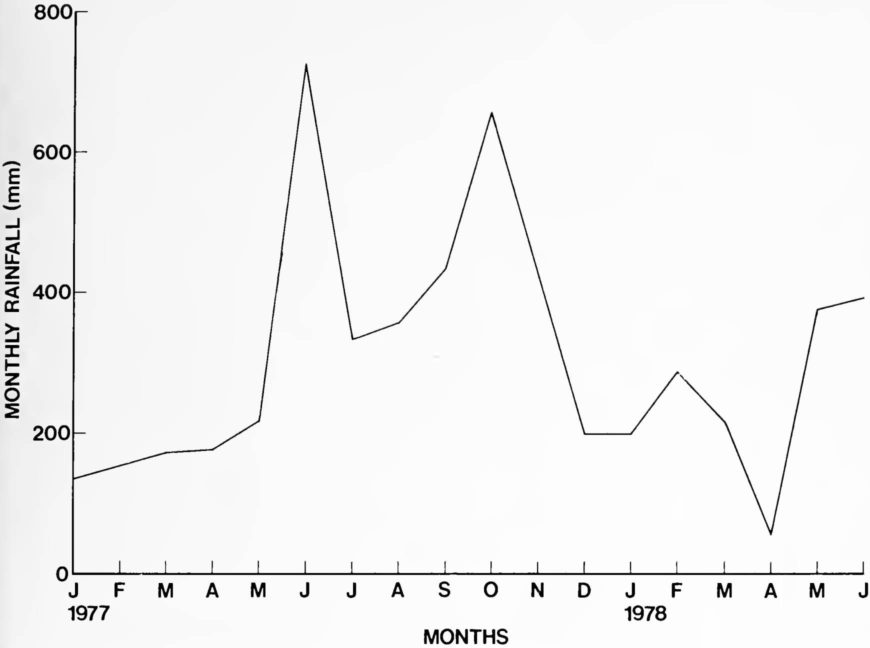

Fig. 3. A typical pattern of rainfall during which some of the studies were made at Finca La Tigra. Note the general depression of rain during January, February and March, and a second, less lengthy dip in April. This pattern is fairly typical over a run of several successive years.

each batch of eggs obtained in this manner on different suspected larval food plants, with an emphasis on comparing larval performance (survival, growth rates) on two major food plants of *M. peleides, Mucuna urens* and *Machaerium seemannii,* both stout woody legume vines associated with forest-edge and secondary habitats (see Young and Muyshondt 1973) in Costa Rica. I also obtained a third-instar larva of *M. granadensis* (determined to be this species from rearing to adult stage) from Philip J. DeVries, who found it on a small "trailside" seedling of *M. seemannii* at "Carillo" (San Jose Province, 600 m elev.). This discovery by Mr. DeVries constituted the only wild record of the species on a particular food plant, as all of my information on life cycle was generated by the rearing of larvae from ova obtained from captive females. Whenever possible, I reared *M. peleides* simultaneously with *M. granadensis,* and using the same food plant material. Because both species are closely related in the *achilles* Linnaeus "superspecies" complex of South America (see Young 1974), I suspected overlap in larval food plants when these rearing tests were initiated.

Additional material was reared independently by Philip J. DeVries, using eggs or larvae collected either at Carillo or "Finca La Selva," the site of my original field study on the adults of this species and others (Young 1972a). In addition to the three species mentioned thus far, two others, *M. theseus* Deyr. and *M. cypris* Westw., are also found at the La Tigra locality. The locality has been the site for studies on the natural history of other forest-associated day-flying Rhopalocera (e.g., Young 1977, 1978a, 1980b).

Results

Distribution

Based upon my own observations in Costa Rica (1968–81) and those of Philip J. DeVries (several pers. comms.), *M. granadensis* is probably distributed within a relatively narrow band of tropical rain forest along the Caribbean watershed of the Cordillera Central, between 100 and 600 meters above sea level. Because specimens of this form are exceedingly rare in museum collections throughout the world, there are few data available on distribution. In Costa Rica, the species is associated with the "Carrillo belt" (see DeVries 1980), extending to the north slopes of the Poas volcano and south to the Reventazon River Valley. Populations probably follow the series of ridges along this imaginary transect. It is probably not found in the lowland coastal areas of the Caribbean watershed and it is absent from the Pacific side of the country, even where tropical rain forest is well developed (e.g., Corcovado National Park on the Osa Peninsula). In contrast, *M. peleides* is widely distributed in several major climatic zones of Costa Rica (Young and Muyshondt 1973; Young and Thomason 1974) and it is one of the most widely distributed species throughout much of Central America, not to mention the broad distribution of related forms in South America (Seitz 1924). Unlike *M. granadensis,* specimens of *M. peleides* from specific localities exhibit considerable marked variation in the markings on the undersides of the wings (A. M. Young pers. obs.). Such variation is often associated with a single batch of eggs (pers. data). The extreme variation in wing markings and coloration in this species has been emphasized (Seitz 1924) and it exists both within and between populations. *Morpho granadensis* has a much more restricted geographical distribution in southern Central America and northern South America (Seitz 1924) and specimens generally lack, in my experience, the marked phenotypic variation so prevalent in *M. peleides.* Further field study in Central America should focus upon the determination of distribution boundaries of *M. granadensis,* suspected to include Nicaragua and Panama (Seitz 1924). The several specimens I have reared over the past four years match very well the two male specimens in the Allyn Museum collection (the forementioned specimen from A. Hall and that of W. J. Kaye, collected at "Pejeballe" in 1926).

Early Stages

The early stages are very similar to those of *M. peleides* (see Young and Muyshondt 1973). Detailed taxonomic separation and a key to early stages in these species and other is awaiting completion of life cycle studies of all Central American species. A good series of eggs and caterpillars for *M. granadensis* and *M. peleides* is available with the author. Some general features are described here. The egg is green and within two days after being deposited, develops a lateral reddish-brown band (Fig. 4). Unlike that of *M. peleides,* this band is distinctly broken into small dots (Fig. 4). But at Corcovado National Park in southwestern Costa Rica, the egg band of *M. peleides* is also broken (P. J. DeVries pers. comm.). Egg hatches in 16 days and first instar is yellow and red (Fig. 4). The second instar (Fig. 4) is similarly patterned but with a marked change in the distribution, coloration, and sizes of setae. For example, distinct rows of long white setae appear at the posterior margins of the second and third thoracic segments (Fig. 4). Setae generally black and evenly distributed on most body segments in the first instar. The second instar develops a set of dorso-lateral groupings of long, filamentous red and white setae on the posterior five abdominal segments, and all body segments have long, whitish lateral setae as well (Fig. 4).

The first instar head capsule of *M. granadensis* possesses a greater number of setae than does that of *M. peleides* (Fig. 5). The medial edge of the mandible in *M. granadensis* (first instars) possesses relatively short protuberances compared to that of *M. peleides* (Fig. 5). The cuticle over most of the head capsule in *M. granadensis,* and exemplified by the area just above the ocelli region, is finely studded with many small protuberances while that of *M. peleides* is relatively smooth (Fig. 6). These micromorphological distinctions in the head capsule appear to be very consistent in separating the first instar caterpillars of these two species.

The third instar is very similar to the second instar, but with further shortening of head capsule setae in the former (Fig. 7). Early instars generally rest on leaves of *Machaerium seemanii* when not feeding (Fig. 7). As in *M. peleides* (Young and Muyshondt 1973), there is a major change in the coloration of the caterpillar in the fourth instar (Fig. 7). The caterpillar becomes shaded in rich hues of brown, pink, and white. There is further reduction and coalescence of setae into sets of distinct tufts (Fig. 7) and the caterpillar generally rests on woody stems of *M. seemanii* when not feeding. The fifth instar is similar to the fourth, but with colors becoming more bland and setae reduced in size. Prior to developing into a highly mobile green prepupa of contracted size, the caterpillar attains a length of about 100 mm and maximal width (laterally) of about 20 mm. The caterpillar stage, as measured on a total of 16 individuals reared, lasts 89–96 days. These estimates may

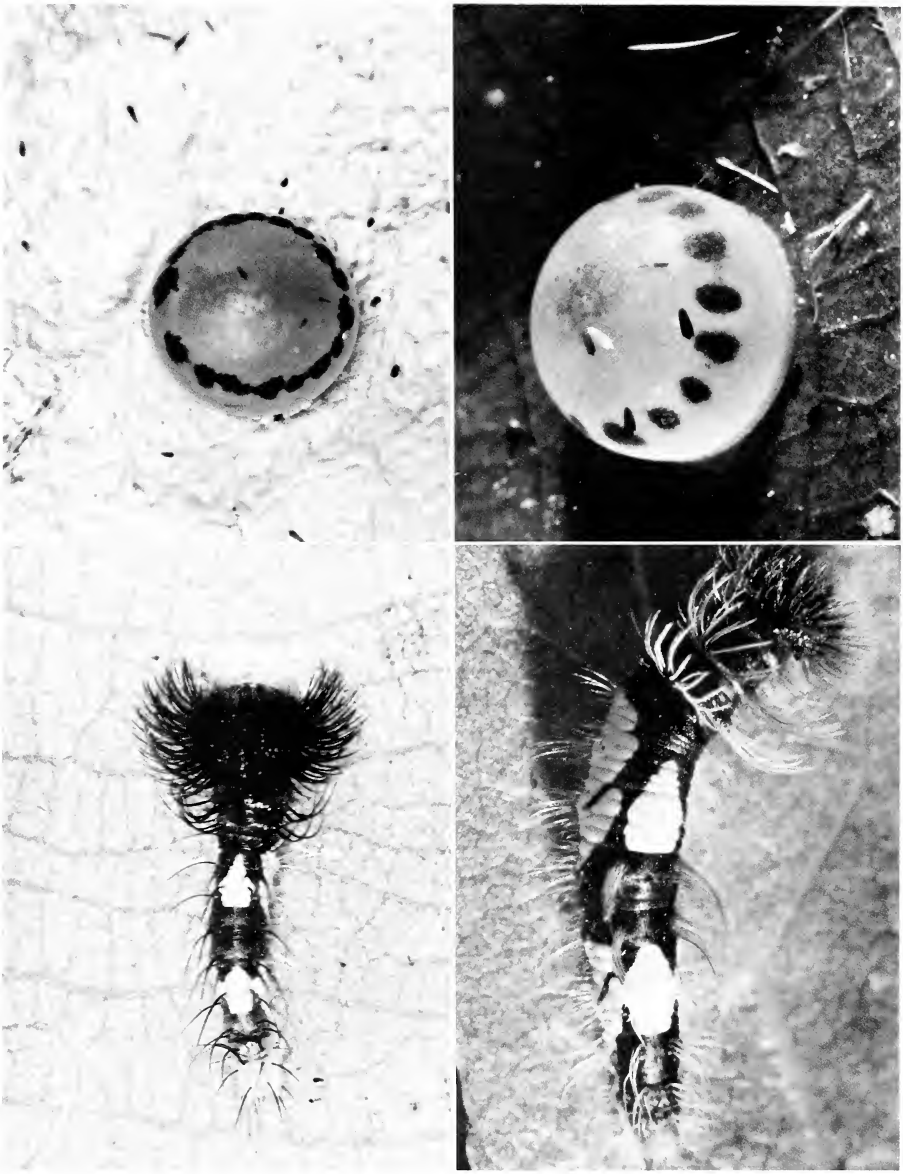

Fig. 4. Early stages of *Morpho granadensis*. Top: egg; note broken "ring" of brownish pigmentation of the hemispherical green egg (about 1.8 mm dia.). Bottom, left to right: first and second instar caterpillars respectively.

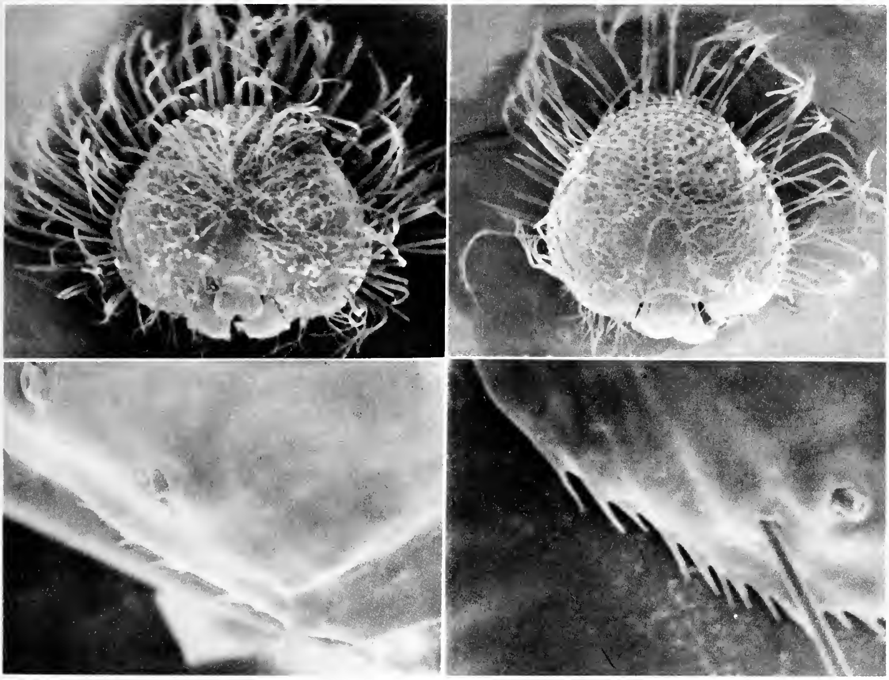

Fig. 5. Some micromorphological differences between the first instar caterpillars of *M. granadensis* and *M. peleides*. Left column: head capsule (SEM, 20× mag.) and right mandible (1,000× mag.) for *M. granadensis*. Right column, same structures and magnifications, but for *M. peleides*. Preparations and SEM work by R. Wolff.

have relatively little biological significance since caterpillars were often transported around considerably while being reared, and therefore subject to different environmental conditions.

The pupa (Fig. 7) is uniformly green with a pinkish-brown cremaster. It is 34–38 mm long and with a maximal dorso-ventral width of 15.5 mm and lateral width of 16.5 mm. Three prominent spiracles adjacent to the wing pads are white, while others are much smaller and pinkish. The marked protuberances of the head region are deep brown or black. The pupa stage lasts about 24 days. Eclosion is extremely rapid, with the wings fully expanded within one hour. Newly eclosed males less than two days old exude a rich fragrance similar to that of rancid margarine.

Behavior

Oviposition-proneness in *Morpho* refers to the readiness of captive fecundated females to deposit eggs on larval food plant cuttings. Females of

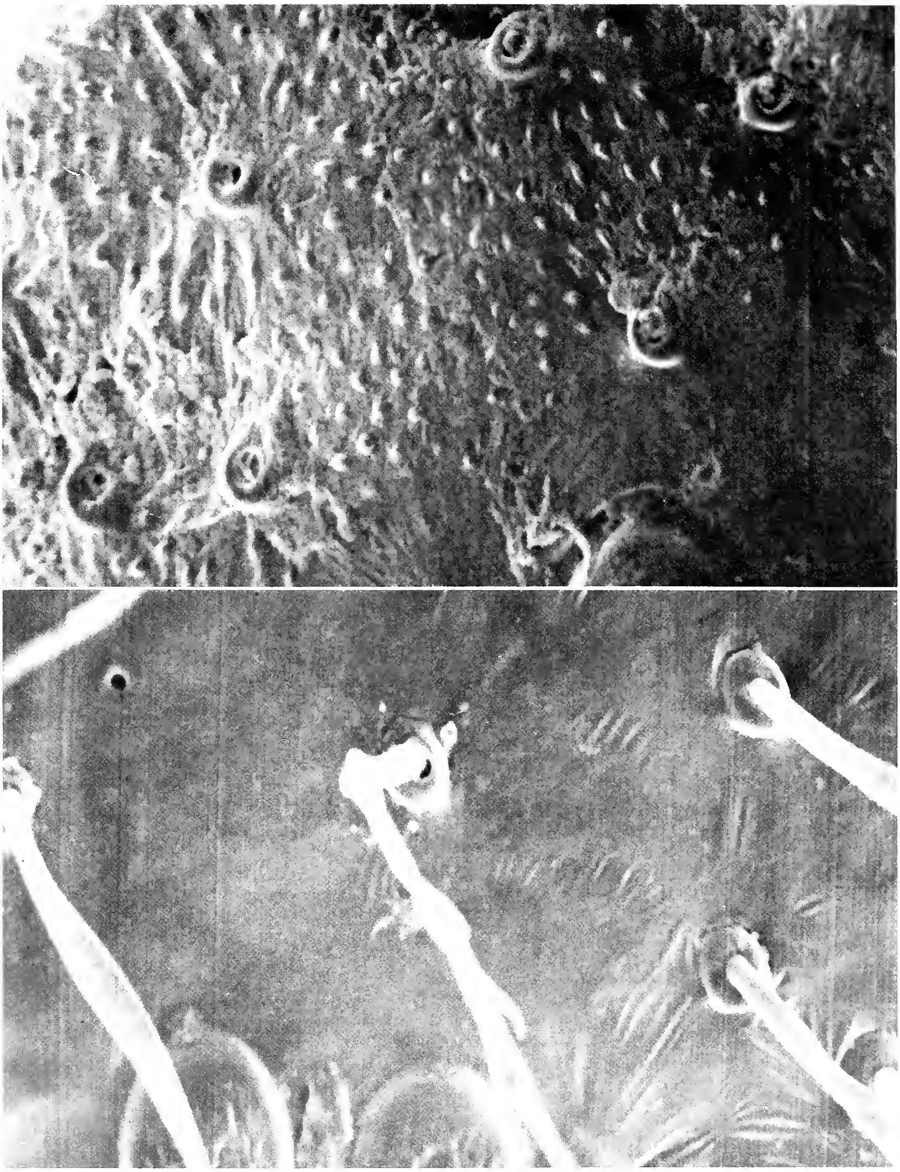

Fig. 6. Sculpturing of the cuticle of the head capsules of first instar caterpillars of *M. granadensis* (top) and *M. peleides* (below) for medial-lateral sections above region of ocelli (500× mag., with SEM). Preparations and SEM work by R. Wolff.

Fig. 7. Early stages of *Morpho granadensis*. Top, left and right: third-instar caterpillars resting on leaves of a larval food plant, *Machaerium seemannii* (Leguminosae). Note leaf damage from feeding in the photograph to the right. Bottom: fourth instar caterpillar (left) and pupa (right).

M. granadensis generally require two to four days before egg-laying is initiated under these conditions, while the response is generally less than two days in *M. peleides*. Successful mating cannot be achieved by confining a virgin female with an active male in a clear plastic bag. In one such test, the two butterflies were kept active for abut two weeks without copulation taking place. The female was clearly a virgin given the large amounts of body fluids exuded in the first few days of confinement, indicating a very recent eclosion. Given tests with both *M. granadensis* and *M. peleides,* it is likely that mating takes place very soon after eclosion in the wild. In captivity, eggs are placed singly on the food plant, and it is known that oviposition is single in the wild in *M. peleides* (Young and Muyshondt 1973). I suspect single oviposition in *M. granadensis* in the wild.

Adults of both species regularly show up at fruit baits (see below) and can sometimes be distinguished by the amount of blue reflectance and size of the wings. At a closer distance, the distinctive coloration of the ocellus markings on the ventral sides of both sets of wings between the two species is very evident (see also Fig. 1). In *M. granadensis,* both the circulus and ocellata associated with each of the three eyespot markings on each forewing, and the set of four such markings on each hindwing are colored in vivid reddish-orange. In *M. peleides,* these areas are yellowish. In *M. granadensis,* the circulus is a very thin reddish-pink or slightly lavender line, while in *M. peleides* it is light blue. In *M. granadensis* the center spot of each eyespot marking is bluish while it is white in *M. peleides*. The number of eyespot markings on the forewings of individual specimens of *M. peleides* is often very variable while seldom so in *M. granadensis*. Relative to *M. peleides,* the dorsal marginal black border of both sets of wings is thinner in *M. granadensis*. Good descriptions of wing coloration for both species is given in Seitz (1924). The above comments are made more in the context of providing a key to an immediate identification of species in the wild. A detailed study of the evolutionary relationship between these two species must understandably await for a detailed study of the genus as a whole, including the examination of early stages and biogeographical patterns.

In laboratory culture, caterpillars of *M. granadensis* exhibit the same "dawn-dusk" feeding rhythm as do the caterpillars of *M. peleides* (see Young 1972b), with the dusk peak being greater than the dawn peak. Presumably similar behavior exists in the wild.

Food Plant Preference

When offered various leguminous food plants, known to be acceptable to the caterpillars of *M. peleides* from sympatric Costa Rican populations, the first instar caterpillars of *M. granadensis* exhibit distinctive patterns of response. For example, of a total of 32 first instars offered fresh leaves of *Mucuna urens,* a very common food plant of *M. peleides* (Young and Muyshondt 1973), all died within five days, and following the actual ingestion of tissues along leaf edges. Similar results were obtained in tests of 17 first instars with the leaves of *Erythrina* sp. From studies of *M. peleides* (e.g., Young 1978b; Young and Muyshondt 1973) it is known that even first instars preferentially eat the tissues from older leaves of *M. urens* and other legumes, and *M. granadensis* in the present tests were offered both young and old leaves. Although *M. peleides* can be succesfully reared to adulthood on the leaves of peanut, *Arachis hypogea* (Young 1974), results are more mixed with *M. granadensis*: in a total of 15 first instars tested, 10 died in that instar, two more survived to the next instar, and the others perished in the third instar (within two days following the molt). At the same time, all but two of an initial group of 12 *M. peleides* were reared to adulthood on the same peanut plants. Although these samples are exceedingly small, they do provide some tentative evidence of a differential response between these two species to legumes. The inference is that *M. granadensis* does not share all of its food plants with the closely related *M. peleides*. A total of 10 caterpillars of *M. granadensis* have been reared successfully on one common food plant of *M. peleides, Machaerium seemannii*. Furthermore, one partially-grown caterpillar was discovered feeding on this plant in the wild (Carillo, San Jose Prov., Costa Rica) by Philip J. DeVries, thus confirming this woody legume vine as a food plant of *M. granadensis* in Costa Rica. This species has also been reared at Finca La Selva by P. J. DeVries. Both butterflies share the habit of placing eggs on seedlings of *M. seemannii* (see also Young 1972a; Young and Muyshondt 1973) since the one caterpillar found in the wild was on a small seedling.

Species abundances

The irregular program of baiting *Morpho* in the same tract of tropical rain forest over several years suggests that *M. granadensis* is less abundant than two other sympatric species, *M. peleides* and *M. amathonte* (Table 1). While samples are small and widely scattered over time, they do reflect the low density property of adult populations of these butterflies, as noted for *M. peleides* in tropical rain forest elsewhere in Costa Rica (Young 1973). In tropical wet regions populations of these butterflies tend to be of low adult densities, except when restricted to a small habitat (e.g., Young and Thomason 1974). The patterns of sex ratio observed in the present study (Table 1) are fairly typical for baited *Morpho,* in which males far outnumber females, regardless of the species (see also Young 1972a, 1973; Young and Thomason 1974). All three species were found to be active at various times of the year, including the drier months of February and March (Table 1 and Fig. 3). As noted in the footnotes to Table 1, there is considerable variation in the production of eggs by individual captive females of *M. granadensis,* although again samples are very small. Although hourly samples are not available, there is clearly considerable feeding at baits during the afternoon hours (Table 1). Based upon a very limited mark-recapture study, there is some evidence that the same individual butterflies may appear at a bait on successive days. For example, the male *M. granadensis* sighted on 20 February 1980 was captured, marked (with a fast-drying white enamel paint—see Young and Thomason 1974 for details of this technique), and released immediately. This male was subsequently resighted at the three baits on 21 and 22 February. Similarly, two males of *M. peleides* marked and released on 22 February 1980 were resighted at the baits, and one of these was seen feeding the following day at noon (Table 1).

Discussion

Because both *M. granadensis* and *M. peleides* are both members of the *achilles* "superspecies" complex (Young 1974), it is not unexpected that their early stages would be of similar appearance and behavior as reported in this present study. Yet consistent morphological differences, including larval characters, adult wing color patterns, and genitalia structure (Young unpubl. data), indicate the forms to be two valid species. Both undoubtedly represent the geographical extension of the *achilles* complex into Central America, although one, *M. granadensis* is far more restricted in this ecological range extension than the other. Elsewhere (Young and Muyshondt 1973), it is argued that *M. peleides* represents the form most successful in the colonization of secondary habitats in both the non-seasonal and seasonal tropical forest zones of Central America and Mexico. *Morpho granadensis,* in contrast, is a restricted tropical rain forest form associated with intermediate elevations along the Caribbean drainage of southern Central America, and the northern part of South America.

The topic of this paper is not to make an attempt to reconstruct what might have been the ecology of a progenitor form to both species, and the selection pressures leading to divergence. Rather, we are at the descriptive stage of trying to gather basic natural history data that provide some clues to present-day patterns of differentiation between the two species in a region of sympatry and ecological overlap. What is of interest in this context is the considerable overlap in the flying seasons of both species, their co-occurrence at baits in tropical rain forest, and a preference for the same habitat. Yet *M. peleides* is a far more widely distributed species than *M. granadensis,* suggesting indirectly that the two forms are not in direct competition for resources. Rather, I tentatively conclude that the ecological requirements of *M. granadensis,* particularly as related to the exploitation of larval food plants, represents a subset of those required by *M. peleides*. The data and other reports (Young and Muyshondt 1973; Young and Thomason 1974) suggest that *M. peleides* has a higher reproductive capacity (defined here

Table 1. Comparative abundance of three species of *Morpho* butterflies at baits of rotting bananas in an approximately 2,000 m^2 block of tropical rain forest in northeastern Costa Rica as seen intermittently over several years.

Dates	Season	Time of day	*Morpho peleides*			*Morpho granadensis*			*Morpho amathonte*		
			♀♀	♂♂	T	♀♀	♂♂	T	♀♀	♂♂	T
VIII-14-77	rainy	1300	0	0	0	0	1	1	0	1	1
VIII-15-77	rainy	1300	0	3	3	0	0	0	0	0	0
XI-30-78	rainy	1200	0	1	1	0	0	0	0	0	0
XII-1-78	rainy	1130	1	0	1	1[a]	0	1	0	2	2
XII-2-78	rainy	1100	0	0	0	0	0	0	0	2	2
XII-3-78	rainy	1330	0	1	1	0	0	0	0	6	6
XII-4-78	rainy	1400	1	0	1	0	0	0	0	2	2
XII-5-78	rainy	1000	0	0	0	0	0	0	0	1	1
III-11-79	dry	1000	1	0	1	0	0	0	0	0	0
III-12-79	dry	1000	1	0	1	0	0	0	0	0	0
IX-28-79	rainy	1400	0	0	0	2[b]	0	2	0	1[c]	1
X-3-79	rainy	1400	0	1	1	0	1	1	0	1	1
II-12-80	dry	1200	1	2	3	0	0	0	0	3	3
II-13-80	dry	1230	1	1	2	0	0	0	0	1	1
II-20-80	dry	1330	0	0	0	0	0	0	0	1	1
II-21-80	dry	1230	0	0	0	0	0	0	0	1	1
II-22-80	dry	1200	0	2	2	0	0	0	0	1	1
II-23-80	dry	1200	0	1	1	0	0	0	0	0	0
VI-13-80	rainy	1400	0	2	2	0	5	5	0	0	0
VI-14-80	rainy	1400	0	0	0	0	2	2	0	1	1
VI-15-80	rainy	1400	0	0	0	0	1	1	0	0	0
VI-16-80	rainy	1400	0	0	0	0	1	1	0	2	2
II-3-81	dry	1500	1[d]	2	3	0	0	0	0	0	0
II-4-81	dry	1500	0	1	1	0	1	1	0	1	1
II-5-81	dry	1500	0	0	0	0	2	2	0	1	1
VII-24-81	rainy	1300	1	0	1	0	2	2	0	1	1
VII-26-81	rainy	1300	1[e]	0	1	0	1	1	0	0	0
Total butterfly sightings:			9	17	26	3	17	20	0	29	29
% rainy season sightings:					46.1%			75.0%			69.0%

[a] In captivity this female produced 53 viable eggs in two weeks.
[b] In captivity one female produced 8 viable eggs in 8 days, the other 24 eggs in 2.
[c] This male fed continuously for at least one hour.
[d] In captivity this female produced 16 viable eggs in 3 days.
[e] In captivity this female produced 26 viable eggs in 5 days.

as the total number of eggs produced by the average female during her lifetime) than does *M. granadensis,* and that this phenotypic trait is associated with the ability of the former species to colonize a broad range of ecological conditions throughout much of the American tropics. Thus the lower abundance of adult *M. granadensis* at baits reflects a smaller breeding population, rather than a necessarily large population dispersed over large areas. It is interesting to note the similarities in adult abundance between

M. peleides and *M. amathonte* in this region. Both of these species are widespread forms throughout the lowland and premontane tropical rain forest region of the Caribbean drainage of Costa Rica, and that ranked abundance with *M. granadensis* is not unexpected (Young 1972a). All three species have single oviposition and legume-feeding caterpillars, conditions that promote widespread distribution. Elsewhere (Young and Muyshondt 1972b) it was proposed that *M. amathonte,* representing the Central American expansion of *M. anaxibia* from South America, with its dazzling blue wing colors in the males, is the dominant form of the genus in lowland tropical rain forests, whereas forms such as *M. peleides,* with more subdued wings, are the dominant representation of the genus at higher forested elevations. *Morpho granadensis* seems to ''fit in'' by being distributed at an intermediate elevation, and perhaps between the two major faunistic regions for the other forms mentioned above. Given some preliminary information available on these and other species of the genus in Central America, I propose the summary of ecological distributions given in Figure 8. This scheme is meant to be a starting point for further study, rather than a conclusion based on a solid background of field data.

Owing to its relatively narrow geographical distribution in Costa Rica and presumably elsewhere, *M. granadensis* is probably a more ecologically-specialized species of mixed primary-secondary tropical rain forest than the more cosmopolitan *M. peleides.* The inability of the caterpillars of *M. granadensis* to exploit one of the most abundant larval food plants of *M. peleides, Mucuna urens,* and their inability to develop successfully on a cultivar such as peanuts, tentatively suggests ecological specialization in a direction away from *M. peleides.* What is lacking is critical data on the scope of larval food plants of *M. granadensis* in zones of overlap with *M. peleides.* If it is assumed that *Machaerium seemannii* is the dominant larval food plant of *M. granadensis,* much of the distribution of this butterfly may be explained by the distribution of this woody vine. Although this vine is abundant at higher elevations in the same region of Costa Rica, where it is exploited by *M. peleides* (Young and Muyshondt 1973), the marked absence of *M. granadensis* from this region suggests the operation of other factors generating this distribution. With an absence of critical biogeographical data, perhaps larval food plant distribution coupled with other factors such as climate play a joint role in limiting *M. granadensis.* Whether or not ecological differentiation within larval food plant populations, in which the defensive chemistry against herbivorous insects is altered geographically, plays a role in the absence of *M. granadensis* from both montane and coastal tropical rain forest zones cannot be ruled out at this time. As pointed out by Ehrlich and Raven (1969), there is a need to consider the evolutionary history of a species in determining patterns of ecological differentiation.

The data on adults suggest that the short, often erratic dry season char-

The species of Morpho butterflies found in premontane-to-lowland tropical wet forest region of northeastern Costa Rica, and their general habits.

SPECIES	MAJOR ADULT HABITAT(S)	FLIGHT HEIGHT RANGE	RELATIVE ABUNDANCE	LARVAL FOOD-PLANT TAXA
M. peleides	various secondary; large forest light gaps	1-3 M	high	several Leguminosae
M. granadensis	advanced secondary; large forest light gaps	1-3 M	low	prob. few Leguminosae
M. amathonte	primary forest	1-6 M	intermediate	prob. few Leguminosae
M. theseus	primary forest	6-30 M	low	prob. few Menispermaceae
M. cypris	primary forest	10-30 M	low	prob. few Leguminosae

Defined here as 0-200meters above sea level.

Fig. 8. A schematic summary of the major ecological attributes for the species of *Morpho* butterflies found in northeastern Costa Rica. Data on habitats, flight ranges, and relative abundance from direct field observations over several years, and larval food plant data from both field and laboratory study, and the literature.

acteristic of this region of Costa Rica does not appreciably affect the population structure of the butterflies. In all three species, adults are active at various times of the year. It is likely that the larval food plants are not deciduous and therefore remain evergreen during dry periods. Thus breeding can be continuous throughout the year. What may vary is the distribution of natural adult foods. I have noticed that during dry periods adults arrive at baits faster than in the rainy season. Increased dryness may result in increased feeding to maintain water balance and it may also result in a decrease in density of suitable foods, which include sweet-smelling rotten fruits and soupy fungal growths (Young 1979, 1980a). Throughout the year, females are rare at baits, possibly the result of a sexual difference in pref-

Table 2. Summary of the major ecological characteristics of *Morpho peleides* and *M. granadensis* in terms of explaining their distribution.[a]

Phenotypic and other characters responding to selection	Determined and/or predicted[b] character states	
	Morpho peleides	*Morpho granadensis*
(1) Geographical range	widespread	restricted
(2) Local endemism and restriction of gene flow	low*	high*
(3) Distribution across marked elevational gradients	high	low
(4) Ability to occupy highly seasonal regions	good	poor
(5) General spatial patchiness of resident populations over approx. 1,000-meter sections of a region	low	high
(6) Dispersal ability of adults	high	moderate-to-low*
(7) Intrapopulational variation	high*	low*
(8) Interpopulational variation	low*	moderate-to-high*
(9) Habitat selection	generalized (low)	grading into specialized (high)
(10) Main habitat	grades of secondary forest	advanced secondary forest
(11) Colonizing ability	high	moderate-to-low*
(12) Local population density	high	low
(13) Regional breadth of larval foodplants	high	low*
(14) Acceptability of each other's larval foodplants	high	low
(15) Relative abundance of larval foodplants per unit area of suitable habitat	high	low*
(16) Oviposition strategy	single and scattered	single and scattered
(17) Oviposition proneness in captivity	high	low
(18) Predation/parasitism on immature stages	high	high[b]
(19) Overall fecundity (average per female)	high	moderate
(20) Egg-adult developmental time	very similar*	
(21) Larval dawn-dusk feeding	present	present
(22) "Bait-ability" of adults	excellent	fair-to-good
(23) Daily turnover of adults at baits	high	moderate
(24) Sex ratio of adults at baits	skewed males	skewed males
(25) Diurnal rhythmicity of adult feeding	present	present
(26) Percent character states in common: 28.0%		

[a] Analyses of these characters should include an examination of breeding populations in both regions of species overlap and non-overlap.

[b] Character states marked with an asterisk are predictions, while unmarked ones are empirical observations from previous studies (Young 1971a, b, 1972a, b, 1973, 1974, 1975a, 1978b, 1979, 1980a; Young and Muyshondt 1973; Young and Thomason 1974) and unpublished data (Young).

erence for feeding on rotten bananas. Rearing studies (Young and Muyshondt 1973) indicate that sex ratio is near unity in egg batches. The complete absence of female *M. amathonte* from baits may indicate, together with the scarcity of females in the other two species, that females have different feeding habits from those of males. Because observations were made at various times of the day, it is unlikely that females were missed at the baits. Rather, their food requirementss may be considerably different from males in all three species, and possibly linked to nutritional demands associated with egg production.

Table 2 summarizes a proposed model for the overall evolution and ecological differentiation of *M. granadensis* and *M. peleides*. This framework is suggested as a means for developing some testable hypotheses on the ecological properties of these two species, a topic of considerable interest since both are members of the same "superspecies" complex and exhibit considerable sympatry at the same time. The proposed model can also be eventually applied to the other species of *Morpho* as natural history data are gathered on them. Basically this model makes some testable predictions about the differences in genetic structure and ecological properties between a pair of species, one of which is geographically and ecologically more restricted than the other in the tropics.

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VLADIMIR NABOKOV 1899–1977: A NOTE ON A LATE ENTOMOLOGIST

"Look, how pretty," said observant Chateau.

A score of small butterflies, all of one kind, were settled on a damp patch of sand, their wings erect and closed, showing their pale undersides with dark dots and tiny orange-rimmed peacock spots along the hindwing margins; one of Pnin's shed rubbers disturbed some of them and, revealing the celestial hue of their upper surface, they fluttered around like blue snowflakes before settling again.

"Pity Vladimir Vladimirovich is not here," remarked Chateau. "He would have told us all about these enchanting insects."

"I have always had the impression that his entomology was merely a pose."

"Oh no," said Chateau.

(from Pnin by V. Nabokov, Garden City, N.Y.: Doubleday, 1957)

Not just Timofey Pavlich Pnin, the title character of his 1957 novel, but many "real" people thought that Vladimir Vladimirovich's—that is, Vladimir Nabokov's—entomology was an affectation, a little marginal coloration on the hindwings of his prolific writing and busy teaching careers. But it wasn't. "My passion for lepidopterological research, in the field, in the laboratory, in the library, is even more pleasurable than the study and practice of literature, which is saying a good deal." (Interview for Wisconsin Studies in Contemporary Literature in 1966.)

Nabokov was born in old St. Petersburg in 1899. By the age of seven he was chasing butterflies across Russian meadows and marshes (see Chapter Six of Speak, Memory: An Autobiography Revisited, New York: Putnam, 1966). In a 1920 entomological article, written during his Western European émigré period, he described some species he observed in the Crimea. It was his first published writing in English, 20 years before he was forced to flee Europe and abandon his "docile" Russian and decided to tame English for his creative purposes. For seventy years, until he died in Montreux, Switzerland in 1977, Vladimir Nabokov pursued Lycaeides and Plebejinae, dissected and drew their genitals, described their haunts and once said, "I have often dreamt of a long and exciting career as an obscure curator of lepidoptera in a great museum." (Interview for Life Magazine in 1964.)

His published lepidoptera is not minor. From 1941 to 1948 he worked very hard and very happily over a microscope at the laboratory of the Museum of Comparative Zoology, Harvard. From 1941 to 1953, at the same time he was writing and teaching, he published some 10 major articles in entomological journals (see pp. 314–335 of Strong Opinions, New York:

McGraw-Hill, 1973). "I am the author or the revisor of a number of species and sub-species mainly in the New World . . . Several butterflies and one moth have been named for me . . . There is also a genus Nabokovia Hemming, in South America." (Interview for Bayerischer Rundfunk in 1971.) At one time he had begun work on an illustrated "Butterflies in Art," from Egyptian antiquity to the Renaissance.

The playful lepidopterological images that flutter across the pages of his stories and novels had a very precise purpose. They established contact between two of the great loves in his life, literature and lepidopterology, "between the precision of poetry and the excitement of pure science." (Interview for the BBC in 1962.)

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BOOK REVIEW

Vectors of Plant Pathogens. Edited by K. F. Harris and K. Maramorosch. Published by Academic Press, New York, London, Toronto, Sydney and San Francisco, 1980. ISBN 0-12-326450-2. Price $48.00. Pp. xiv + 467.

This 17-chapter book, authored by 21 contributors from 8 different countries of the world, is the third in a multi-volume series of treatises on the general topic of vectors, pathogens and plant diseases. The two preceding volumes, namely "Aphids as Virus Vectors" and "Leafhopper Vectors and Plant Disease Agents," appeared in 1977 and 1979, respectively.

Each one of the first 10 chapters of the book, with a certain exception concerning Chapter 8 (see below), deals with a different taxonomic group of insects which is known to contain species that act as vectors of plant disease agents. Chapters 14–17 are devoted to taxa other than Insecta that include vectors, to wit: mites, nematodes and fungi.

Two vector-borne plant diseases which in recent years have gained world notoriety were quite understandably allotted special chapters rather than being treated in the relevant chapters dealing with their respective vector group. The diseases are: (a) Dutch elm disease, a barkbeetle-borne fungal pandemic, prevalent mainly in temperate regions of the world (Chapter 8); and (b) lethal yellowing of coconut palm, a devastating disease in the tropics and subtropics, which is presumably caused by a mycoplasma-like organism, though its vector transmission still requires unequivocal proof (Chapter 11). The singling out of these two plant diseases by apportioning a separate chapter to each one of them in a book which is chiefly concerned with animal vectors, seems nevertheless justifiable in view of the worldwide impact of these diseases on both the economy and the environment. Moreover, thanks to the editors' apparent prudence there is no duplication of coverage between Chapter 8 handling the beetle-borne Dutch elm disease and Chapter 7 which comprehensively deals with beetles vectoring plant pathogens, in spite of the fact that the two chapters were written by different authors.

The same virtually holds true for Chapters 12 and 13 which review the involvement of insects in the transmission of bacterial and fungal phytopathogens, respectively. By narrowing the scope of the chapters on the taxonomic groups of insects down to vectors of viral pathogens mainly, the editors managed to preclude any unnecessary repetitiousness likely to occur in these two chapters dealing with the transmision by insects of nonviral plant pathogens *viz.* bacteria and fungi.

It may perhaps be argued that Chapter 1 (aphids, leafhoppers and planthoppers) is apparently redundant since the two preceding volumes of the series bear the titles of "aphid vectors of plant viruses" and "leafhopper vectors and plant pathogens." However, in a rapidly developing area of research like the transmission of plant pathogens by homopterous vectors, a tri- or even biennial updating of a review is certainly not unwarranted, let alone the fact that the chapter under discussion (written by one of the editors—K. F. Harris) has been condensed into a mere 12-page synoptic review. At any rate, it would be utterly inconceivable to omit, for whatever reason, a chapter on aphids and leafhoppers from a textbook entitled "Vectors of Plant Pathogens."

A marked improvement in the References lists concluding each chapter, as compared to the two previous volumes of the series, is the providing of full titles of the cited publications. This will undoubtedly be very much appreciated by all users of the book.

In a reference book like this, comprising 17 individual contributions of different authors, a good index, going down to exhaustive detail, is more than essential. The challenge was indeed well taken up here in the form of a 29-page index, listing some 2,800 items.

Thus, the careful choice of top expert authors, coupled with a good measure of skillful judgment exercised by the editors, and the highly professional presentation on the part of the publishers, have all together resulted in a most welcome, comprehensive and updated compilation of core reference and background information on its subject. It will doubtlessly be indispensable in providing the most up-to-date handbook on vector transmission of plant disease agents currently available. As a university instructor charged with the teaching of a course on this very subject, I can state with a great deal of gratitude that the book has definitely made my task very much easier now. Without any hesitation I thoroughly recommend this book to specialists and non-specialists alike who have an interest in vector-related plant pathology, and/or phytopathogen-related entomology, whether it be from the research or teaching point of view.

I. Harpaz, *Hebrew University of Jerusalem, Rehovot, Israel.*

Handbook of Plant Virus Infections: Comparative Diagnosis. E. Kurstak, ed. Elsevier-North Holland. 944 pp. $192.75.

Plant virus infections can spread in various ways and the most prevalent is by means of insect vectors. Therefore the subject of this treatise is of special interest to entomologists. Hundreds of plant virus diseases have been described all over the world, but the causative viruses were often inadequately identified and, in many instances, the viral nature of the diseases not properly ascertained. In fact, more than 200 viruses, incompletely characterized by 1981, remain ungrouped, and only 23 virus groups and 2 families of viruses have been accepted as properly characterized. There exists a real need for a comprehensive text that would facilitate the proper diagnosis of plant virus infections, and the present volume is the first attempt to fill the existing gap.

Many of the basic procedures used for the description and diagnosis of viruses are described in detail by the contributors of this book. In most instances the natural means of transmission is highly diagnostic, but there are certain virus groups with specific vectors, others where vectors are as yet unknown, and still others transmitted by seed, pollen, or by vegetative means. The comprehensive contents of this book are divided into 6 parts. The first deals with plant virus taxonomy, the second with non-enveloped RNA viruses, the third with enveloped RNA viruses, the fourth with elongate RNA viruses. The fifth part deals with DNA viruses and the last one with viroids.

Entomologists will be especially interested in the chapters in which insect and other invertebrate vectors and their interactions with plant-pathogenic viruses are presented. Chapter 2 describes maize chlorotic dwaft and its only natural leafhopper vector *Graminella nigrifrons*. The third chapter deals with the identification of Tymoviruses, transmitted by beetles. The Tombusviruses (Chapter 4) have but a few known natural vectors, such as the flea beetles of the genera *Phyllotreta* and *Psilliodes* for turnip crinkle. Chrysomelid vectors, *Lema melanopa* and *L. lichensis,* as well as *Ceratoma trifurcata* transmit southern bean mosaic virus (Chaper 5). Luteoviruses are transmitted by more than a dozen specific aphid vectors and the persistent virus-vector interaction accounts for the distribution of infected plants in the field (Chapter 6). Chapter 8 deals with Comoviruses, transmitted mainly by chrysomelid beetles. There are very good electron micrographs of the pea enation mosaic virus (Chapter 10) but none of the virus in its major aphid vector *Acyrthosiphon pisum,* in which the virus is known to multiply. The ubiquitous Cucumoviruses (Chapter 11) are transmitted in nature by some 75 aphid species. Their biological aspects and vector control have been described in great detail. Among the Ilarviruses (Chapter 13) one, tobacco streak, is transmitted by a thrips, *Franklinella* sp., another (Prunus ringspot) by a mite, *Vasates fockeni.* Alfalfa mosaic virus (Chapter 14) is transmitted by many aphid species in the nonpersistent manner. On the other hand, Reoviruses (Chapter 15) are transmitted biologically by leafhoppers and planthoppers. This chapter contains detailed tables concerning vector species as well as outstanding electron micrographs by Prof. E. Shikata of Hokkaido U., Japan, of virions in fatbody cells of *Nephotettix cincticeps* infected with rice dwarf virus, and of *Unkanodes albifascia* with rice black-streaked dwarf virus. The use of immune electron microscopy for the identification of plant reoviruses is among the highlights of this chapter. In the following chapter (No. 16) there is an excellent tabular presentation of rhabdovirus vectors, and of the world-wide distribution of the diseases. Electron micrographs of virions in cells of infected plants illustrate this chapter, prepared by R. I. B. Francki (Australia), E. W. Kitajima (Brazil) and D. Peters (Netherlands), the three foremost authorities on these ubiquitous viruses. The thrips-borne tomato spotted wilt virus is described in Chapter 17. The diagnosis of aphid-borne Potyviruses is in Chapter 23. The plant DNA Caulimoviruses (Chapter 25) are transmitted by *Myzus persicae* and *Brevicoryne brassicae* aphids. Some of the Geminiviruses (Chapter 26) have vectors belonging to the cicadellid leafhoppers, such as *Orosius argentatus* and *Nesoclutha pallida,* while others are transmitted by whiteflies, *Bemisia tabaci.*

The constant growth of the world population increases the need for more food and fiber, and in light of this it is important to reinforce current knowledge of plant virus diseases and of plant virus-vector interactions, so as to control the numerous diseases more efficiently. Plant pathologists, entomologists, teachers and students will find this large volume to be an outstanding source of information. Because of its cost, however, it will most likely be limited to libraries at colleges and universities.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers–The State University, New Brunswick, New Jersey.*

Insects and Other Invertebrates of the World on Stamps. William E. Stanley, ed. Biology Unit, American Topical Association Handbook No. 98. 140 pp. $10.—ATA, 3306 North 50th St., Milwaukee, WI 53216.

This 140-page handbook is the only complete data source on insects and other invertebrates, illustrated on stamps of the world. It brings together in a concise form in three sections (1) butterflies and moths, (2) other insects and (3) other invertebrates. Taxonomic listings by phyla, classes, subclasses, orders and families, with Latin and common names, as well as country listings follow the style of earlier biological stamp handbooks issued by ATA. The checklist specifies the country, date of issue, Scott, Minkus or Stanley Gibbons stamp catalog numbers, face value, Latin name and authority, as well as an indication of whether the reproduction is in natural colors. This little handbook will be a must for entomologists who collect insects on stamps.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers University.*

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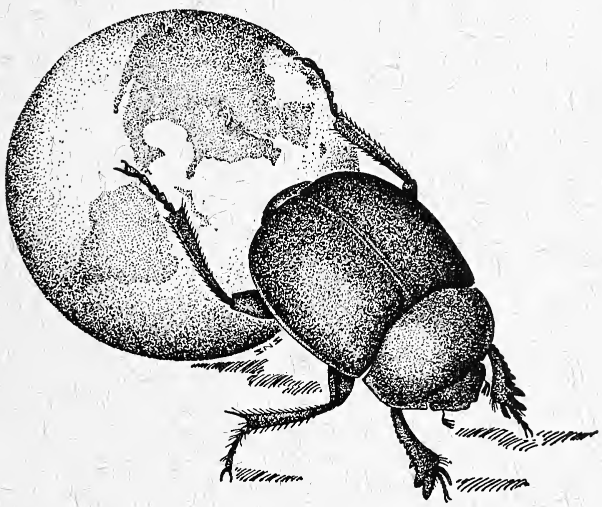

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HABITAT EFFECT ON FUNGAL SUBSTRATE SELECTION BY A LEAF-CUTTING ANT

Harold G. Fowler

Abstract.—Colonies of the grass-cutting ant, *Acromyrmex landolti fracticornis,* ranked potential fungal substrate in field preference bioassays as a function of the dominant grass species in the field in which they were located. Mahalanobis distances between and among colony preferences between and among habitats revealed that there was less variability among colonies within any habitat than between habitats. These results suggest that fungal substrate preferences are environmentally induced, probably as a result of early experience of workers.

The extreme catholicism demonstrated by leaf-cutting ants (genera *Atta* and *Acromyrmex*; Formicidae: Attini) in harvesting vegetation to serve as fungal substrate is one of the most intriguing and applied problems confronting researchers in Latin America. Yet, despite the efforts of many workers, why leaf-cutting ants do what they do is still unknown, although patterns are beginning to emerge. Cherrett (1968) and Rockwood (1976, 1977) have argued for a conservative management of vegetative resources by colonies of leaf-cutting ants based upon their experience with tropical forest species. Recently, Fowler and Stiles (1980) have suggested that a more parsimonious explanation, based upon the patchiness of the vegetative resources, might better explain the patterns observed by Cherrett and Rockwood.

There is now strong evidence that fungal substrate selection is based, in part, on plant chemistry (Cherrett and Seaforth 1970; Cherrett 1972; Littledyke and Cherrett 1975, 1978; Rockwood and Glander 1979; Stradling 1978; Hubbell and Wiemer 1981). This fact alone, however, cannot explain plant selection, especially by colonies in different habitats (Rockwood 1976, 1977). I now report on the effect of habitat in determining plant selection in a leaf-cutting ant. These studies were conducted near Asuncion, Paraguay, in 1976.

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Methods

Based on a previous study (Fowler and Robinson 1977), the ranked preferences for 5 species of introduced forage grasses were determined from laboratory colonies. These ranked preferences were *Digitaria smutsii, Hyparrhenia rufa, Digitaria decumbens, Tripsacum laxum,* and *Pennisetum ciliare*. Thirty field bioassays were conducted on colonies in each of three essentially mono-specific habitats of *D. smutsii, D. decumbens,* and *P. ciliare*. Each bioassay consisted in clearing vegetation from nest mounds, enclosing the mound with a wire and plastic enclosure to prevent foraging, and then offering 10 uniform pieces of each of the 5 grasses to the colony in a random array, and recording the numbers taken. Bioassays were terminated when all of one type of grass was entered into the nest.

Data analysis consisted in subjecting the acceptance data to a multivariate analysis of variance (Morrison 1976) to test for an overall habitat effect, and the use of discriminant analysis (Morrison 1976) to obtain the Mahalanobis distances separating the preferences of colonies established in distinct habitats.

Results

The mean number of pieces picked up by the ants and entered into the nests is given in Table 1. Overall ranking of the grasses taken in each habitat were the same, with the exception of the ranking by colonies located in *P. ciliare* monocultures.

When these data were subjected to a multivariate analysis of variance, it was found that the vectors characterizing habitat-specific colony preferences for the 5 forage species (Table 2), were highly significant (Pillai's trace = 0.5306, $F_{(10,168)} = 6.0$, $P < 0.0001$) indicating an important effect of habitat on the resulting preferences of the colonies located within them. In particular, these differences arose from the colony selections relating to *P.*

Table 1. The effect of habitat on grass-selection by *Acromyrmex landolti fracticornis* colonies located in mono-specific stands of forage in Paraguay.

	Mean (±SD) of 10 grass pieces taken by colonies located in fields of:		
Grass species taken	*D. smutsii*	*D. decumbens*	*P. ciliare*
Digitaria smutsii	7.57 ± 2.49	8.83 ± 2.15	7.83 ± 2.03
Hyparrhenia rufa	7.50 ± 2.03	6.23 ± 2.71	6.63 ± 2.52
Digitaria decumbens	6.77 ± 2.63	4.86 ± 2.78	6.93 ± 2.76
Tripsacum laxum	2.60 ± 1.69	3.20 ± 2.66	2.30 ± 1.66
Pennisetum ciliare	1.93 ± 1.62	3.20 ± 2.56	5.43 ± 3.02

Table 2. Characteristic roots and vectors of E inverse × H matrices, where E is the error sum square and cross product matrix, and H is the type IV sum square and cross product matrix for habitat effect on the preferences of colonies located in the 3 habitats of Table 1.

Characteristic root	Characteristic vector				
	D. smutsii	*H. rufa*	*D. decumbens*	*T. laxum*	*P. ciliare*
0.428	−0.0155	−0.0069	0.0116	−0.0208	0.0396
0.300	−0.0198	0.0200	0.0312	−0.0194	−0.0159
0.000	−0.0083	0.0034	0.0099	0.0456	0.0049
0.000	0.0180	0.0414	−0.0078	0.0044	0.0096
0.000	0.0397	0.0056	0.0211	0.0002	−0.0026

ciliare and *D. decumbens* (ANOVA F values of 15.41 and 5.32 respectively for pick-up per habitat).

An analysis of the covariance matrices of grass-selection by colonies in each habitat (Table 3) revealed a significant deviation from homogeneity

Table 3. Covariance matrices of grass-species preferences exhibited by field colonies of *Acromyrmex landolti fracticornis* in habitats where they occur, and a pooled covariance matrix for overall preferences (intra-habitat). Habitat is indicated in parenthesis.

Grass species:	*D. smutsii*	*H. rufa*	*D. decumbens*	*T. laxum*	*P. ciliare*
			(*D. smutsii*)		
D. smutsii	6.18	−2.53	0.34	−0.90	0.04
H. rufa		4.12	−0.16	−0.07	0.28
D. decumbens			6.94	1.14	−0.33
T. laxum				2.86	−0.34
P. ciliare					2.62
			(*D. decumbens*)		
D. smutsii	4.63	0.73	1.49	−0.21	1.03
H. rufa		7.36	−1.73	−0.53	−0.05
D. decumbens			7.71	1.03	2.23
T. laxum				7.06	3.68
P. ciliare					6.58
			(*P. ciliare*)		
D. smutsii	4.14	−2.79	0.47	−0.39	0.49
H. rufa		6.38	−2.58	0.08	0.58
D. decumbens			7.65	1.06	−0.28
T. laxum				2.77	−1.79
P. ciliare					9.15
			(Pooled—all habitats)		
D. smutsii	4.98	−1.53	0.77	−0.50	0.52
H. rufa		5.95	−1.49	−0.17	0.27
D. decumbens			7.43	1.08	0.54
T. laxum				4.23	0.52
P. ciliare					6.11

Table 4. Mean Mahalanobis distances of substrate preferences from colonies of each habitat to the habitat mean substrate preferences.

	Mahalanobis distance to:		
Substrate preferences for colonies in habitats of	*D. smutsii* habitat mean preferences	*D. decumbens* habitat mean preferences	*P. ciliare* habitat mean preferences
Digitaria smutsii	6.723	10.980	9.457
Digitaria decumbens	8.843	8.753	9.653
Pennisetum ciliare	11.899	11.628	7.783

($\chi^2 = 52.26$, $P < 0.0033$). Thus, the overall pick-up of grass species in each habitat was determined by the characteristics of the colonies within those habitats, and a global pattern of substrate ranking and preference cannot be extracted across habitat boundaries.

Because of the lack of homogeneity in the covariances, a quadratic discriminant function was needed to separate the habitat specific pick-up responses of colonies. From this, it possible to calculate the generalized squared distances (Mahalanobis distances) for the habitat specific preferences (Table 4). Without exception, the preferences of colonies located in *D. smutsii* habitats are more dissimilar to those of colonies located in *P. ciliare* than they are to the preference means of colonies located in *D. decumbens*. Since the overall preferences of these 2 grasses are relatively high (Table 1), this result is expected. However, colonies located in the low preference *P. ciliare* habitats showed a highly variable selection of grasses (Table 1), because all of the offered grasses were of superior rank. Yet, these colonies did not harvest significantly more of these than the grass it was normally foraging, *P. ciliare* (Table 1).

Discussion

The results presented here suggest that conditioning can greatly affect the patterns of plant selection in leaf-cutting ants, and may explain, in part, the intra-colonial differences in substrate selection noted in tropical rain forests (Rockwood 1976, 1977). In a tropical forest, the surrounding vegetation pattern is much more complex than that discussed here for grass-cutting ants in mono-specific pastures. However, the foraging territories of these species is undoubtedly characterized by its own characteristic vector of plant species. If worker ants learn, probably through early experience (Jaisson 1980), the characteristics of its habitat, it is very likely that the colony specific foraging patterns noted by Rockwood (1976, 1977) could be induced.

The results of this paper also suggest that a more tractable analysis of the foraging behavior of leaf-cutting ants could probably result from studies in less complex habitats instead of tropical rain forests. In less complex habitats, many complicating and intertwined parameters are naturally elimininated, which would allow for an analysis of leaf-cutter foraging behavior from basic to complex elements, instead of complex to basic elements as is by necessity dictated by studies in tropical rain forests.

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A NEW SPECIES OF *TRACHYMYRMEX* FUNGUS-GROWING ANT (HYMENOPTERA: MYRMICINAE: ATTINI) FROM PARAGUAY[1]

Harold G. Fowler

Abstract.—A new species of fungus-growing ant, *Trachymyrmex* **kempfi**, is described from the Chaco Basin of Paraguay. This species necessitates an expansion of the concept of the generic limits of *Trachymyrmex*.

Specimens of a new species of *Trachymyrmex* were collected in northwestern Paraguay (Chaco Basin). Correspondence with the late W. W. Kempf indicated that this species was common in central Brazil and northern Argentina. At the time of his untimely death, Dr. Kempf was in the process of revising the species of *Trachymyrmex*, in which this species was to be included. Since no generic revision is imminent, I felt it imperative to provide a description and an available name for this common species.

Trachymyrmex **kempfi**, n.sp.

Figures 1–3

Holotype.—Worker holotype and 18 worker paratypes, Teniente Enciso, Departamento Nueva Asuncion, Paraguay, 16 August, 1975 (J. Guerrero). Holotype and 5 paratypes deposited in the Museum of Comparative Zoology. Additional paratypes are deposited in the American Museum of Natural History and the author's personal collection.

Diagnosis.—Similar to *T. iheringi* but differing in the following features: frontal carina vestigial or weakly defined in *T. iheringi*, prominent in *T. kempfi*; lobe of antennal scape 2.5× longer than broad in *T. kempfi*, less than this in *T. iheringi*; pronounced tubercle at base of epinotal spine in *T. kempfi*, absent or vestigial in *T. iheringi* (Fig. 2).

Description.—Holotype worker (all measurements in mm): (TL) total body length, 4.2; (EL) maximum length of compound eye, 0.16; (OMD) distance between lower margin of compound eye and mandibular base, 0.15; (SL) scape length, 0.73; (WL) Weber's length of alitrunk, 1.67; (HW) head

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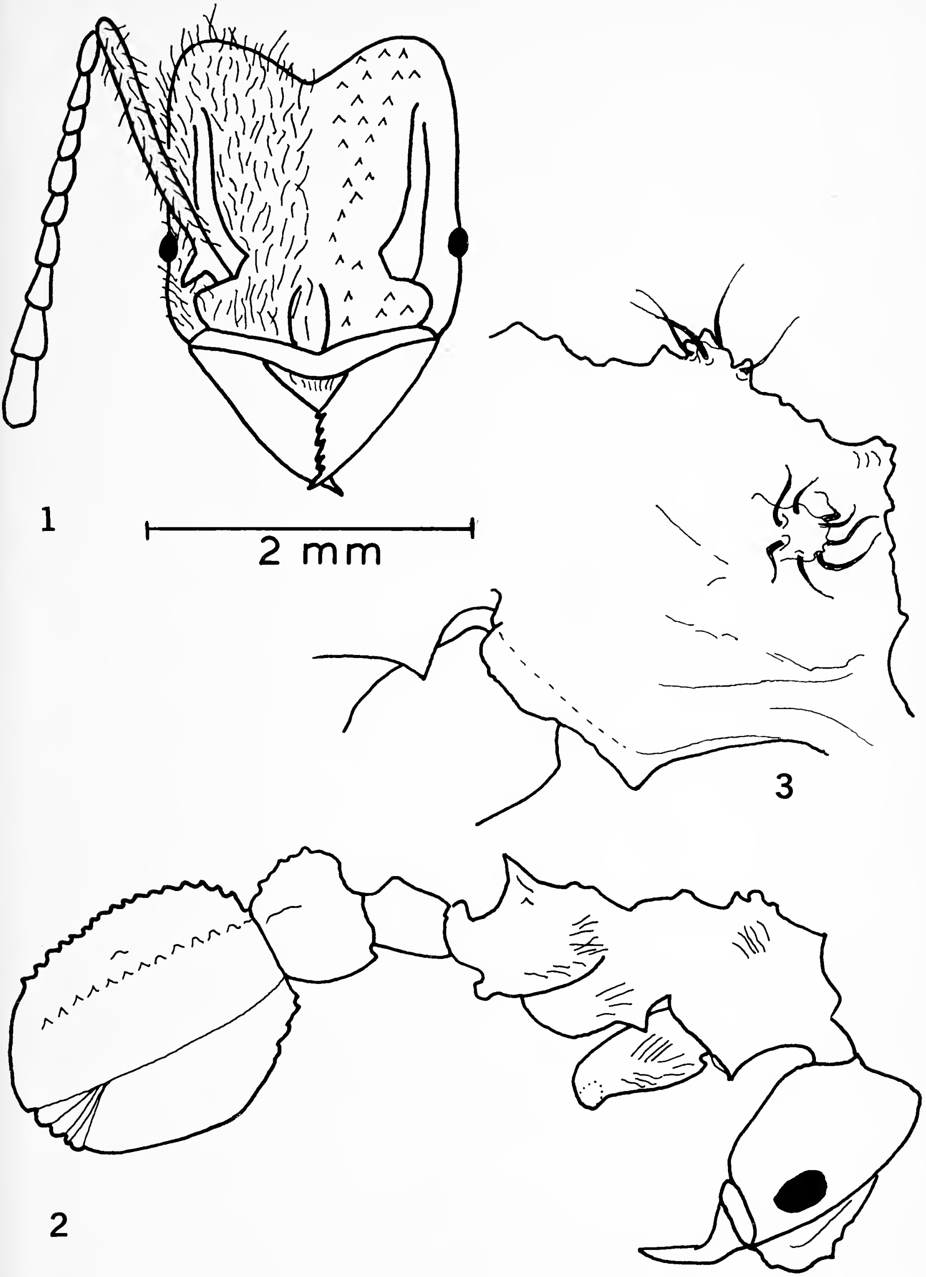

Figs. 1–3. *Trachymyrmex kempfi* new species: 1. Paratype worker head, frontal view, 2. Paratype worker, lateral view without appendages, 3. Paratype worker mesonotum; lateral view.

width across occiput, 1.02; (HL) head length from anterior clypeal margin to occipital margin, 1.02; (PW) pronotum width between anterior mesonotal crests, 0.57; (ML) mandible length, 0.49; (SI) scape index ((HW/SL)(100)), 139; (CI) cephalic index, ((HW/HL)(100)), 100.

Head: (Fig. 1) In full frontal view, as broad as long, tubercles numerous on frons and occiput; lobe of frontal carina expanded, covering antennal condyle (Fig. 1); erect setae covering antennal scape, appressed fine setae covering flagellomeres; scape fitting tightly into frontal carina; gena with erect setae; compound eye slightly raised above gena; base of antennal scape with a pronounced, protruding lobe; gula with appressed setae. Alitrunk: (Figs. 2, 3) anterior mesonotal crest 2× as long as basal width, trilobed; posterior mesonotal spine poorly developed; propodeal crest poorly developed; propodeal spine 2× as long as basal width, sharply pointed, with large tubercle laterally at base; propodeum with numerous tubercles dorsally and laterally; setae long and erect on propodeal spine and on dorsum of alitrunk. Prothoracic femur: expanded. Petiole: (Fig. 2) dorsum of node evenly convex; setae of dorsum short and erect, longitudinally long and appressed. Postpetiole: (Fig. 2) dorsum with long, erect setae. Gaster: (Fig. 2) first segment with many short tubercles arranged in four longitudinal rows, from which arise long, semi-erect setae; venter smooth, with short, thinner appressed hairs. Color: reddish brown.

Holotype worker bears red/handwritten label: *Trachymyrmex kempfi*/HOLOTYPE/H. Fowler 1981. Paratype workers bear green/handwritten label: Trachymyrmex kempfi/PARATYPE/H. Fowler 1981.

Paratypes.—TL, 3.34–4.24; EL, 0.15–0.17; OMD, 0.15–0.17; SL, 0.73–0.78; WL, 1.62–1.67; HW, 0.98–1.07; HL, 0.90–1.03; PW, 0.48–0.57; ML, 0.45–0.53; SI, 134–142, CI, 97–108.

Etymology.—This species is named in honor of the late W. W. Kempf. His cheerfulness and prompt identifications benefitted many researchers in Latin America, and his untimely death has created a void that will not easily be filled.

Discussion

The similarities of *T. kempfi* with *T. iheringi* are numerous, yet these species are easily distinguished. Emery (1887) has discussed in detail these morphological traits which distinguish *T. iheringi,* and which also hold for *T. kempfi*.

Kempf (personal communication) indicated that *T. kempfi* has a broad geographical range, extending from the Chaco Basin to Rio Grande do Sul, Brazil, and that it is much more common than *T. iheringi* which tends to occur further to the south.

Nests of *T. kempfi* consist of a small tumulus of excavated soil with one entrance hole located on the tumulus. The workers described above were foraging on fresh leguminous vegetation, a habit common in most rangeland *Trachymyrmex,* although generally more characteristic of the genera *Atta* and *Acromyrmex* (Weber 1972).

This description of *T. kempfi* necessitates a new interpretation of the genus *Trachymyrmex.* Although *T. kempfi* is weakly polymorphic, as other species of *Trachymyrmex,* its large size overlaps with some castes of species of *Acromyrmex.* Also *T. kempfi* lacks pronounced sharp spines or large tubercles posteriorly on the head, unlike other taxa of *Trachymyrmex,* although small spines bearing tuberculate setae are present. Also, the thoracic and propodeal spines of *T. kempfi* are not well developed, which is generally characteristic of the genus. However, the alitrunk is much smoother in lateral view than is usually observed in *Trachymyrmex.* Nevertheless, *T. kempfi* will key out as a *Trachymyrmex* in the generic key of Weber (1972).

Acknowledgments

The late W. W. Kempf initially identified the species as new, and encouraged further collection of the Paraguayan fauna. N. A. Weber, R. B. Roberts, and M. DuBois all read and offered useful criticisms of the manuscript, and their interest is gratefully acknowledged.

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EXPERIMENTAL REMOVAL OF 17-YEAR CICADA NYMPHS AND GROWTH OF HOST APPLE TREES

Richard Karban

Abstract.—Seventeen-year cicada nymphs feed on xylem sap of most species of deciduous trees. They attain very great densities in apple orchards and are known to damage apple trees during oviposition. Newly hatched nymphs were removed from certain apple trees in 1979 and the growth of these trees was compared to trees where the nymphs had not been removed. During 1980, trees without cicada nymphs experienced significantly increased annual wood accumulation compared to control trees with cicadas. There was no difference in growth between the 2 treatments in 1979 (the emergence year). Despite the small sample size, these results suggest that cicada nymphs reduce apple tree wood increment in the years following the emergence.

Most deciduous woody tree species in the eastern U.S. serve as hosts for cicada (*Magicicada* spp.) nymphs (Butler 1886; Dybas and Lloyd 1974; Lloyd and White 1976; White 1980). Commercial apple, peach, pear, plum and cherry trees are often heavily infested (Marlatt 1907; Asquith 1954; Graham and Cochran 1954; Banta 1960; Hamilton and Cleveland 1964). Adult periodical cicadas, which emerge only every 17 years at any locality in the northern part of their range, are known to be extremely abundant (Marlatt 1907; Dybas and Davis 1962). The adults live for two to four weeks and females oviposit in pencil sized twigs (3–11 mm diam). The damaging effects of egg laying are well established (Riley 1885; Hopkins 1897; Cory and Knight 1937; Smock and Neubert 1950; Graham and Cochran 1954; Hunter and Lund 1960; Lloyd and Dybas 1966; Smith and Linderman 1974; White 1980).

Periodical cicadas spend their 17 or 13 year nymphal development underground. As nymphs, they feed by sucking relatively great quantities of xylem fluid, an extremely dilute source of nutrients (Cheung and Marshall 1973; White and Strehl 1978). Few studies have considered the effects of root sucking nymphs. Assessing the impact of feeding nymphs is very difficult; trees supporting cicadas are not killed and are still capable of growth

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and reproduction. Banta (1960), Hamilton (1961) and Hamilton and Cleveland (1964) observed that apple trees with cicada nymphs were experiencing a cessation of growth and a reduction of yield. They were unable to reduce chemically the cicada population, in a replicated manner, required to test their hypothesis that cicadas were responsible for the "apple orchard decline." Karban (1980) compared the growth of parasitized and unparasitized scrub oak trees (*Quercus ilicifolia* Wang.). Parasitized and unparasitized trees did not differ in the amounts that they grew during the years preceding the cicada emergence, indicating that microenvironmental differences between parasitized and unparasitized trees were not causing differences in growth. In the emergence year and the years following the emergence, trees without cicadas grew significantly more (ca. 30% more radial wood accumulation) than those which supported nymphs.

The purpose of this investigation is to remove cicada nymphs from certain trees but not others (controls) in order to test the effect of root xylem fluid feeding on wood increment of apple tree hosts.

Methods and Site Description

A heavy emergence of *M. septendecim* (L.) and *M. cassini* (Fisher) occurred in the Jenkins-Leuken orchard near New Paltz, Ulster Co., N.Y. during the 1st week in June 1979 (Brood II). I selected eleven 'Nothern Spy' apple trees (*Malus pumila* Mill.) (Fig. 1). By late June all of these trees contained many freshly constructed eggnests. Apple trees of other varieties

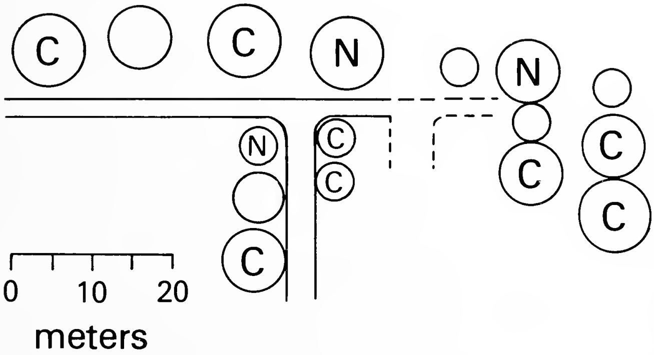

Fig. 1. Scale diagram of the study area. Circles with letters are 'Northern Spy' apple trees that are included in the study. Circles without numbers are either a variety other than Spy or were dead, hollow, or rotting Spy trees. The size of the circle represents the approximate extent of the canopy of each tree. There is no apparent relationship between canopy diam and tree growth. Trees in which cicadas were removed in 1979 are marked "N"; trees with cicadas are marked "C." The location of an overgrown farm road is indicated.

Fig. 2. Bed sheets are set up under one of the experimental trees. As nymphs hatch they fall from the twigs to the ground to begin their subterranean development. Sheets are used to remove the nymphs from the experimental trees.

and trees which were dead, had fallen or had rotting or hollowed trunks were not included. None of the eleven trees in this experiment had been cropped in 1979 or 1980; previous cropping history is unknown.

Three of the eleven trees were selected at random and served as experimental trees. Cotton bed sheets, used to entrap the newly hatched nymphs, were spread under the canopies of the experimental trees on July 2, 1979. The sheets were raised off the ground by wooden stakes at their corners and rocks were placed in them to keep them from flapping in the wind and discharging their contents (Fig. 2). The sheets allowed rain water to pass through but caught the nymphs and unwanted debris. Nymphs were removed from the debris which was then placed on the soil under the sheets. Eight trees had no sheets placed under their canopies and serve as controls.

Once a female places her eggs in a twig they require 6 to 10 weeks to hatch. The 1st instars hatch from their twig-borne eggs, fall to the ground and burrow into the soil. Nymphs from the experimental trees were intercepted in the sheets as they attempted to fall to the ground, leaving the experimental trees free of cicada nymphs.

The density of 1st instars was estimated for the experimental trees by placing five aluminum trays (29 × 23 × 11 cm) on the ground under the canopy in a manner so that they were not covered by bed sheets. Each tray was filled with a saturated picric acid solution and intercepted an area equal to one-fifteenth of a square meter (White 1973; Karban in press). The trays were not allowed to dry out, overflow, or be covered by spider webs. The trays were set out on July 16 and were removed on Aug. 30 after all the nymphs had hatched out and fallen.

The 3 experimental and 8 control trees were cored on Dec. 6, 1980 with an increment borer. The cores were stained with a solution of 1% phloroglucinol in 95% ethanol. To prevent bias, an assistant who did not know which of the cores were from the experimental trees, measured the annual wood increment with a dissecting microscope and an ocular micrometer. Annual wood increment was measured for a 10-year period from 1971 to 1980. Although it was possible to measure more years, the probability of counting a false ring increases as more years are included. One of the control cores was particularly difficult to measure and is not considered in the analysis.

Results

The radial growth increment for the 1980 growing season for each tree is presented in Table 1. There is a 7-fold difference (0.5 to 3.5 mm) in radial growth for 1980 among the trees, irrespective of treatment. From year to year, some trees grow consistently more than others; this is undoubtedly due to habitat, cropping, competitive and predator differences. Comparing

Table 1. 1980 and 1979 annual radial increments (mm) for control trees with feeding cicada nymphs (with cicadas) and experimental trees without cicadas (no cicadas). The 1979 season, which was the emergence year, and the 1980 season are compared to the 8-year (1971–1978) average for each site.

Treatment	8-year average increment (1971–1978)	1980 increment	1980 increment / 8-year average	1979 increment	1979 increment / 8-year average
No cicadas	1.45	1.4	.97	1.8	1.24
No cicadas	1.91	1.8	.94	0.6	.31
No cicadas	2.88	3.5	1.22	2.0	.69
With cicadas	1.50	1.0	.67	1.2	.80
With cicadas	2.09	2.0	.96	2.3	1.10
With cicadas	2.33	1.8	.77	3.1	1.33
With cicadas	1.38	0.7	.51	0.6	.43
With cicadas	2.96	0.9	.30	2.1	.71
With cicadas	2.46	2.8	1.14	3.3	1.34
With cicadas	1.23	0.5	.41	0.7	.57

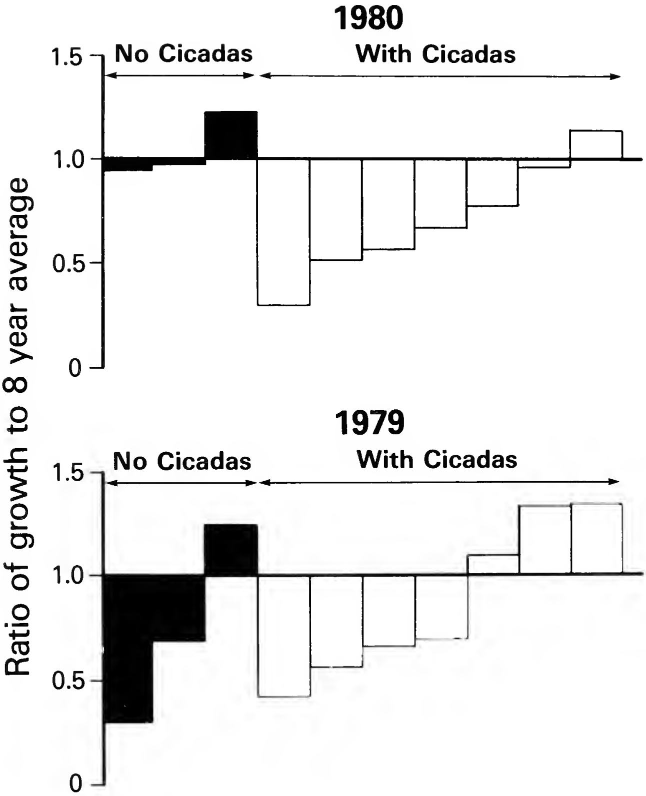

Fig. 3. The ratio of annual wood increment for 1980 and 1979 compared to the 8-year average (1971–1978) for each tree. Trees without cicadas are shown as shaded bars, trees with cicadas are shown as unshaded bars. In 1980, trees without cicadas were ranked 1, 3, and 5. In 1979 trees without cicadas were ranked 3, 7, and 10.

the 1980 annual wood increment with an 8-year average (1971–1978) increment for each tree provides a more meaningful estimate of the effects of the removal of cicadas on tree growth than considering 1980 growth alone. By comparing the 1980 growth to the 8-year average for each tree, the effects of other factors, which each year create differences in growth between the trees, are controlled. There is less than a 3-fold difference in average wood increment over an 8-year period between the trees (1.23 to 2.96 mm). Table 1 and Fig. 3 present the ratio of 1980 increment to the 8-year average for each tree. The ranks of this ratio are compared using a Mann-Whitney U test. The null hypothesis is that there is no effect on radial wood increment of removing the nymphs, i.e. that the samples from the experimental and control treatments come from populations having the same distribution. This null hypothesis can be rejected with 94% certainty ($U = 3$, $n_1 = 3$, $n_2 = 7$, $P = .058$).

This same analysis was applied to the annual radial wood increment for the 1979 growing season (the emergence year). Table 1 and Fig. 3 present the ratio of the 1979 increment to the 8-year average for each tree. The hypothesis that trees without cicadas added relatively more wood than those with nymphs during 1979 is not supported by the data ($U = 7$, $n_1 = 3$, $n_2 = 7$, $P = .258$).

There is no relationship between canopy diameter and tree growth. Mean canopy diameter of the three experimental trees was 7.467 ± 1.746 m and mean canopy diameter of the eight control trees was 6.625 ± 2.271 m (Mann-Whitney $U = 5$, $n_1 = 3$, $n_2 = 7$, $P = .133$). Canopy diameter was not correlated with average radial growth over the 8-year period of 1971 to 1978 (Kendall rank correlation $N = 2$, $n = 10$, no significance). Canopy diameter was not correlated with the ratio of radial growth in 1980 to the 8-year average (Kendall rank correlation, $N = 30$, $n = 10$, no significance).

The density of first instars was estimated by catching a sample of those falling from the tree. The estimated density and SE for each of the three experimental trees is: 777 ± 56, 1,404 ± 144 and 1,914 ± 252 first instars per m^2. This range of densities corresponds to 20–40 adult cicadas per m^2 (Karban in press) and is comparable to nymphal densities found in other studies in apple orchards (Hamilton 1961; Forsythe 1976; Maier 1980).

Discussion

In a previous study the effects of cicada nymphs on annual wood increment were most apparent in the years immediately following the emergence year (Karban 1980). In this study experimental removal of cicadas resulted in increased radial growth of apple trees in the year following the emergence. The reduction in wood increment associated with cicadas has now been shown for apple trees as well as scrub oaks.

Experimental trees, without cicadas, added on average, 61% more radial wood in 1980 than did control trees, with cicadas. This result was not due to other differences between experimental and control trees. However, the experimental trees added 12% more wood over the 8-year period (1971–1978) than did the control trees. Scrub oaks, without cicadas added 30% more wood, on average, than trees with cicadas (Karban 1980).

No signficant differences in annual wood accumulation during the emergence year, 1979, were found between apple trees without cicadas and trees with cicadas. This is in contrast to a previous study in which scrub oaks with no eggnests in their canopies added significantly more wood during the emergence year than did those with eggnests (Karban 1980). This suggests that the negative effect on tree growth observed for the scrub oaks during the emergence year probably resulted from oviposition damage.

Periodical cicada nymphs feed on root xylem fluid (White and Strehl 1978). Amination, the process of incorporation of inorganic nitrogen into organic compounds, takes place largely in growing root cells; most of the nitrogen ascending the stem is already in the form of amino acids (Bollard 1957; Raven et al. 1976; Tromp and Ovaa 1976; Dickson 1979). Wiegert (1964) points out that xylem feeding insects may be extremely costly to their host plant because they consume the nitrogen which the plant requires for growth.

This study has shown that 1st instar cicadas can negatively affect the radial wood increment of apple trees. However, the small sample size, both in terms of the number of trees in the study and in terms of the number of years in which the effect has been found, suggest caution about generalizing from this result.

Acknowledgments

I wish to thank Mr. Jack Leukin and Mr. Ray Jenkins for permission and encouragement to work in their orchard. Andrea White and my father helped in the field. The Mohonk Trust graciously provided a campsite. Leeanne Omrod measured growth increments. This paper was writen in Chapel Hill where JoAnn White created a 'writers retreat,' second to none. I benefitted greatly from the comments of Monte Lloyd, Frank Slansky, Alan Smith, JoAnn White and Truman Young. This work was supported by NSF grant DEB-7914039.

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ALTERED HATCH SEQUENCE OF MALES AND FEMALES FROM UNCHILLED EGGS OF A "NON-DIAPAUSE" GYPSY MOTH STRAIN (LEPIDOPTERA: LYMANTRIIDAE)

Nancy Fike Knop, Marjorie A. Hoy and Michael E. Montgomery

Abstract.—Larvae hatching from unchilled egg masses of a "non-diapause" gypsy moth strain (*Lymantria dispar* Linnaeus) were reared to determine the hatch sequence of males and females. Males tended to hatch from non-diapause egg masses before females, which is the reverse of the hatching sequence of chilled wild egg masses. These results were obtained with an outcrossed non-diapause strain as well. The reversed hatch sequence is not due to a skewed sex ratio or to differential mortality.

The gypsy moth (*Lymantria dispar* Linnaeus) has been intensively studied in North America even though it has been a difficult laboratory animal. Development of an artificial diet (Leonard and Doane 1966; ODell and Rollinson 1966) and a "non-diapause" strain (Hoy 1977, 1978a, b) have made laboratory rearing easier. The non-diapause strain facilitates continuous laboratory rearing for parasite or virus production since the gypsy moth eggs will hatch within 31 days of deposition without exposure to cold. Wild type gypsy moth eggs require 90–120 days of chill to obtain a good level of hatch.

The non-diapause strain had been selected simultaneously for early hatch and hatch without chilling (Hoy 1977, 1978a, b). Beginning with generation 5, the first 60% of larvae to hatch from each egg mass were reared and larvae hatching later were discarded. In generation 6 the first 40% of larvae to hatch were reared, and in generation 7 only the first 20% to hatch were reared. At the same time, the sex ratio of the adults reared from these fractions of egg masses shifted; progressively higher frequencies of males were produced in each succeeding generation. This study was undertaken to determine whether the excessive number of males produced was due to a change in sex ratio in the non-diapause strain or to a change in the time of hatch of males and females in this strain. Accordingly, all larvae hatching from twenty-three unchilled non-diapause egg masses were reared.

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Materials and Methods

Intact, unsterilized egg masses were held individually in plastic petri dishes (100 × 15 mm). They were supplied with a block of synthetic diet (Media 722A, BioServ, Inc., Frenchtown, N.J.). Larvae began hatching about 30 days after egg deposition. Newly hatched larvae were collected daily from 10 non-diapause (selection generation 8 (Hoy 1977, 1978a)) egg masses. These larvae were reared in groups of 20 in 475 ml unwaxed cardboard containers supplied with diet in small cups. Egg masses and larvae were maintained at 21–22°C and 16 h light. Sex was determined by examining pupae.

To see if the apparently skewed sex ratio could be modified by outbreeding with a wild gypsy moth stock, an outcross was made of the selected non-diapause strain to adult moths reared from field-collected wild eggs. This was followed by a backcross of the F_1 progeny to the non-diapause strain. The resulting strain was selected for "non-diapause" for 3 generations. Larvae from 13 egg masses of the 4th outcrossed non-diapause generation were group reared as above except larvae from 4 of the 13 egg masses were reared individually in 100 × 15 mm petri dishes to reduce larval mortality due to disease.

Results and Discussion

All three groups of egg masses had the same male-female hatch sequence (Fig. 1). High frequencies of male pupae were reared from the first collections and progressively lower proportions were reared from subsequent collections (Fig. 1). This hatch sequence is the reverse of that reported for chilled wild gypsy moth eggs. Leonard (1968) reported that the first larvae to hatch from field collected eggs consisted of ca. 30% males while the last larvae to hatch were ca. 65% males. We observed this wild-type hatching sequence repeatedly in our own laboratory (Hoy and Knop, unpubl. data). Mortality data are given in Fig. 2.

Greater susceptibility to mortality factors of females in first collections and males in later collections might produce a pupal (male-female) sequence such as we observed. Our data for the group with the lowest mortality (individually reared outcross non-diapause, Fig. 1, Fig. 2C) show that the male-female pupal sequence cannot be eliminated even if we include the dead larvae in the sex ratio calculations. Even if we assume that all the dead larvae in collections 1–5 were female and all the dead larvae in collections 10–14 (no. pupae > 10, Fig. 1) were male, collections 1–5 are more than 65% male and collections 10–14 are less than 40% male. Also, the number of male pupae in the first collection is significantly greater (χ^2, $P < .001$) than the number of female pupae and dead larvae combined in

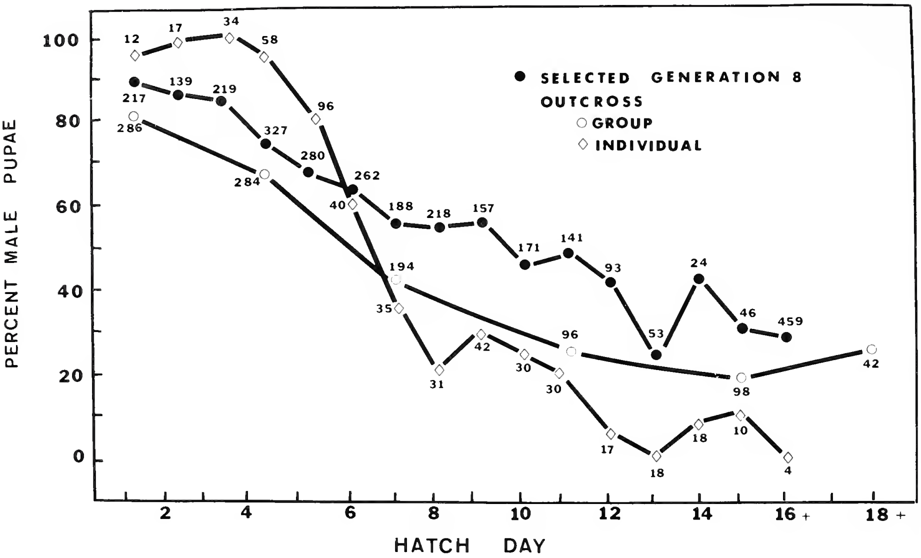

Fig. 1. Percentage male gypsy moth pupae reared from collections of larvae hatching from non-diapause (selected generation 8) and outcrossed non-diapause egg masses, group reared and individually reared. Numbers of pupae are indicated at each point.

each of the other groups (Fig. 1, Fig. 2A, B). We conclude that a male-female hatch sequence occurs in these non-diapause strains.

The overall sex ratios of the non-diapause and the outcrossed non-diapause strains are not different from the wild strain. Higher proportions of males (58–59%) were produced in group rearing but this was the result of higher mortality among late-hatching (mostly female) larvae (Fig. 2A, B). Individual rearing eliminated this skewed distribution of mortality (Fig. 2C) and pupae were 52% male.

Reversal in male-female hatching in the non-diapause gypsy moth strains is not due to a change in sex ratio or to differential mortality. We do not know if the reversal is a pleiotropic effect of the non-diapause trait, or is correlated with it through linkage or through correlated selection. Hoy (1978b) speculated that the "non-diapause" strain still has a short diapause, the selection having influenced diapause duration and the requirement for chilling. Wild egg masses that are chilled for less than the optimal time produce males first (Montgomery, unpubl. data). The occurrence and duration of chill may be important in determining hatch order in wild and "non-diapause" strains. (Chilled non-diapause egg masses hatch rapidly (Hoy 1978a) and any alteration in hatch order is obscured.)

The non-diapause gypsy moth strain was developed to facilitate contin-

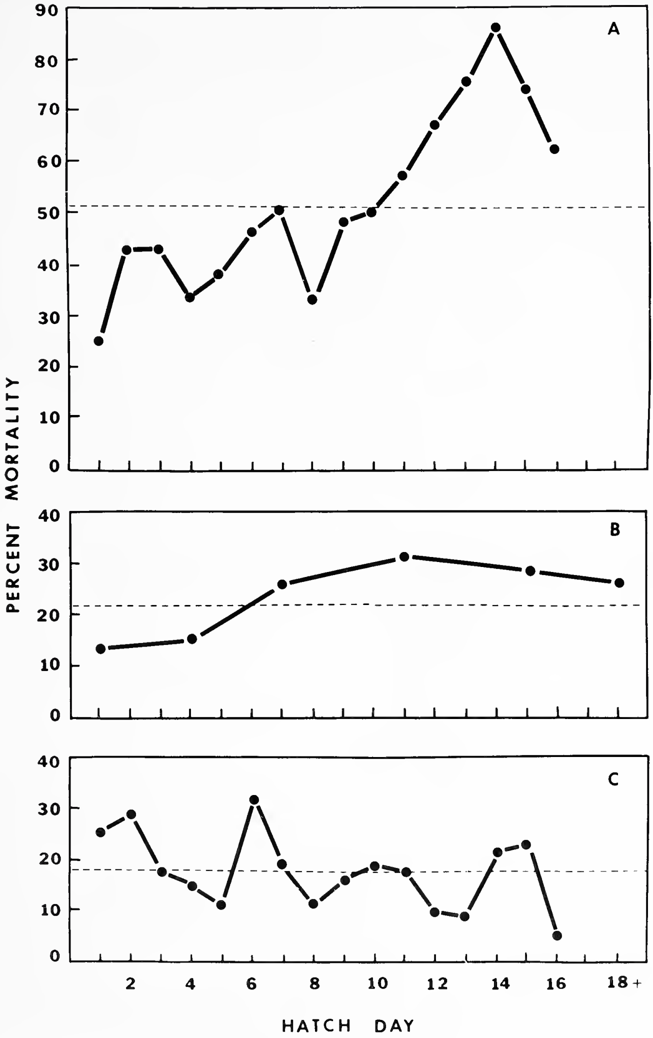

Fig. 2. Percentage developmental mortality in collections of gypsy moth larvae hatching from group reared non-diapause (selected generation 8) (A), and outcrossed non-diapause egg masses either group reared (B) or individually reared (C). The broken line indicates overall percent mortality.

uous rearing of gypsy moth parasites. The data presented here should facilitate maintenance of a desired sex ratio in larvae hatching from unchilled egg masses of this non-diapause strain. A higher proportion of adult females will result if the first non-diapause larvae to hatch are discarded. This would be advantageous if the caterpillars were being reared to yield nuclear-polyhedrosis virus since a higher yield is obtained from females than from males. Conversely, if sterile males were being reared for a genetic control program, it would be most profitable to rear only the first 30% of the larvae to hatch.

Acknowledgments

We wish to thank Karen Ocorr, Marion Winslow and Arthur Bridgeforth for their assistance during the course of this project.

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COMPARATIVE FEEDING BEHAVIOR OF TWO APHID SPECIES: BEAN APHID (*APHIS FABAE* SCOPOLI) AND PEA APHID (*ACYRTHOSIPHON PISUM* (HARRIS)) (HOMOPTERA: APHIDIDAE)

Ronald P. Salyk and Daniel J. Sullivan S.J.

Abstract.—A comparative feeding site preference and competition study was performed in the laboratory on two species of aphids, the bean aphid, *Aphis fabae* Scopoli, and the pea aphid, *Acyrthosiphon pisum* (Harris). The two species were raised separately and together on broad bean, *Vicia faba*. When raised separately, *A. fabae* was found about equally on leaves and stems, and preferred leaf undersides to leaf uppersides by a 2:1 ratio. *A. pisum,* however, strongly preferred leaves to stems, and leaf undersides to leaf uppersides, both by more than 90%. But, when raised together, *A. fabae* developed a noticeable change in preferences, preferring leaves by 83% and leaf undersides by 90%. No major change was seen in preferences of *A. pisum*.

Introduction

The preferences in feeding sites of aphids have long been of interest to a wide variety of entomologists. Feeding site preferences have implications for the type of damage done to plants, the ease with which chemical and biological controls can affect the aphids, the accuracy of standard sampling methods, and the breeding of resistant plant varieties.

Leaf age.—Preferences in leaf age were studied by Kennedy et al. (1950) and Kennedy and Ibbotson (1950). They found that *Myzus persicae* (Sulzer) and *Aphis fabae* Scopoli preferred young or early senescent leaves, while avoiding mature leaves on the sugar beet and spindle tree. Similar results were obtained by Wearing (1972) for *M. persicae* and *Brevicoryne brassicae* (Linnaeus) on brussel sprouts. This preference, however, was stronger in *M. persicae*. Kennedy and Booth (1951) later found that the reproductive rate was also similarly affected by leaf age. Preference in *M. persicae* for older leaves on potatoes was found by Taylor (1955), but he failed to find any difference in *Aphis nasturtii* Kaltenbach. Differences between the two races of *M. persicae* were reported by Tanaka (1957), who found the green

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race preferring younger leaves to a greater extent than the pink race, which preferred the older.

Position on plant.—Preferences in position on the whole plant have also been studied. Shands et al. (1954) studied 3 aphid species on potatoes: *Myzus persicae, Macrosiphum solanifolii* (Ashmead), and *Aphis abbreviata* (Patch). *M. solanifolii* had the highest percentage on the top leaves of the 3 species studied. Even on the same leaf, *A. abbreviata* and *M. persicae* had preferences for different leaflets. Doucette (1961), while studying 3 other species, found that *Macrosiphum scoliopi* (Essig) preferred undersides of lower leaves of Easter lily, while *Aphis gossypii* Glover preferred edges of undersides of top leaves. *Myzus solani* (Kaltenbach) preferred young leaves and buds near the tip.

Leaf uppersides or undersides.—Whether uppersides or undersides of leaves are chosen by aphids has also been the subject of some study. With the aphid, *Eucallipterus tiliae* (Linnaeus), feeding on lime (*Tilia* spp.), Kidd (1976) found that both uppersides and undersides were colonized in the laboratory, while only undersides were colonized in the field. Dixon and Logan (1973) reported an underside preference in *Drepanosiphum platanoides* (Schrank). Cruz and Bernardo (1971) found a similar behavior for *Aphis gossypii.* Contrasting these studies, Wyatt (1965) noted that a majority of aphids on the terminal buds of chrysanthemum were on the upper surface, although this preference was reversed on the lower leaves. Uppersides were also preferred by *Hyalopterus prunii* (Geoffroy) on peach and plum in a study by El-Kady (1971). Four aphids on potatoes prefer undersides: *Macrosiphum euphorbiae* Thomas, *Myzus persicae, Aphis nasturtii,* and *Aulacorthum solani* (Kaltenbach) (Gibson 1972).

Bean aphid and pea aphid.—In direct relation to this present research, *Aphis fabae* Scopoli, the bean aphid, and *Acyrthosiphon pisum* (Harris), the pea aphid, have been the subjects of a number of studies on feeding as well.

1) Leaves vs. stem: Bond and Lowe (1975) found resistant varieties of *V. faba* to be colonized by *A. fabae* approximately 50% on the leaf and 50% on the stem, while susceptible varieties were more heavily colonized on the leaves. Lowe and Taylor (1964) found that both green and red races of *A. pisum* preferred leaves to stems of *V. faba,* with from 86% to 98% of the green preferring leaves, and from 91% to 98% of the red preferring leaves. Lowe (1967), studying only those *A. fabae* that settled on leaf undersides, found that they fed only on veins, ignoring lamina and margins. *A. pisum,* on undersides, were found to be on veins 93.3% of the time. On the same plant at the same time, Tambs-Lyche and Kennedy (1958) found that *A. pisum* was more numerous on the leaves than *A. fabae.*

2) Leaf uppersides or undersides: In reference to the uppersides or undersides of leaves, Dixon and Wratten (1971) reported that *A. fabae* feeds

on either surface of *V. faba*. However, this was not true in the research by Hull (1964) who found only underside feeding on the sweet pea. *A. pisum* was also an underside feeder, ranging from 93% to 98% on leaf undersides. It should be noted, however, that a different host plant was used in the study. *A. pisum* on *V. faba* was found to be primarily an underside feeder by Muller et al. (1974).

In this present research, two types of positional preferences were studied in the laboratory: leaf or stem preference, and upperside or underside preference, using both the bean aphid, *Aphis fabae,* and the pea aphid, *Acyrthosiphon pisum*. These preferences were measured in the aphids as they colonized broad bean, *Vicia faba,* separately, and as they colonized it together. Preferences and changes in preferences between the two species raised separately and then raised together were recorded.

3) Aggregation: Aggregation has been found in both species. Kennedy and Ibbotson (1951) found aggregation in *A. fabae* on spindle trees and sugar beets, while Strong (1967) found aggregation in 1st and 2nd instar nymphs of *A. pisum*. The results of the present research will be related to these studies of aggregation.

Materials and Methods

Two species of aphids were used in this study: the bean aphid, *Aphis fabae* Scopoli, and the pea aphid, *Acyrthosiphon pisum* (Harris). The broad bean, *Vicia faba* Linnaeus (Windsor variety), served as the host plant for both aphids. Seeds were obtained from the W. Atlee Burpee Co., and germinated in a mixture of Baccto potting soil and vermiculite in a ratio of 2:1. Prior to planting, the seeds were dusted with a powdered fungicide, Orthocide, to inhibit the growth of fungi.

Two rows of 4 seeds each were planted in plastic trays and placed in a dark cabinet for approximately 5 days to ensure germination. When the seeds had sprouted, they were transferred to an insect cage illuminated with continuous light by 1 Sylvania Gro-Lux 40 W bulb and 1 Westinghouse 40 W cool white fluorescent bulb. Temperature in the cage varied between 18° and 25°C.

For the first 8 weeks of the experiment, 2 trays were selected and 6 sprouts were left in each tray through the removal of any stunted or incompletely sprouted seeds. One apterous aphid was placed on each of these 6 sprouts, using a camel's hair brush. Sprouts selected for the aphids were approximately 5 cm in height. The gravid females were selected from stock cultures of aphids reared on broad bean. One tray of broad bean sprouts, therefore, had 6 gravid bean aphids, one to a plant, and the other tray 6 gravid pea aphids, one to a plant. These were placed in separate insect cages.

Counts were taken on the 2nd, 5th and 7th days. Aphids were counted and recorded in 3 categories: aphids on stems, on leaf uppersides, and on leaf undersides. At the end of the 7th day count, the tray was discarded and a new tray begun.

During the final 4 weeks of the experiment, the procedure was similar except for the addition of a third tray of 6 sprouts. On each sprout of this tray, one gravid bean aphid and one gravid pea aphid were placed. This tray was placed in a third separate continuous light insect cage, and similar counts were made on the 2nd, 5th and 7th days.

Results and Discussion

1) *Reared separately: leaves vs. stem.*—a) The bean aphid reared by itself showed no preference in feeding site, being evenly divided between leaves (49.4%) and stems (50.6%). These results were very similar to those of Bond and Lowe (1975) who reported a division of 50% leaf to 50% stem.

b) Pea aphids reared by themselves were much more particular, with 95.0% preferring leaves to stems. This was parallel to the results of Lowe and Taylor (1964), who found that the green race of the pea aphid preferred leaves by a percentage varying from 86% to 98%. Tambs-Lyche and Kennedy (1958) also reported that the pea aphid preferred leaves to a greater extent than did the bean aphid when the two were raised separately.

2) *Reared separately: leaf uppersides or undersides.*—a) Those bean aphids found on the leaf preferred the underside of the leaf (64.5%) to the upperside (35.5%) by a 2:1 ratio. Dixon and Wratten (1971) noted feeding on both the uppersides and undersides of leaves of *Vicia faba* by the bean aphid, but did not quantify these observations. Hull (1964) found only underside leaf feeding in the bean aphid on sweet pea, but these results may not be directly comparable due to the different host plants.

b) Pea aphids were again more particular, with 93.4% of them preferring the underside. This is also similar to the results of Hull (1964), who found the pea aphid preferring leaf undersides on sweet pea from 93% to 98%. Muller et al. (1974) also found the pea aphid to be primarily a leaf underside feeder on *Vicia faba*.

3) *Reared together: leaves vs. stem.*—No previous studies have measured differences or changes in feeding site preferences between these two species when reared together as compared to their behavior when reared separately. In the present study, the 2 species raised together showed some dramatic behavioral changes for the bean aphid, but little change for the pea aphid.

a) Bean aphids reared together with pea aphids developed a much stronger preference for leaves rather than stems: 83.1% compared to the original 49.4% ($P < .0001$, Chi square test).

b) Pea aphids reared together with bean aphids showed no noticeable

Table 1. Results of experiment on feeding site preferences.

1) Reared separately	Leaf		Stem	
	No.	%	No.	%
Bean aphid	677	49.4	693	50.6
Pea aphid	3,104	95.0	165	5.0
	Leaf upperside		Leaf underside	
	No.	%	No.	%
Bean aphid	240	35.5	437	64.5
Pea aphid	205	6.6	2,899	93.4
2) Reared together	Leaf		Stem	
	No.	%	No.	%
Bean aphid	723	83.1	147	16.9
Pea aphid	1,250	94.3	75	5.7
	Leaf upperside		Leaf underside	
	No.	%	No.	%
Bean aphid	70	9.7	653	90.3
Pea aphid	106	8.5	1,144	91.5

change in behavior, preferring leaves by almost the same percentage (94.3%) as when reared alone.

4) *Reared together: leaf uppersides or undersides.*—a) When reared together with the pea aphid, the bean aphids on the leaves also developed a much stronger preference for leaf undersides (90.3%) ($P < .001$).

b) The pea aphid preference changed only slightly, with 91.5% preferring undersides, compared to 93.4% when reared separately. This change, although small, was statistically significant ($P < .01$).

The results of both parts of the study are presented in Table 1. In summary, the presence of the pea aphid seemed to cause the bean aphid to move from stems to leaves and from leaf uppersides to leaf undersides. No major change was seen in the pea aphid preferences.

Intraspecific aggregation: A possible explanation of these results might involve the phenomenon of aggregation. Individuals in many aphid species have been shown to have a strong preference for locations on the host plant in close proximity to groups of other aphids of the same species. This intraspecific aggregation behavior is independent of the quality of the feeding site. That is to say, given apparently equal feeding sites, aphids often choose one near another aphid or group of aphids. Kennedy and Ibbotson (1951) found such aggregation in the bean aphid on spindle trees and sugar beets, and it is said to be well known in other cases (Heathcote 1972). Aggregation has also been reported in the pea aphid by Strong (1967) who found it in 1st and 2nd instar nymphs.

Interspecific aggregation: It is conceivable that an interspecific aggregation has occurred in this research. The pea aphid showed an unchanging but strong preference for leaves and leaf undersides throughout the study, regardless of the presence or absence of the bean aphid. The bean aphid, however, which was found to a great degree on both stems and leaf uppersides when reared separately, strongly preferred leaf undersides when raised with the pea aphid. This appears to be a form of interspecific aggregation or an enhancement of the bean aphid's tendency to aggregate, and may be to the bean aphid's advantage in some way, possibly for protection. This apparent aggregation was surprising in that an expected result of such a combination of two species might have been a form of niche splitting. It would have been thought that increased competition for feeding sites might have logically led to the bean aphid's leaving the leaf undersides to the pea aphid and concentrating on stems and leaf uppersides for feeding sites, where interspecific competition would be minimal. Surprisingly, the opposite occurred. Aggregation for protection or some other advantage is the suggested partial answer.

Other possible factors which could affect the feeding site preferences of these aphids that were not studied here include the relative nutritional quality of the stems, leaf uppersides and leaf undersides, and the age of the plant when first colonized by the aphids. These two factors of nutrition and age will be explored in future work.

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SEASONAL FLIGHT OF THE CRANBERRY GIRDLER[1] DETERMINED WITH PHEROMONE TRAPS[2,3]

J. A. Kamm and L. M. McDonough

Abstract.—The seasonal flight of the cranberry girdler, *Chrysoteuchia topiaria* (Zeller) was monitored with pheromone traps for 3 years. Daily trap captures averaged at 5-day intervals were a better indicator of seasonal flight than single-day catches. Peak flight occurred at different calendar dates but was close to the mean summation of heat units (857°C degree-days) for 3 years. More than 90 percent of the flight period occurred within 30–35 calendar days. Even though pheromone traps measured both flight activity and population density, a combination of pheromone trap data and cumulative heat units provided a reasonable estimate of the seasonal abundance of adults, excluding data obtained during periods of cool rainy weather.

The cranberry girdler, *Chrysoteuchia topiaria* (Zeller) occurs throughout North America in habitats that vary from coastal cranberry bogs to high mountain parks. The sex pheromone of this polyphagous feeder has provided a new way to monitor the seasonal flight of adults (McDonough and Kamm 1979; Kamm and McDonough 1980). The extent to which trap captures reflect population density is unknown because various factors influence the number of insects captured in pheromone traps, e.g. weather, population density, and various behavioral modes of the insect (Lingren et al. 1981). Unlike many moths, the cranberry girdler is diurnal and weather conditions during the day also influence the number responding to pheromone traps.

The accumulation of heat units (degree-days) is also useful in monitoring insect populations (Sevacherian et al. 1977). Since temperature is known to have a major influence on diapause development of the cranberry girdler (Kamm 1973), heat unit summations may also have value in monitoring

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[1] Lepidoptera: Pyralidae.

[2] Contribution of Agric. Res. Serv., USDA in cooperation with the Agric. Exp. Sta., Oregon State Univ. Technical Paper No. 5744 of the latter.

[3] Mention of a commercial or proprietary product in the paper does not constitute an endorsement of this product by the USDA.

girdler populations. The present paper describes the seasonal flight period of the cranberry girdler determined with pheromone traps in relation to daily weather and heat unit summations.

Materials and Methods

Tests were conducted near Corvallis, Albany, and Woodburn, Oregon, in commercial seed fields of Kentucky bluegrass or orchardgrass infested with a natural population of the cranberry girdler. Procedures and methods for preparing the test baits are described elsewhere (Kamm and McDonough 1980). Pherocon 1C traps were baited with natural rubber septa that contained 1.0 mg (*Z*)-11-hexadecenal and 0.05 mg (*Z*)-9-hexadecenal.

The flight period of adults was monitored with 6 pheromone traps deployed throughout each field. Traps were serviced daily in the weather study, and trap catches for 5 consecutive days were averaged each calendar day of the flight season to obtain a moving average. Otherwise traps were serviced 2 or 3 times weekly, and trap captures were averaged every 5 calendar days during the flight season. Light intensity was measured at 0900 daily with a General Electric light meter, and 3 classifications of sky conditions were established: (1) Cloudy—total cloud cover, 26–28,000 foot candles (fc); (2) Partially cloudy—39–50,000 fc; and (3) Sunny—66–67,500 fc. Since the calling period of females occurs primarily between 0700–1100 (Kamm 1974), sky conditions during the afternoon were disregarded. No light intensity values fell between established classifications.

Temperature data were obtained from the Oregon State University weather station. Wintering prepupae of the girdler were capable of some development at 10°C, and 5.5°C was considered the developmental threshold (Kamm 1973). Daily heat units (degree-days) were computed by adding the maximum and minimum temperature, then dividing by 2 and subtracting 5.5°C.

Results and Discussion

Daily weather and trap capture of males during the flight period is shown in Fig. 1. Substantial day-to-day variation in trap capture occurred throughout the flight period that could be attributed to weather. For example, trap captures during rainy periods were considerably less than captures made during favorable weather that preceded the rain. Notice also that trap catch was reduced on cloudy or partially cloudy days when preceded by a sunny day. Weather clearly exerted a dominant influence on trap catch, and therefore trap catch on any given day may not provide a reasonable estimate of population density. Such variation in trap catches is believed to be the rule rather than the exception.

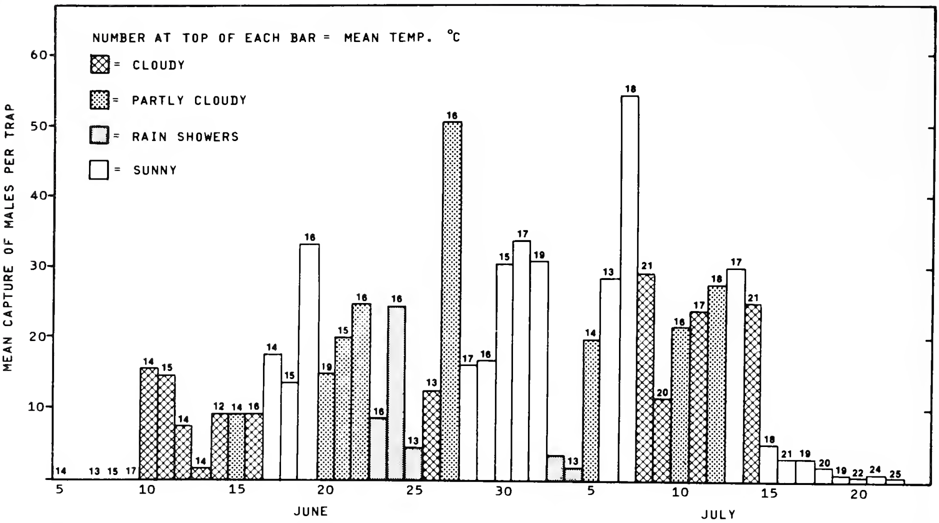

Fig. 1. Weather records and pheromone trap catch of male cranberry girdler in a commercial seed field of bluegrass.

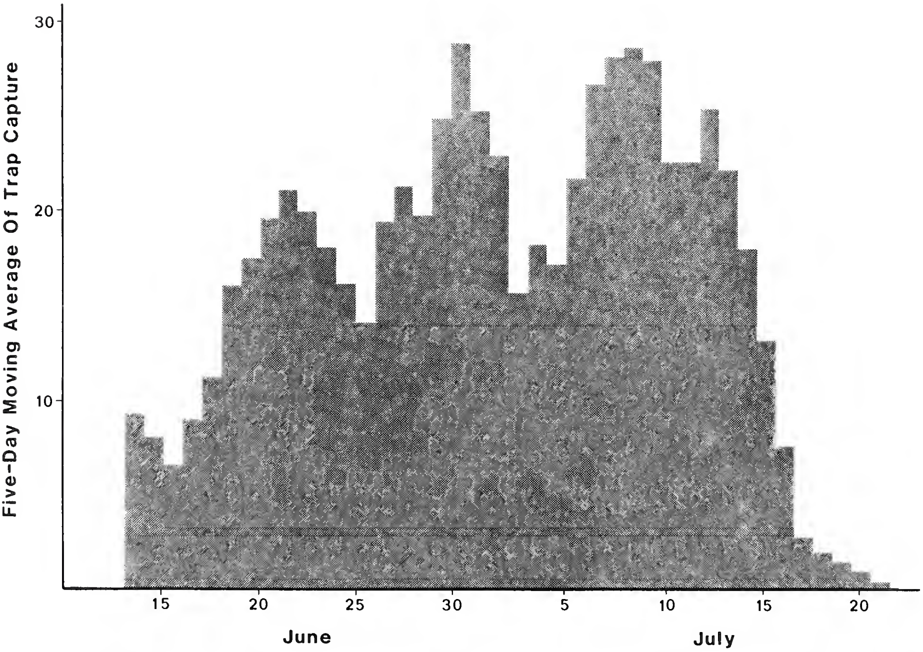

Fig. 2. Five-day moving average of seasonal pheromone trap catch of male cranberry girdler.

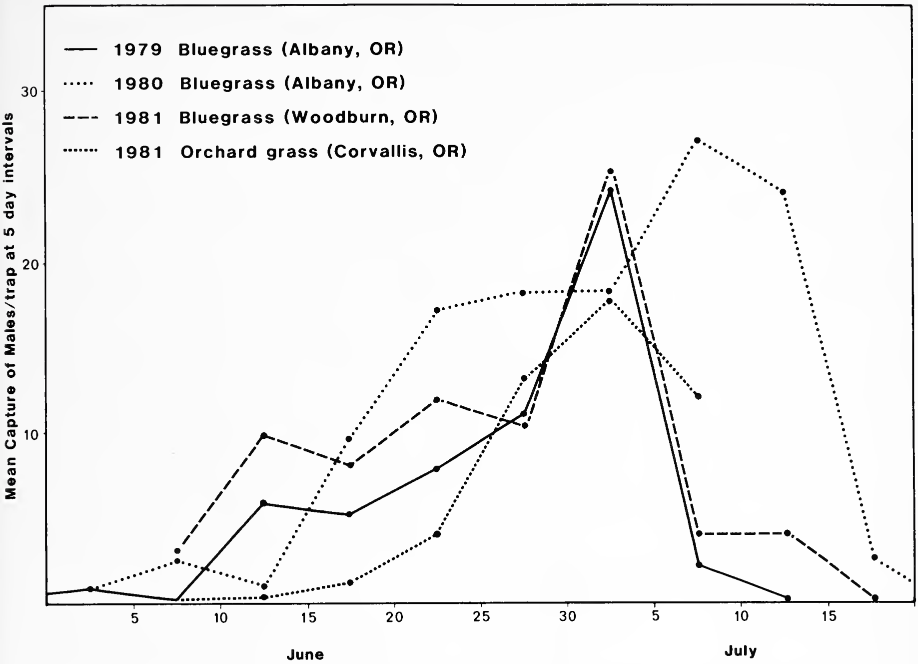

Fig. 3. Seasonal flight of the cranberry girdler in 4 fields in different years and locations.

Daily variation in trap data (Fig. 1) can be reduced by computing a 5-day moving average (Fig. 2). The resulting histogram closely approximates seasonal abundance and duration of the flight period determined with light traps (Crawford and Harwood 1964). Even though pheromone traps measured both flight activity and population density, the traps provided a reasonable estimate of seasonal abundance except when trap catches decreased during the two periods of cool rainy weather (near June 24 and July 3).

Fig. 3 shows the adult trap captures in 4 fields in different years and locations when trap captures are averaged every 5 calendar days. Notice that populations peaked July 1–5 in 1979 and 1981 and July 5–10 in 1980. The cumulative heat units since Jan. 1 for each year at peak flight were:

Year	Date of peak flight	Cumulative heat units °C at peak flight
1979	July 1–5	877
1980	July 5–10	847
1981	July 1–5	849

The mean cumulative heat units for the 3 years was 857, and peak flight in all three years occurred remarkably close to the mean. Peak flight for each of the three years would be close to the mean summation of 857 heat units even though peak flight occurred on different calendar dates. Notice also that 90 percent of the moths were captured in each field over a period of 30–35 days. The decline of the adult population may be accelerated when fields are windrowed for harvest by elimination of canopy shelter. However, none of the bluegrass fields was windrowed for harvest before July 11, and in 2 of these fields the population had declined drastically before windrowing.

Information about population density in advance of larval damage is difficult to obtain, and often the stand of grass is damaged before the infestation becomes noticeable. Since pheromone traps measure both flight activity and population density, it is nearly impossible to forecast precise population density with 90–95 percent accuracy. Nevertheless, we feel a combination of pheromone trap data and cumulative heat units provides a useful estimate of population density during the flight period. For example, by June 10, 1979, 1980, and 1981, the cumulative heat units were 631, 551, and 577°C, respectively. Therefore, the 1980 population would be expected at a later calendar date than the 1979 and probably the 1981 population. With this information, trap data obtained after June 10 should indicate about when the population will peak and whether the population is sparse, moderate or dense, excluding data gotten during cool and rainy weather.

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NOTES ON THE INTERACTION OF THE SKIPPER BUTTERFLY *CALPODES ETHLIUS* (LEPIDOPTERA: HESPERIIDAE) WITH ITS LARVAL HOST PLANT *CANNA EDULIS* (CANNACEAE) IN MAZATLAN, STATE OF SINALOA, MEXICO

Allen M. Young

Abstract.—The hesperiid butterfly *Calpodes ethlius* is very widely distributed in the subtropical and tropical regions of North, Central, and South America, where the larval stage is a specialized herbivore of various Cannaceae, mostly *Canna.* The larvae are known to be occasional defoliators of cannas, including ornamental species. Some quantitative aspects of the interaction between *C. ethlius* and several patches of an ornamental species *Canna edulis,* were examined at Mazatlan, State of Sinaloa, Mexico, at the beginning of the dry season. Defoliation from *C. ethlius* was very severe during the previous wet season as indicated by aging conspicuous leaf damage to most plants in all patches, lack of new vegetative growth, and an abundance of old fecal pellets from larvae. Only a few late instar larvae and adults were present at this time. A large number of pupae were found in the host plant patches but more than 90% were parasitized, apparently by a chalcid wasp. Although *C. edulis* blooms profusely here in the early dry season, very few flowers and fruits were present. Presumably the larval population of *C. ethlius* peaks during the latter half of the wet season following a period of steady increase in response to an abundant food supply. The dry season interrupts this trend in abundance and the population drops off. Severe attack by chalcid parasites in the late wet season intensifies this change in population structure. The parasites cause mortality in the pupal stage thus precluding any regulatory effects on the larval population. Such interactions lower the ability of the infested larvae to produce flowers and fruit. Other aspects of these interactions are discussed.

Calpodes ethlius Stoll (Hesperiidae) is a well known medium-sized brown skipper butterfly with an extensive geographical range comprising predominantly southern North America, Central America, and much of South America (Klots 1951: MacNeill in Howe 1975). Several early studies re-

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vealed a life history pattern for *C. ethlius* in which the larvae feed on cannas (*Canna* spp., Cannaceae—see Tietz 1972). Although the Cannaceae is a tropical and subtropical family, native to the West Indies and Central America (Heywood 1978), the widespread popularity of cannas as ornamentals has been a probably significant ecological factor in accounting for the extensive range of this butterfly (MacNeill in Howe 1975). Although the life cycle and association of *C. ethlius* larvae with cannas has been examined (e.g. Cockerell 1892; Scudder 1889; Seitz 1924; Klots 1951, and several other references) and it has been noted that the larvae are sometimes severe defoliators (Klots 1951), there are no published studies on the quantitative aspects of the butterfly's interaction with the host plant. The purpose of the present paper is to report one short-term study on the abundance of larvae and pupae of *C. ethlius* in different patches of *Canna edulis* in Mazatlan, State of Sinaloa, Mexico at the beginning of the dry season, and to make a preliminary assessment of the possible ecological impact of the butterfly on the host plant. This is not an attempt to establish broad generalizations about the population biology of this obviously very successful species, as to do so would require long-term studies in many regions.

Locality and Methods

The distribution and abundance of larvae and pupae, along with notes on adults, of *C. ethlius* were studied in Mazatlan (18°02′N; 96°54′W), State of Sinaloa, along the Pacific Coast of Mexico, 12–14 November 1979. This region is best described as coastal tropical dry forest, with mostly open and scattered scrub forest (Fig. 1) save for large tracts of experimental agricultural lands for *Citrus* and other crops. A strong and long dry season occurs here each year, usually from the end of October through June. A large portion of the natural plant communities of the region go deciduous during the dry season.

Within the last seven years, Mazatlan experienced a large expansion of the tourist industry, resulting in the construction of several major hotels with extensive gardens and recreational grounds containing numerous ornamental plants, including numerous patches of *Canna* plants (Fig. 2). Discussions with three local gardeners employed by hotels revealed that the patches of *Canna* were generally less than six years old. In the central (old) section of the city, however, *Canna* has been present in scattered small patches in homes. At the time of this study there was a total of eight patches of *Canna* associated with two hotels and one small shopping center in the tourist area. Other patches of *Canna* were undoubtedly present at other hotels but these were not examined.

I counted the number of *C. ethlius* larvae and pupae (including empty and parasitized pupae [Fig. 3]) in eight different patches of *Canna*. This was

Fig. 1. The open scrub forest habitat characteristic of the Mazatlan region.

done by carefully examining each plant within a patch, unfolding rolled leaves and opening the characteristic tent-like structures made by the larvae. The relatively large final instar larva (60–65 mm) and pupa (38–42 mm) make it easy to locate *C. ethlius* on its host plants. The size distribution of larvae was noted. With the exception of four larvae taken for rearing to confirm species, the larvae and living pupae were left undisturbed following the census. Samples of obviously parasitized (dead) pupae were also taken. The number of plants in each patch was recorded, along with the heights of the plants and numbers of flowers and fruits. An estimate of defoliation activity by *C. ethlius* was obtained by counting the numbers of leaves with at least 20% surface area missing and bearing the easily-recognized defoliation pattern of the larger larvae of this species. The ground beneath each patch was also examined for the presence of fresh and old feces of the larvae. The incidence of successfully-eclosed *C. ethlius* in each patch was estimated by counting the number of empty pupal cases (Fig. 3). The pupae and pupal cases of *C. ethlius* can generally be counted accurately as they are usually protected within the individual tent-like structures made by the larvae prior

Fig. 2. (A) Typical hotel garden environment in the tourist area of Mazatlan where patches of *Canna edulis* (Cannaceae) are grown as ornamentals. (B) Typical patterns of leaf destruction from larvae of *Calpodes ethlius* on its host plant, *Canna edulis*; usually only 1–2 per leaf.

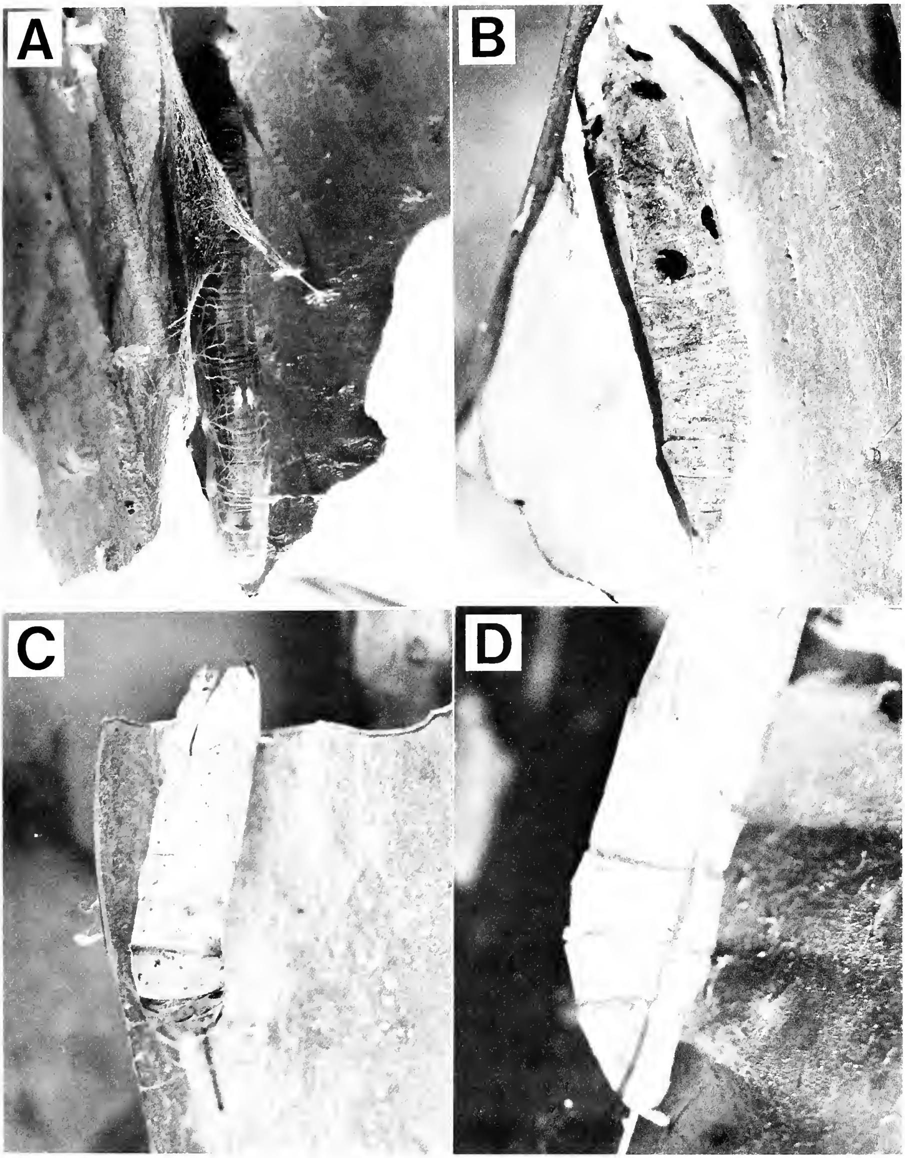


Fig. 3. (A) Final instar larvae of *C. ethlius*. Note internal structures visible through thin cuticle and the silk netting lining the opened tent-like structure. (B) Parasitized pupa of *C. ethlius* showing exit holes of apparently chalcid wasps. (C–D) Intact pupal shells following adult eclosion; note the long proboscis case (D) characteristic of *Calpodes*. Healthy, parasitized, and empty pupal shells are found inside the tent-like structures built by the larvae.

to pupation. Most or all individuals pupate on the host plant, or within a patch of the host plant. The host plant patches selected for study were widely distributed with most inter-patch distances being greater than 30 meters, but with the closest distance between one particular pair being 500 meters, and between another pair, only one meter. Records were kept on the coniditions of plants in these patches to determine whether or not there was a pattern of plant healthiness with the abundance of *C. ethlius*. Other ornamentals were examined briefly to check for signs of defoliation. A sample of healthy larvae was brought to Milwaukee for completion of the life cycle. Various patches of flowers in the many surrounding gardens were examined for adult *C. ethlius*, as this particular skipper is well known to visit flowers (Klots 1951). Searches for adults were also made at the larval host plant patches.

Results

The sizes of the eight *Canna* patches studied as host plant resources for *C. ethlius* ranged from 10 to 150 mature plants. These patches (Figs. 4–6) showed varying but noticeable levels of defoliation by larval *C. ethlius* (Fig. 7) with the percentage of defoliated plants (Fig. 4) ranging from 90–100%. The percentages of defoliated leaves (Fig. 7) in patches ranged from 80–95%. The herbivore damage on most plants in all of the patches was not fresh. The damaged leaf edges were generally brown and dry. When cut with a knife, leaf edges of *Canna* do not become brown for at least three days and probably considerably longer. A large patch of about 100 plants contained about 500 leaves whereas small patches, those with 10–15 plants, contained about 100 leaves. Height range was very similar for all eight patches, being 0.75 to 1.5 meters. The abundance of flowers (Fig. 7) was very low: there were 0–3 flowers among the different patches. Fruits were absent from three of the patches with the following distributions among the patches: 26 fruits on 13 stalks, 22 fruits on 9 stalks, 8 fruits on 4 stalks. Of the total of 56 fruits present, 50 were brown and partly dehisced with the hard black seeds exposed; the remaining few were green. Fruits (Fig. 6) were scarce relative to the numbers of plants in the patches. Only close to full-grown larvae and empty pupal shells were present at this time (Fig. 3). A total of 11 larvae were found, with none found in four of the patches. One patch of about 100 plants had more than 1,000 old fecal pellets beneath them, while another patch of only 48 plants also had more than 1,000 pellets. Of 135 pupae found, 132 or 97% were parasitized, all by the same species of an undetermined chalcid wasp. The parasite exit holes were the same (Fig. 3) in all of these pupae, suggesting a single species of parasite. Only two eclosed pupae were found, and one living pupa. No other insects were found feeding on the cannas at this time. A total of four adult *C. ethlius*

Fig. 4. One of the patches of *Canna edulis* examined for defoliation by *Calpodes ethlius* in Mazatlan. This patch contains 97 plants; note flower stalks above the leaf canopy.

were seen at two different flower patches on a single morning during a two-hour observation period split between the patches. The adults exhibited considerable home-range movements at the flower patches, darting off from perches on leaves (Fig. 8) only to return a short time later. One other skipper, *Quinta cannae* (Herrich-Schaffer), presumably another *Canna*-feeder, was seen at the flower patches. Larvae or pupae of *Q. cannae* were not found in the patches studied.

The larva of *C. ethlius* builds at tent-like structure (Fig. 7) folding over the edge of a leaf and anchoring it in place with two widely-spaced multi-stranded bands of silk. Owing to a very thin cuticle (Fig. 3) it is probably very vulnerable to desiccation, especially in dry areas such as Mazatlan. Larvae feed primarily after dusk and on the same leaves where their tents are located (Fig. 7). In the laboratory in Milwaukee, the pupa stage lasted 11 days, with a rapid darkening within 48 hours of eclosion. Full eclosion is also very rapid, the adult requiring only about four minutes to fully expand the wings (Fig. 8).

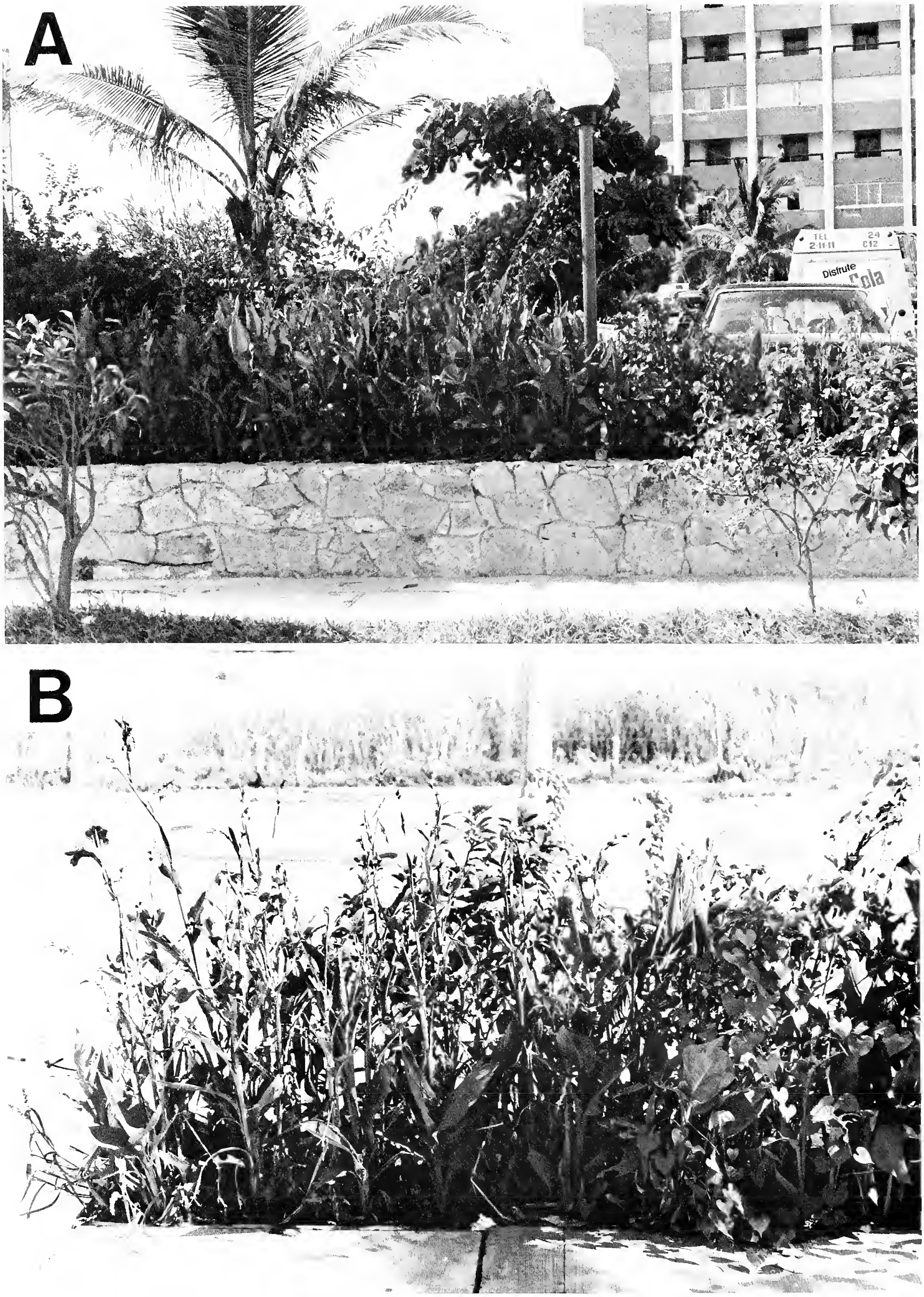


Fig. 5. (A–B) Two other patches of cannas in Mazatlan examined for *C. ethlius*. Note the considerable "thinning out" of leaves from larval feeding (B).

Fig. 6. (A–B) In addition to large patches of cannas, there were also two small patches studied. Both large and small patches exhibited signs of considerable defoliation by *C. ethlius* larvae.

Discussion

Peaks in adult populations of *C. ethlius* in the Mazatlan area, and perhaps in other very seasonal tropical and subtropical regions, are predicted to be synchronized with the growing (wet) season, based upon the age-structure of the population studied here. The low abundance of larvae, pupae, and adults indicates that the population was beyond its period of greatest abundance. My discovery of predominantly old herbivore damage and old fecal pellets indicates further that the period of intense larval abundance had passed. Although the larvae of *C. ethlius* are well known to be occasional severe defoliators of *Canna* (Klots 1951), the impact of the larvae on the host plant population may be a very seasonal occurrence in regions such as Mazatlan. The generation time of *C. ethlius* is probably on the order of 40 days, given the observed duration of the pupa stage and my own experience studying butterfly life cycles in the tropics for the past 11 years. A wet season period of about five months permits three, and possibly four, generations of *C. ethlius*. For many tropical plants, the wet season is the period of maximal vegetative growth (Janzen and Schoener 1968), thus providing an expanded resource base for many herbivorous insects inhabiting seasonal

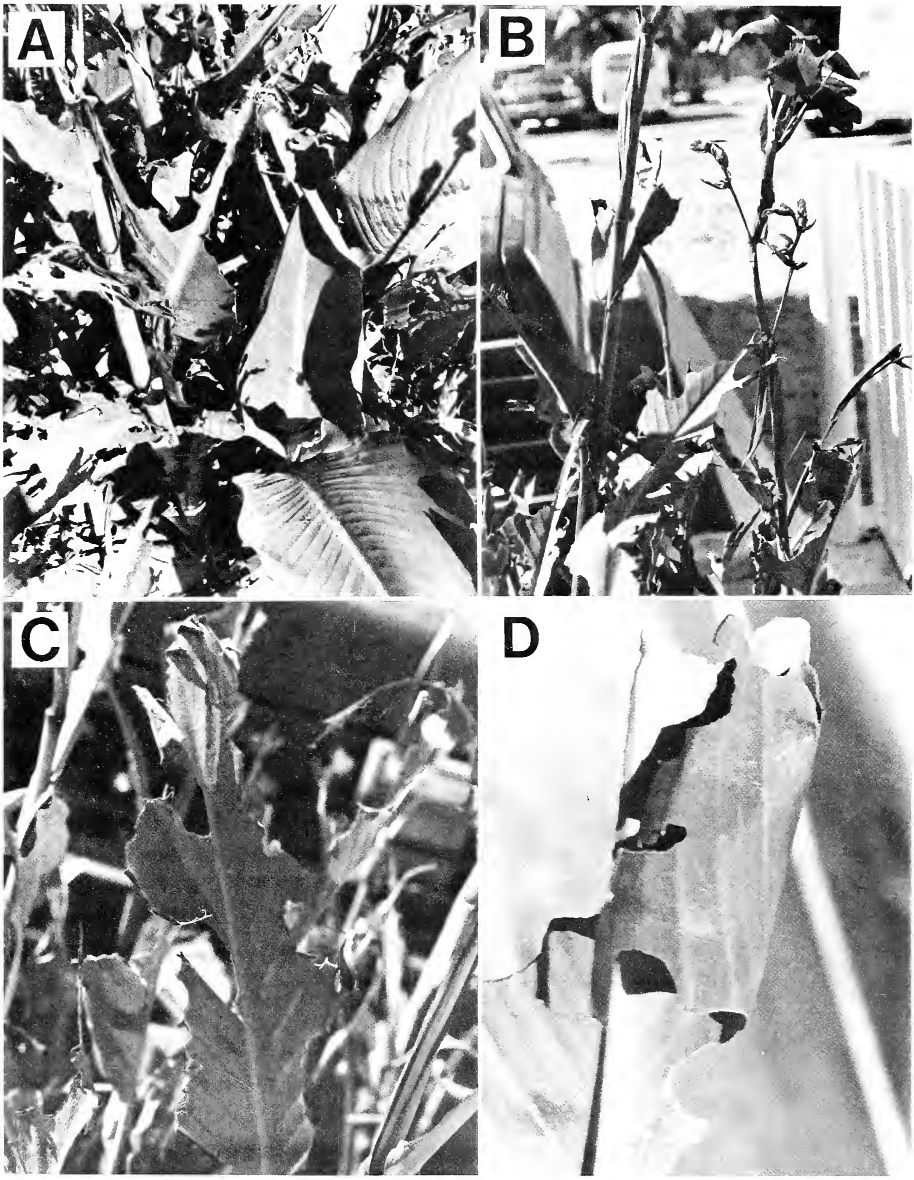
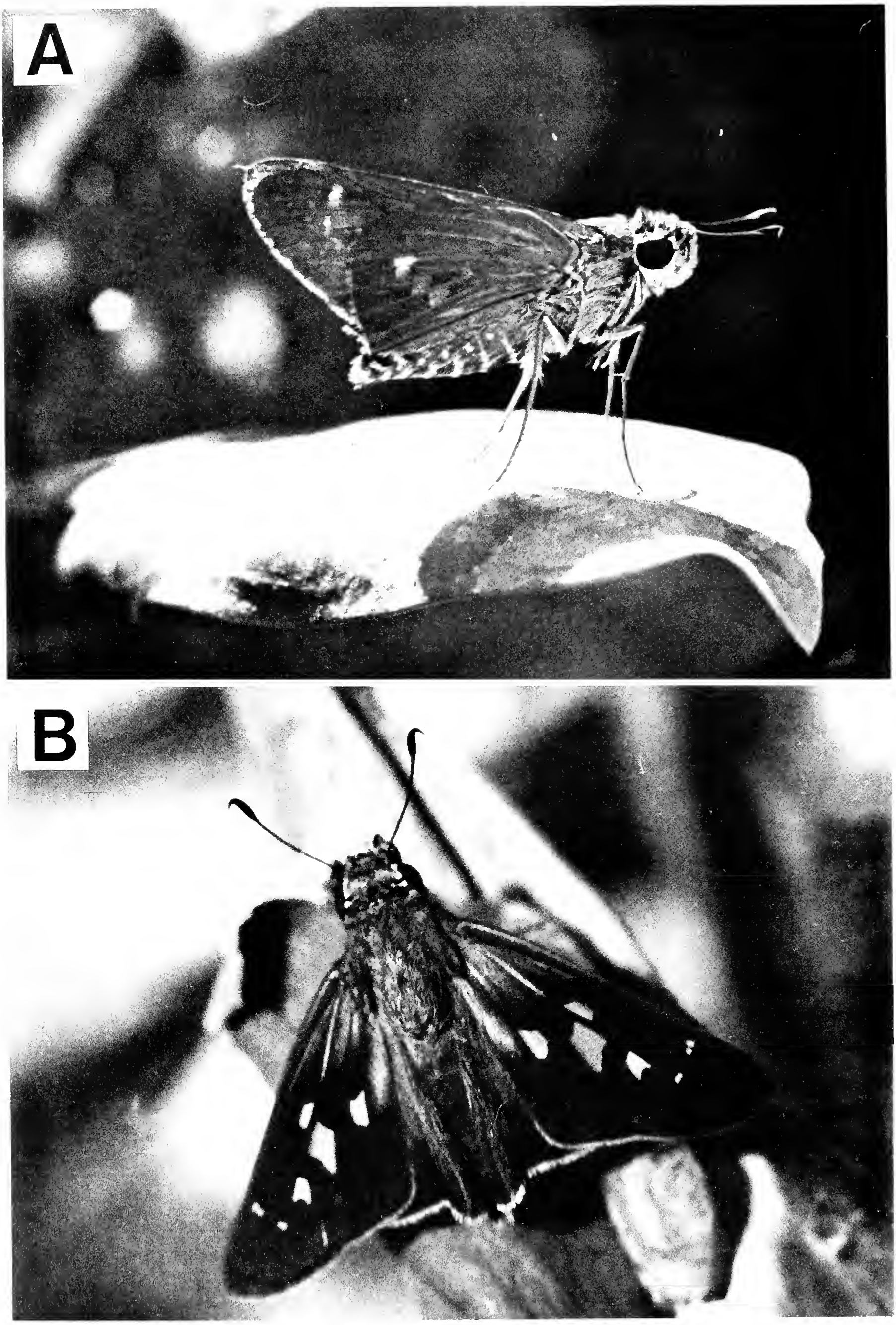


Fig. 7. (A) Generally more than 90% of the leaves within a single patch of cannas were heavily defoliated by *C. ethlius*; the contrast between a few surviving intact leaves and defoliated leaves is shown here. (B) Very few plants possessed the very conspicuous red flowers even though blooming is generally high early in the dry season. (C) Generally between 20–90% of the leaf surface area were devoured by *C. ethlius* larvae in each patch of cannas studied. (D) *In situ* tent-like structure housing a *C. ethlius* larva; the larva feeds on the same leaf.

environments (Wolda 1978). Under such conditions, there will be strong selection for synchronization of maximal breeding with the wet season in herbivorous insects such as *C. ethlius*. Yet the presence of the tail-end of the immature population during the very early dry season at Mazatlan indicates that such synchronization is somewhat variable, with some overlap between the seasons. The tent-building behavior of the larvae of *C. ethlius* may be adaptive in permitting completion of a generation in the early phase of the dry season in that the shelter, and after-dusk feeding, reduce the chances of larval death from severe desiccation in the open exposed habitats of this region. Such behavior may also preadapt this species to occupy new environments otherwise impenetrable owing to dry conditions, thus contributing to the widespread geographical distribution of the butterfly. Clearly more extensive and long-term field studies are needed to confirm these ideas on the survival of *C. ethlius* in very seasonal environments. As a basis for such studies, a preliminary prediction from my observations in Mazatlan in the early dry season would be that *C. ethlius* attains peak abundance and reproductive activity in the latter half of the wet season, and the population experiences a drastic decline by the beginning of the dry season. Severe herbivore damage of *Canna* patches also occurs in the latter half of the wet season. The age-structure of the *C. ethlius* population during this period consists primarily of adults and larvae, particularly the first three instars. Larvae of two or more generations are abundant at this time. By the beginning of the dry season, the age-structure shifts to a reduced number of adults and very few larvae if any at all. Whether or not adult *C. ethlius* breeds during the long dry season of this region or enters into a reproductive diapause is not known at this time. The observed age-structure of the population at the beginning of the dry season suggests a very depressed abundance of adults at this time.

Calpodes ethlius probably has its greatest impact on the *Canna edulis* population during the latter half of the wet season, a time in which the larval population is peaking in abundance. A good example of this impact is seen in the fact that virtually all plants in the eight patches studied were severely defoliated by *C. ethlius*. Very little new growth was present and the plants were entering into a period of synchronized flowering and fruiting. I learned from two different gardeners familiar with some of the patches studied that (1) flowers are most abundant near the end of the wet season, and fruits during the first half of the dry season, and (2) these patches show signs of severe defoliation each year. The observed high incidence of parasitized pupae suggests that most larvae, even those parasitized, complete the larval stage and pupate, and such mortality therefore does little to regulate herbivore pressure on the host plant. It does, however, reduce recruitment of


A
B

new adults. Whether or not earlier generations in the wet season experience intense parasitism needs to be studied.

The point at which larvae are parasitized is another unknown factor is this system. It is clear, however, that the last major wave of pupae in the population were heavily parasitized and resulted in very low recruitment of new adults. Therefore, it is most likely that seasonality molds the population dynamics of this butterfly. The advancing wet season results in a build up of the population and a gradual depletion of food supply so that when the dry season arrives, food supply is even further reduced by lack of new growth and the breeding population declines. The availability during the late wet season or early dry season of a reduced larval population consisting of later instars, provides a suitable resource base for a hymenopterous parasite which in turn reduces the adult population even further. The early dry season may also be a period very favorable for the parasites thus increasing their impact as a regulatory factor on the *C. ethlius* population. Many parasites are generalists on several species of Lepidoptera in a region, and as some of these host species ''drop out'' of the herbivore community as the wet season closes, such generalists concentrate on the few remaining species.

Given the size and pattern of emergence holes of the parasites seen on the *C. ethlius* pupae, the suspected parasite is a chalcid wasp, and perhaps a species of *Spilochalcis*. The exit holes and their distribution on pupae resembles very closely *Spilochalcis* parasitism of *Opsiphanes tamarindi sikyon* Fruhstorfer in Costa Rica (Young and Muyshondt 1975). Cockerell (1892) reported high incidence of egg parasitism of *C. ethlius* by another hymenopterous parasite, *Trichogramma* sp., and suggested that such mortality regulates the abundance of this butterfly in Jamaica. With the exception of this observation and that presented here, little is known about the parasites of *C. ethlius*. Whether or not the population in Mazatlan experienced egg parasitism is not known, although perhaps not since larvae were very abundant in at least the late wet season as indicated by the abundance of pupae at that time.

When large larval populations build up on *Canna* patches, they will have a severe defoliating effect, perhaps to the point of reducing leaf surface area to the point where differentiation of flowers and fruit is impaired. Very few

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Fig. 8. (A) *Calpodes ethlius* perched on the leaf of an ornamental plant in a garden in Mazatlan (13 November 1979, 1100 hours). The butterfly is set for flying off as the species exhibits considerable home-range movements involving sudden darting flights and perching periods. (B) A fresh *C. ethlius* within five minutes after eclosion (in Milwaukee, 24 November 1979, 1500 hours).

flowers and fruit were present in all eight patches studied and this scarcity of reproductive structures on mature plants could have been due to the interplay of severe herbivore pressure from *C. ethlius,* and the synchronization of flowering with another time of the year. These observations suggest that herbivore damage by *C. ethlius* reduces the abundance of flowers and fruits in infested patches of *Canna* in Mazatlan. The interaction between *Canna edulis* and *C. ethlius* is intensified further by the observation that this butterfly is a specialized herbivore of Cannaceae, and primarily *Canna* (Scudder 1892; Seitz 1924; Klots 1951; Tietz 1972; MacNeill in Howe (1975) although the Cannaceae share a very close phylogenetic history with the bananas (Musaceae), gingers (Zingiberaceae) and arrowroots (Marantaceae) (Heywood 1978), checking members (ornamental species) of these groups in Mazatlan revealed no larvae or pupae of *C. ethlius,* nor any signs of extensive herbivore damage indicative of larval *C. ethlius.*

Based upon the above considerations, I suggest that Klots's original remark (Klots 1951) about *C. ethlius* larvae that "sometimes they are abundant enough to be destructive" be expanded to consider the interplay of seasonality of climate, vegetative growth patterns of the host plants, and impact of parasites. Another factor to be considered in long-term studies of this interaction relates to the status of *Canna* species as ornamentals. A major portion of the geographical distribution of *Canna* species results from these plants being used as ornamentals in regions where wild species do not occur. Apparently the group had its origin in Central America (Heywood 1978) thriving primarily in moist or wet forest areas. The expansion of these plants as ornamentals into drier regions such as the Mazatlan area provides an evolutionary opportunity for the herbivores normally associated with wild populations to "track the environment" and penetrate new regions where the plants have been introduced. Whether or not under such conditions *C. ethlius* leaves behind its natural regulatory agents (predators and/or parasites) associated with it on wild host plants needs to be determined. Sometimes when a herbivorous insect enters into a new adaptive zone (host plant) it leaves behind its natural enemies (Janzen 1973). If wild host plants are scarce or absent from the region where the ornamentals are being introduced, *C. ethlius* as a colonizing species will concentrate on infesting patches of the ornamentals. It would not be surprising to discover that virtually all patches of *Canna edulis* in the Mazatlan area are severely damaged each year from such an effect. Given the climatic regime of this area, it is unlikely that wild patches of host plant exist, and the known distribution of this butterfly through Baja California and mainland Mexico (MacNeill 1975) is probably largely determined by the presence of ornamental cannas. Being a very strong flier and having the habit of depositing eggs singly on the host plant contribute to *C. ethlius* successfully dispersing itself among patches of cannas. Depending chiefly upon (1) the intensity of seasonal conditions affecting phenological patterns of vegetative and reproductive growth of the host plants at a locality, (2) the relative abundance of wild and ornamental host plant patches, and (3) the kinds of predators and parasites present, *C. ethlius* adult populations will vary in size at different times of the year. Thus population structure and dynamics of *C. ethlius* will vary considerably both spatially and temporally, to varying degrees. The impact of this insect as a specialized herbivore on cannas is also expected to vary considerably, even to the extent that under some conditions it is one of the determinants influencing the spread of the host plant once the latter is established as an ornamental in a new area.

Acknowledgments

This field research was accomplished while I was attending the 27th Tropical Region Meeting of the American Society for Horticultural Sciences held in Mazatlan, State of Sinaloa, Mexico. I thank Richard I. Smith (ICI de Mexico) and Miguel Holle (CATIE, Turrialba, Costa Rica) for their assistance with identifying the species of *Canna.* I thank Lee D. Miller (Allyn Museum of Enotmology) for confirming the identification of the butterfly, and also for assistance with some of the early references cited in this paper. This paper is dedicated to the gardeners at the several hotels along the northern "tourist strip" in Mazatlan.

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BOOK REVIEW

Butterflies of the Rocky Mountain States. Clifford D. Ferris and F. Martin Brown, eds. U. Oklahoma Press. 442 p. 4 color plates. 1981. $35 hardbound; $15.95 softbound.

This book is a comprehensive and updated field guide that will be most welcomed by butterfly collectors who could no longer obtain the out-of-print *Colorado Butterflies* by Brown, Eff, and Roger (1957). The prefactory chapters describe the biogeography and geology of the region from the Canadian border to northern New Mexico, as well as some butterflies from the Black Hills and the Pine Ridge Escarpment of South Dakota and Nebraska. All of the species and most of the butterfly subspecies of North America in the four major families, Hesperioidea, Papilionoidea, Lycaenoidea, and Nymphaloidea are illustrated by black-and-white photographs and many are shown in the 4 color plates. Life histories, flight periods, habitats, as well as common names are included. There is a complete glossary of terms, a general bibliography, and distribution maps. The excellent illustrations and well-organized text add to the usefulness of this book. This very reasonably priced field guide will serve not only the serious collector, but also a wide audience, including weekend naturalists and young butterfly collectors.

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OVIPOSITION BY TWO *HELICONIUS* SPECIES: COMMENTS ON A PAPER BY DR. A. YOUNG

L. E. Gilbert

Abstract.—Corrections and comments are made concerning the paper by A. Young on *Heliconius cydno* and *H. sapho* and their host plants.

I disagree with a number of observations and with the taxonomy in Young's paper on host-plant relations of *Heliconius cydno* and *sapho* (N.Y. Entomol. Soc. 88, 1980, pp. 217–227). Young places *H. sapho* in the "*melpomene*" group with *H. cydno*. However, the paper cited by Young (Benson et al. 1976) clearly places *H. sapho* with *H. hewitsoni, H. eleuchia,* and *H. congener*. These species are more closely allied with the "*erato*" group as they share the trait of pupal mating (Gilbert 1976). The "*sapho* group" is also known to utilize only the *Astrophea* subgenus of *Passiflora* (Benson et al. 1976), one of which, *P. pittieri,* is widespread in Costa Rican rainforests, from low to middle elevation.

I have cultured *H. cydno, H. sapho* and *H. hewitsoni* in tropical insectaries here in Austin and my students and I have observed these and other species oviposit in the field. *H. cydno* is a generalist (Smiley 1978); ovipositing on most available *Passiflora* in forest understory and in light gaps. It typically lays single eggs but will place two eggs on a shoot when shoots are limited (see Williams and Gilbert 1981). On the other hand, Atlantic side *H. sapho* and its close relative on the Pacific side of Costa Rica, *H. hewitsoni,* are strictly monophagous on *P. pittieri*. This plant has a tree-like growth form but can also be a liana. It grows in spurts punctuated by total absence of new growth. *H. sapho* and *H. hewitsoni* always place clusters on young shoots. In fact, females of these species are very choosy, using only a restricted stage of shoot development. (Beyond a certain point, young larvae would be unable to feed on maturing leaves which are extremely tough in this *Passiflora* species.)

In Costa Rica *H. cydno,* a mullerian mimic of *H. sapho* and its close relative, *H. pachinus,* a mullerian mimic of *H. hewitsoni,* both occasionally oviposit on *P. pittieri* but have a lower per capita survivorship on those

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shoots than the clusterlaying specialist (J. Longino, personal communication).

Young's *Passiflora* identifications require corrections. The individual labelled "*Granadilla* A" (fig. 1B) is unmistakably *Passiflora pittieri* Masters, an Astrophea. The other "*Granadilla* A" (fig. 2A, B) is equally unmistakably *Passiflora ambigua* Hemsl., a common liana in Costa Rican rainforests. *P. ambigua* is a member of *Granadilla* and is a recorded host for both *H. cydno* and *H. pachinus* in Costa Rica (Benson et al. 1976). Both *P. pittieri* and *P. ambigua* lack tendrils as young understory plants and develop tendrils as mature vines. In rearing both of these *Passiflora* from seedlings, I have noticed several consistent features which allow identification. The best character for young plants is the placement of extra floral nectaries. There are typically ½ to ⅔ of the way along the petiole toward the leaf base in *P. ambigua* as can be clearly seen in Young's fig. 2A, B. Extra floral nectaries of *P. pittieri* are conspicuous at the leaf base in unfolded new leaves (Young's fig. 4C) but hidden under the leaf at the apex of the petiole in older leaves (Young's fig. 1B, fig. 3A).

An additional problem concerns the specific identification of these mimetic *Heliconius*. The black and white butterfly depositing "large clusters" on *P. pittieri* is *H. sapho,* not *H. cydno.* For example, fig. 4A, p. 223 show *H. sapho,* not *H. cydno.* The shape of the white fore-wing patch, clearly visible in Young's fig. 4A, is diagnostic of *H. sapho.*

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ERRATA: OVER-EXPLOITATION OF LARVAL HOST PLANTS BY *HELICONIUS* BUTTERFLIES

Allen M. Young

I take this opportunity to agree with, and to thank, both Drs. Keith S. Brown, Jr. and Lawrence E. Gilbert for expressing their concern for the errors I made in the paper discussed by Gilbert (1982). My errors were initially pointed out to me by a letter from Dr. Brown, and subsequently I received a copy of an earlier version of Dr. Gilbert's manuscript. In this note I wish to explain the sources of my errors appearing in Young (1980).

My error in confusing *Passiflora pittieri* for a species of *Granadilla,* as pointed out by both Drs. Brown and Gilbert, arose from a superficial comparison of a photograph with the plant shown in figs. 1–3 (Young 1980), which was determined by Brown (pers. comm., 30 April 1977) to be *Granadilla*. Gilbert (1982) disagrees with this determination. My error was compounded by not having a voucher specimen for determination. I hesitated to collect the individual plant in question because I wanted to observe possible repeated *Heliconius* oviposition on both plants over a year or longer. Neither plant was therefore collected. *Granadilla* and *P. pittieri* are systematically far apart from one another in the evolution of the Passifloraceae (Benson et al. 1976). Furthermore, Laurifoliae is a series, not a subfamily (Benson et al. 1976).

My misidentification of *Heliconius sapho* as *H. cydno* in fig. 4 (Young 1980) came from missing the clearly diagnostic small red patch at the base of the hindwing, very visible in the ovipositing butterfly and in the photograph (fig. 4) as a small light area. The butterfly had not been collected to make a confirmative determination. At the time it did not occur to me that the shape of the white fore-wing patch (seen in my fig. 4A) is also diagnostic of *H. sapho* as pointed out by Dr. Gilbert in the accompanying note. I simply did not know this. *Heliconius sapho* is not in the *melpomene* group (Benson et al. 1976) as I incorrectly stated in my paper.

Members of the *H. sapho* group customarily lay large numbers of eggs on individual host plants (Benson et al. 1976; Brown 1981), thereby explaining the high abundance of eggs I reported (Young 1980). *Heliconius sapho* typically lays 10–40 eggs on a rapidly growing meristem (Brown 1981). Dr.

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Brown (pers. comm.) believes that the reproductive strategy of members of the *H. sapho* group includes the possibility of sometimes laying many more eggs on an individual host plant than can survive, so it is sometimes observed that only one or two larvae make it to pupation. This may be related to the frequent "explosive" mode of growth of young shoots on the *Astrophea* host plants (Benson et al. 1976). Thus one may assume that the high density of eggs observed on the second host plant in my study is typical oviposition behavior of *H. sapho,* and that the butterfly exhibits the same behavior on large host plant individuals as well as on small ones which are expected to grow rapidly.

Gilbert, in the accompanying note, has comprehensively summarized detailed information on the oviposition behavior of both *H. cydno* and *H. sapho* in relation to larval host plants, and has clarified how to distinguish the larval host plants in my study.

In the study discussed here, I was not able to follow two standard procedures I use for confirming the identifications of host plant and butterfly species used in my other published field studies in Costa Rica. I did not, in Young (1980), collect the butterfly or host plant material, thereby increasing markedly the potential for my margin of error.

In closing, I am appreciative of the professional concerns expressed by Drs. Brown and Gilbert in relation to the errors appearing in my paper (Young 1980). I thank the editor of this journal for giving me the opportunity to clarify the nature of these unfortunate mistakes. I offer particular thanks also to Dr. Keith S. Brown, Jr. for his encouragement and assistance with clarifying these errors, and for reading over an earlier draft of this note.

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MIRIDAE AND COLEOPTERA ASSOCIATED WITH TULIP TREE FLOWERS AT ITHACA, NEW YORK

David Andow

Abstract.—The Miridae and Coleoptera on tulip tree (*Liriodendron tulipfera* L.) flowers were examined in June, 1979 at Ithaca, New York. The mirids are mainly *Lygocoris caryae* and *L. omnivagus,* and are probably attracted to tulip tree to feed on the flowers. The mirid-flower association changes with the age of the flower; young flowers support a larger mirid fauna than older flowers. The Coleoptera are mainly Cantharidae and Cephaloidae. Notes on the feeding behavior of these insects are recorded. These are the first feeding records for *Cephaloon lepturides, Cantharis scitulus, C. rectus,* and *Podabrus brunnicollis,* and the first records for *Lygocoris caryae, L. omnivagus, L. tiliae, L. hirticulus,* and *L. belfragii* on tulip tree.

The tulip tree or yellow poplar, *Liriodendron tulipifera* L. is an important hardwood in the Appalachian region. It is distributed from central Massachusetts to Ontario and Wisconsin, and southwest to Florida, Mississippi, and Arkansas (Wiegand and Eames 1925), and is relatively common in rich, light, loamy woodland soils. Its northern limit passes through upper New York State.

More than 100 species of insects have been reported to feed on the leaves and stems of tulip tree (Felt 1905; Felt and Rankin 1932; Herrick 1935; Doane et al. 1936; Burns and Gibson 1968; Burns 1970; Peigler 1976; Futuyma and Gould 1979). The pollinators of *L. tulipifera* are not known but may be similar to those on *Magnolia acuminata* L. (Downes 1973; Thien 1974; Thien et al. 1975).

Flowers are an important resource for insects. Current research on pollination ecology has focussed on competition between pollinators for flower products and between plants for pollinators (Feinsinger 1976; Heinrich 1976; Rathcke and Poole 1977; Poole and Rathcke 1979). However, parasitoids, predators, and herbivores also consume flowers and flower products. Evans and Murdoch (1968) found that 68 percent of the adult insect fauna of an old field in Michigan were flower feeders. The insects utilizing many species of flowers have been described (Kerner 1878; Robertson 1928); Wheeler and

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Henry (1976) present observations on five species of mirids that feed on honey locust flowers, and Henry (pers. comm.) has observed both nymphs and adults of *Neurocolpus nubilus* feeding on and damaging petals of tulip tree in Pennsylvania. This paper describes the associations of flower feeding mirids and Coleoptera on *Liriodendron tulipifera* flowers at Ithaca, New York.

Materials and Methods

Two individuals of *Liriodendron tulipifera* on Turkey Hill in Ithaca, New York were observed on the edge of a weedy lawn, surrounded by poplar, yellow birch, white pine, white ash, basswood, hickory, and oaks. The trees are about 50 feet tall, and first started blooming on June 7, 1979, continuing through June 25.

On June 8 and 9 general collections were made from about 300 flowers. On June 10, all the insects were removed from the open flowers on four low branches, and haphazardly twenty of these flowers were designated as "old flowers." Eight "young flowers," opening between the mornings of the 10th and 11th, were also identified. Insects were collected from these flowers for the next five consecutive mornings between 0600 and 0700 hours. On June 14, five more newly opened flowers were added to the young flower sample.

On June 10 at 0700 hours, twenty mirids in six flowers were marked with fluorescent dusts sprayed into the flowers. No insects left these flowers immediately after marking. At 0800 the following morning, all the mirids in those six flowers were collected and identified.

Results and Discussion

A total of 55 Miridae and 47 Coleoptera were collected in 150 flower-days of sampling (Table 1). Most of the Miridae (96 percent) were species of the genus *Lygocoris*, and most of the Coleoptera were represented by the families Cantharidae (55 percent) and Cephaloidae (38 percent).

Miridae.—All the mirids were observed feeding in the flowers, mainly on the lower portion of the carpels. It is not known if they damage the seed. No nymphs of any of the species were seen on tulip tree during the period of observation. *L. tulipifera* is probably only an adult feeding host for these insects.

Lygocoris caryae breeds on hickory (*Carya ovata*, and *C. alba*), and to a lesser extent on pecan, and walnut (Knight 1917; Blatchley 1926; Smith 1940; Kelton 1971). It has also been found on *Rhus typhina*, *Tilia americana*, *Robinia pseudoacacia*, *Quercus* sp., and *Juniperus virginiana* (Knight 1941; Kelton 1971). It can cause economic damage on peaches and pears (Caesar 1920; Ross and Caesar 1921, 1927; Garman 1936; Smith 1940; Knight 1941),

Table 1. Number of insects caught in young and old *L. tulipifera* flowers. A single flower-day sample consists of the insects accumulating in one flower during one 24 hour period. *L. belfragii* was collected while general collecting on June 8 and 9. All insects were identified by the author, and are deposited in the Cornell University collection under C.U. Lot #1108.

	Young flowers 50 flower-days	Old flowers 100 flower-days	χ^2
Miridae	37	19	
Lygocoris caryae (Knight)	18	9	13.5*
L. omnivagus (Knight)	14	7	10.5*
Other mirids**	5	3	—
Cantharidae	12	14	1.92
Cantharis scitulus Say	0	3	—
C. rectus Melsheimer	9	9	2.25
Podabrus spp.†	3	2	—
Cephaloidae			
Cephaloon lepturides Newman	7	11	0.29
Other Coleoptera††	2	0	—

* $P < 0.005$, all others n.s.

** *L. tiliae* (Knight), *L. hirticulus* (Van Duzee), *L. belfragii* (Reuter), *Taedia* sp., and *Monosynamma bohemani* (Fallen).

† *P. brunnicollis* Fab. and *P. rugulosus* LeConte.

†† *Grammoptera haemetites* (Newman) [Cerambycidae] and *Orsodacne atra* (Ahrens) [Chrysomelidae].

migrating as far as 300 yards into orchards, returning to hickory to oviposit. Its economic damage is often severe, but highly variable in space and time.

Lygocoris omnivagus has been reported from a large number of hosts, breeding on oaks (*Quercus alba, Q. rubra,* and *Q. coccinea*), and to a lesser degree on *Cornus florida, C. circinata, Castanea* sp., and *Viburnum acerifolium* (Knight 1917; Blatchley 1926; Knight 1941). Kelton (1971) reports it from numerous other species. It too can cause significant damage to peaches and pears (Ross and Caesar 1921, 1927; Garman 1928, 1936; Kelton 1971), migrating to orchards to feed, and returning to its host plants to oviposit.

L. tulipifera is a new feeding record for both of these species, and also for *Lygocoris tiliae, L. hirticulus,* and *L. belfragii*. The individuals I caught probably migrated to tulip tree from nearby host trees, where they will return to oviposit. Many of the individuals I observed were covered with tulip tree pollen, so they may be pollinators. But many bees and wasps were also observed working the flowers, so the importance of mirids as pollinators is unknown.

Coleoptera.—Little is known about the biology of the Cantharidae. *Cantharis* spp. are known to feed on aphids, mealybugs, and plant materials such as pollen and nectar (Motizambert 1908; Essig 1926; Fluke 1929; Balduf 1935; Claussen 1940). *Podabrus* spp. also feed on aphids and pollen (Webster 1876–83; Blatchley 1910; Wilson 1913; Essig 1926; Fluke 1929; Smith 1936; Claussen 1940; Fender 1973).

The cantharids on *L. tulipifera* flowers were observed feeding on the pollen and other litter that collects in the bottoms of the flowers. My observations are the first feeding records for *Cantharis scitulus, C. rectus,* and *Podabrus brunnicollis*. Although *P. rugosulus* is known to eat aphids (Blatchley 1910; Fluke 1929), this is the first record of it eating plant material.

The association of adult *Cephaloon lepturides* with *L. tulipifera* is the first published ecological record for adults of this species. This is an active beetle, more so than the smaller cantharids, and moves rapidly inside the flowers. It is not known if these beetles eat plant material. In captivity, I observed *C. lepturides* to kill and eat an adult of *L. caryae* and *L. tiliae* in a manner similar to the cantharids (Motizambert 1908; Tilden 1950).

The insect-flower associations change with age, young flowers supporting a different mirid fauna than old flowers (Table 1). This was also observed in the general collections on the 8th and 9th. *Lygocoris caryae* and *L. omnivagus* were more abundant in young flowers than old flowers. All the beetles appeared in flowers older than 3 days. Since these beetles are pollen feeders, they may be attracted to flowers after anther dehiscence.

The mirids may be displaced from the older flowers by the cantharids and *Cephaloon lepturides*. The beetles move around inside the flowers much more than the mirids, often bumping into them. The mirids stop feeding to move and avoid the beetles. These interruptions may limit feeding time so that the mirids leave the older flowers that have beetles to find a better, more available food resource. Also, since these beetles may be potential predators, the mirids may be avoiding predation.

Alternatively, flower quality may decline with age and the mirids are avoiding low quality flowers. Of the marked mirids, only 55 percent stayed in the same flower for a day. None of these flowers contained beetles, so this shows that the mirid-flower association is ephemeral and that mirids move enough to be able to respond rapidly to factors such as changes in flower quality and availability.

Even in such a temporary resource as flowers there are regular changes in herbivore presence. Be it a decline in flower quality with time or displacement by beetles, the mirid fauna changes rapidly, apparently exploiting just a portion of a flower's life.

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SUSCEPTIBILITY OF GYPSY MOTH LARVAE TO SEVERAL SPECIES OF ENTOMOGENOUS FUNGI

S. S. Wasti and G. C. Hartmann

Abstract.—Several species of fungal entomopathogens were tested for infectivity on larvae of the gypsy moth, *Lymantria dispar* (L.). Spore suspensions in varying dosages were administered to the larvae via surface treatment of sterilized oak leaves. High levels of mortality were obtained for most of the test species of fungi. *Conidiobolus thromboides, Fusarium* sp., *Hirsutella thompsonii,* one strain of *Paecilomyces farinosus* and *Verticillium* sp. were non-infective to gypsy moth larvae under the conditions of the experiment.

Introduction

The infectivity of entomogenous fungi on gypsy moth larvae has been demonstrated on the basis of qualitative and histopathological studies (Hartmann and Wasti 1974, 1976; Wasti and Hartmann 1975, 1978; Wasti et al. 1980). Toxicity tests on non-target invertebrate and vertebrate hosts have established the environmental safety of these candidate biological control agents (Donovan-Peluso et al. 1980; Hartmann and Wasti 1976, 1980; Hartmann et al. 1979; Wasti et al. 1980). Quantitative studies on the effect of specific dosage levels on mortality of gypsy moth larvae were the primary objectives of the present study.

Methods

Larvae of the gypsy moth, *Lymantria dispar,* were reared from eggs supplied by the Forest Insect Disease Laboratory, Hamden, Connecticut. Entomogenous fungal species tested for infectivity against these larvae were:

1. *Beauveria bassiana* (Bals.) Vuill. Russian strain
2. *Beauveria bassiana* (Bals.) Vuill. (*B. tenella*) ATCC 26156
3. *Cordyceps militaris* (Fries) Link ATCC 26848
4. *Conidiobolus thromboides* Drechsler (*Entomophthora virulenta*) (Hall & Dunn) Latge et al. (1980) ATCC 14270
5. *Fusarium* sp. (local strain)

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6. *Hirsutella thompsonii* (Fisher) ATCC 24874
7. *Metarhizium anisopliae* (Metsch.) Sorokin ATCC 22099
8. *Paecilomyces farinosus* (Dicks. ex Fr.) Vuill. ATCC 24319
9. *Paecilomyces farinosus* (Dicks. ex Fr.) Vuill. USDA, Hamden, Ct. strain
10. *Paecilomyces fumoso-roseus* (Wize) Brown & Smith ATCC 16312
11. *Nomuraea rileyi* (Farlow) Samson, Missouri strain
12. *Verticillium* sp. (local strain)

Stock cultures of the various species of fungi were subcultured on Potato-dextrose agar and yeast extract (PDAYE) under procedures outlined by Hartmann and Wasti (1974). Culture isolates of the test species were then passed in serial succession through larvae of the wax moth, *Galleria mellonella* L. in order to increase virulence by passage through an easily inoculated host.

Infectivity studies were considered initially using the surface treatment technique recommended by Garcia and Ignoffo (1978) for infecting larvae with entomogenous fungi. Spore suspensions representing calibrated dosages of the fungal species were administered in sterile Petri dishes (dia. 60 mm) by spreading them over the surface of artificial gypsy moth diet under conditions recommended by O'Dell and Rollinson (1966). Results with this technique were unsatisfactory and the method proved unsuitable. There was difficulty in distributing low spore concentrations uniformly over the surface and infection rates with early instars were extremely low. Elimination of the antifungal agents in the diet increased the likelihood of infection by non-target saprotrophic fungi.

As an alternative, the leaflet technique described by Garcia and Ignoffo (1978) was used for the infectivity studies and was found to provide satisfactory results. Fresh oak leaves were surface-sterilized by immersion for several minutes in a one per cent solution of sodium hypochlorite and thoroughly rinsed with sterile distilled water. Appropriate dilutions of fungal spore suspensions were applied to the surface and each leaf was placed in a sterile Petri dish.

Fifty second instar larvae were surface-sterilized by immersion in a solution of Zephirine chloride (1:750) followed by a sterile water rinse, placed in each Petri dish, and allowed to feed on the leaves for 48 hours. Subsequently, the larvae were transferred to individual plastic chambers and observed at 24 hr intervals. The following spore dosages of each test organism were administered: 50, 100, 500, 1,000, 5,000 spores/mm^2. Untreated leaves were set up as controls and fed to a group of 100 2nd instar larvae used as controls. Each spore dosage was administered to 50 larvae.

Infected larvae were placed on sterile Petri dishes containing Potato Dextrose agar plus 0.5% yeast extract (PDAYE). One half gram Streptomycin

Table 1. Percentage mortality of gypsy moth larvae treated with surface applied suspensions of entomogenous fungi.

	50		100		500		1,000		5,000	
Dosage spores/mm^2	72 hr	120 hr	72 hr	120 hr	72 hr	120 hr	72 hr	120 hr	72 hr	120 hr
B. bassiana	56	92	88	88	92	92	90	90	96	96
B. tenella	80	96	90	98	90	90	92	92	98	98
C. militaris	66	90	88	92	92	98	90	98	100	100
M. anisopliae	72	94	94	100	94	100	98	100	98	100
N. rileyi	80	96	90	100	98	100	100	100	92	100
P. farinosus	72	96	88	98	88	98	88	100	100	100
P. fumoso-roseus	84	100	88	100	92	100	96	100	88	100

and 0.5 g Penicillin G were added after the PDAYE was autoclaved for 15 min at 15 pounds pressure. The target organisms were recovered in all cases.

Results

The mortality rates of gypsy moth larvae to various dosages of entomogenous fungal spore suspensions have been summarized under Table 1. Control larvae showed 3% mortality after 72 hours and 5% mortality at the end of 120 hours. Of the 12 test species, 5 were considered non-infective under the conditions of the experiment. These were, *Conidiobolus thromboides, Fusarium* sp., *Hirsutella thompsonii, Paecilomyces farinosus* (Hamden, Ct. strain) and *Verticillium* sp.

Paecilomyces fumoso-roseus, Metarhizium anisopliae and *Nomuraea rileyi* were considered highly infective as 100% mortality was recorded within 120 hours of treatment with dosage levels as low as 100 spores per square millimeter of leaf surface. There was a linear dosage-mortality response and five of the seven infective species produced 100% mortality at the high dosages of 1,000 and 5,000 spores/mm^2. The target fungus was recovered from dead larvae and survivors did not show any adverse effects as a result of the treatment.

These tests simulate natural conditions as leaf surfaces were used for administration of the dosages. Entomogenous fungi exhibit varying levels of mortality against gypsy moth larvae and 5 of the 12 test species were non-infective.

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HABITAT DIFFERENCES IN FEEDING HABITS AND BODY SIZE OF THE PREDATORY STINKBUG *PERILLUS CIRCUMCINCTUS* (HEMIPTERA: PENTATOMIDAE)

Edward W. Evans[1]

Abstract.—Near Ithaca, New York, *Perillus circumcinctus* reproduces in stands of *Bidens cernua* and *Solidago* spp. (Compositae) in early summer. Nymphs of this predator consume larvae and adults of the beetle *Calligrapha californica coreopsivora* (Chrysomelidae) in stands of *B. cernua,* and primarily larvae of *Trirhabda* spp. (Chrysomelidae) in stands of *Solidago.* Newly molted adults of *P. circumcinctus* in stands of *Solidago* are larger than newly molted adults of *P. circumcinctus* in stands of *B. cernua.* It is suggested that differences in the physical structure of the two habitats result in nymphs of *P. circumcinctus* experiencing more difficulty in harvesting prey in stands of *B. cernua.* Increased difficulty in harvesting prey results in smaller adult sizes.

Introduction

The predatory stinkbug *Perillus circumcinctus* Stal (Hemiptera: Pentatomidae) is a specialized predator of beetles of the family Chrysomelidae (Hart and Gleason 1907; Vestal 1913; Knight 1923; Parshley 1923). In the Ithaca, New York, area this univoltine predator usually oviposits in stands of goldenrod (*Solidago* spp.) and reproduction is timed so that nymphs mature by feeding almost entirely on beetle larvae of the genus *Trirhabda* (Chrysomelidae) (Evans 1982a). While studying the habits of *P. circumcinctus* near Ithaca, I found this species in only one additional habitat, stands of *Bidens cernua* (Compositae). A comparison of the seasonal patterns, feeding habits, and adult body sizes of *P. circumcinctus* in *B. cernua* and *Solidago* provides a perspective on the ability of this predator to exploit chrysomelid beetles as prey.

Observations

On 3 July 1979, a dense but very local population of *P. circumcinctus* was found in stands of *B. cernua* on the edge of a small pond (Bull Pasture Pond,

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Cornell University Golf Course). Both nymphs and adults of the predator were feeding on larvae and adults of *Calligrapha californica coreopsivora* Brown (Coleoptera: Chrysomelidae). Voucher specimens of both predator and prey have been placed in the Cornell University Insect Collection under Lot 1086. The age structure of the *P. circumcinctus* population on *B. cernua* was very similar to that of populations of the predator on or about the same date in stands of goldenrod (Evans 1982a): fourth- and fifth-instar nymphs and adults predominated, although younger nymphs (including a group of newly hatched first-instar nymphs) were also present. Several clusters of hatched eggs of *P. circumcinctus* were found on the vegetation. Relatively few late-instars of larvae of the beetle were present but adults were common.

Twenty meters distant grew a small (20 × 10 m) but dense stand of goldenrod where nymphs and adults of *P. circumcinctus* also occurred. Adults of *P. circumcinctus* were collected in both habitats. Vernier calipers were used to measure length from the anterior tip of the pronotum to the posterior tip of the abdomen and width across the widest part of the abdomen. Adults of *P. circumcinctus* from goldenrod at Bull Pasture Pond and other localities were of similar size. However, adults from *B. cernua* were unusually small (Tables 1 and 2; $P < .001$ for length and width of both sexes in t test comparisons of adults from *B. cernua* vs. from goldenrods at all sites).

All adults of *P. circumcinctus* were marked and released in both habitats, after measuring them. No marked individuals were recaptured. By mid-July, individuals of *P. circumcinctus* were much less numerous in both habitats and most individuals were adults. No larvae of *C. californica coreopsivora* were found and adults were also much less abundant than formerly. Adult

Table 1. The mean ($\bar{x}$) ± two standard errors (SE), range, and sample size (N), of lengths and widths (mm) of *P. circumcinctus* females captured on comparable dates in early and mid-July in 1979 in stands of *B. cernua* and *Solidago* (BPP: Bull Pasture Pond, Brk: Brooktondale; descriptions of the Brooktondale and Whipple sites appear in Evans 1980).

				Length		Width	
Vegetation	Site	Date	N	$\bar{x}$ ± 2 SE	Range	$\bar{x}$ ± 2 SE	Range
Bidens	BPP	July 3	9	7.9 ± 0.1	7.8–8.1	5.5 ± 0.1	5.4–5.6
Solidago	BPP	July 3	2	8.3 —	8.1–8.5	5.6 —	5.5–5.7
	Brk	July 3	10	8.4 ± 0.1	8.2–8.7	5.8 ± 0.1	5.5–6.0
	Whipple	July 1	22	8.5 ± 0.1	8.2–8.8	5.8 ± 0.1	5.6–6.1
Bidens	BPP	July 18	4	7.9 ± 0.1	7.6–8.2	5.4 ± 0.1	5.3–5.7
Solidago	BPP	July 18	2	8.4 —	8.3–8.4	5.6 —	5.6–5.7
	Brk	July 17	3	8.3 ± 0.1	8.3–8.4	5.8 ± 0.2	5.6–6.0
	Whipple	July 19	11	8.3 ± 0.2	7.5–8.7	5.6 ± 0.1	5.2–5.8

Table 2. The mean ($\bar{x}$) ± two standard errors (SE), range, and sample size (N), of lengths and widths (mm) of *P. circumcinctus* males captured on comparable dates in early and mid-July 1979 in stands of *B. cernua* and *Solidago* (BPP: Bull Pasture Pond; Brk: Brooktondale).

				Length		Width	
Vegetation	Site	Date	N	$\bar{x}$ ± 2 SE	Range	$\bar{x}$ ± 2 SE	Range
Bidens	BPP	July 3	17	7.3 ± 0.1	6.9–7.6	5.1 ± 0.1	4.9–5.4
Solidago	BPP	July 3–4	4	7.7 ± 0.2	7.6–7.9	5.5 ± 0.2	5.3–5.7
	Brk	July 3	13	7.7 ± 0.1	7.4–8.0	5.4 ± 0.1	5.2–5.6
	Whipple	July 1	11	7.6 ± 0.1	7.3–8.2	5.3 ± 0.1	5.0–5.6
Bidens	BPP	July 18	4	7.4 ± 0.1	7.3–7.5	5.1 —	5.1
Solidago	BPP	July 18	3	7.6 ± 0.1	7.5–7.7	5.3 ± 0.1	5.2–5.4
	Brk	July 17	6	7.3 ± 0.2	6.8–8.2	5.1 ± 0.2	5.0–5.6
	Whipple	July 19	11	7.4 ± 0.1	7.2–7.6	5.1 ± 0.1	4.8–5.4

females of the predator from *B. cernua* were still unusually small in comparison to females in goldenrod stands (Table 1; $P < .01$ for length, $P = .10$ for width in t test comparisons). However, adult males did not differ significantly in either length or width in the two kinds of vegetation (Table 2).

On 5 July 1979 I visited a second stand of *B. cernua* at the edge of a small pond several km west of Ithaca. *Calligrapha californica coreopsivora* was very abundant (much more so that at Bull Pasture Pond), but only a few nymphs and two adult males of *P. circumcinctus* were found in an extensive search. Sparse stands of goldenrod grew on hillsides surrounding the pond. In one of these stands, a single *P. circumcinctus* adult male was collected. As at Bull Pasture Pond, this individual was larger (length: 7.5 mm, width: 5.4 mm) than the two males collected from *B. cernua* (7.3 and 7.0 mm in length, 5.0 and 4.8 mm in width, respectively).

Discussion

The predator-prey relationship of *P. circumcinctus* and *C. californica coreopsivora* in stands of *B. cernua* bears strong resemblance to the relationship between the predator and its prey (*Trirhabda*) in stands of goldenrod (Evans 1982a). Both prey have sluggish larvae which briefly occur in great densities in early summer. Nymphs of *P. circumcinctus* easily subdue the sluggish larvae of *Trirhabda* (Evans 1982b). The weak responses of *C. californica coreopsivora* larvae when probed with a pencil suggest that these larvae are also easily captured by stinkbug nymphs. The similarity in age structure of *P. circumcinctus* populations in stands of goldenrod and *B. cernua* in July suggests that the predator's timing of reproduction is similar in both habitats. Thus the development of *P. circumcinctus* nymphs apparently is well synchronized with availability of *C. californica coreopsivora* larvae as prey in stands of *B. cernua* in fashion similar to patterns of predator and prey observed in goldenrod stands (Evans 1982a).

The major difference between individuals of the predator in the two habitats is the difference in body size of newly molted adults. The rate that nymphs consume prey has a dramatic effect on subsequent adult size in *P. circumcinctus* (Evans 1980). Thus the striking difference in body size of adults maturing at the same time in adjacent stands of *Solidago* and *B. cernua* suggests that the food supply differed in these two habitats. In particular *P. circumcinctus* nymphs may have experienced greater difficulty in seeking out prey on *B. cernua* than on *Solidago*. Stands of *B. cernua* were less dense than *Solidago* stands, and individual plants touched each other less frequently in *B. cernua* than in *Solidago* stands. Many plants of *B. cernua* were isolated even more because they grew in shallow water. These attributes of *B. cernua* presumably hampered the searching abilities of *P. circumcinctus*; hence *C. californica coreopsivora* was probably protected from the predators by a "moat effect" (Eickwort 1977). In goldenrod stands, predators travelled readily from plant to plant and hence larvae of *Trirhabda* received little protection (Evans 1982b). Further study of the hunting habits of *P. circumcinctus* should reveal the degree to which the physical structure of these two habitats influences this predator's ability to exploit its prey.

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BOOK REVIEW

The North American Grasshoppers. Vol. I. Acrididae: Gomphocerinae and Acridinae. By Daniel Otte. Harvard University Press. 275 p. 1981. $45.

All known species of the slant-faced grasshoppers of North America, including the Caribbean Islands, are illustrated by detailed drawings and 16 full color plates prepared by the author. Keys for genera and species, distribution maps, habitat preferences, as well as grasshopper ecology, behavior and life cycles are discussed in detail. Taxonomic changes made in this volume are included in Appendix I. Genera and species of Gomphocerinae and Acridinae are in Appendices II and III. A glossary of terms and a taxonomic index complete the volume. The book is carefully written, the format of the volume is excellent and typographical errors are rare. The author, Associate Curator of Entomology at the Academy of Natural Sciences in Philadelphia has provided a valuable contribution to the taxonomy of grasshoppers and a definitive reference that will be especially appreciated by all who are interested in these grazing herbivores and pests, as well as by taxonomists, ecologists, and economic entomologists. The forthcoming volumes II and III will comprise the Oedipodinae, Melanoplinae, Romaleinae and other smaller groups.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers University.*

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BOOK REVIEW

Insects: An Anthology of Arthropods Featuring a Bounty of Beetles. Paintings by Bernard Durin, introduction by Paul Armand Gette, entomological commentaries by Gerhard Scherer. Translated from German by Georg Zappler. Hudson Hills. Distributed by Simon & Schuster. 108 p. 34 full color plates. 1981. $50.

This beautiful, large (11″ × 14″) format volume can only be described in superlative. It contains 34 remarkably well reproduced illustrations by Bernard Durin of butterflies, grasshoppers, beetles, wasps, flies, and a scorpion. The full color plates give the impression of superb color photographs, because of the faint shadows in the background. The illustrations of arthropods are unquestionably among the best ever published. Gette's introduction provides a link between art and science, with an anthology of poems and writings about insects by Nabokov, Lewis Carroll, Thoreau, Poe, Heine and others. The delightful book is a treasury of fact and fancy for entomologists as well as for wildlife lovers and all those who appreciate art and fine books. The authors, particularly Bernard Durin, one of the foremost illustrators, and the publishers are to be congratulated for making available this art book to entomologists and nature lovers. The volume will constitute a valuable addition to any university and public library. Its price, justified for an art book with such fine reproductions of the dazzling paintings, unfortunately puts it out of the reach of all but the most affluent entomologists.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers University.*

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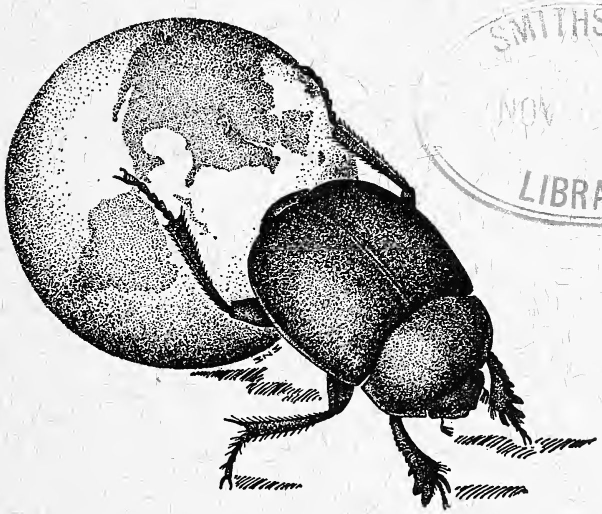

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NEW YORK ENTOMOLOGICAL SOCIETY
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ONSET OF PHONOTAXIS AND AGE AT FIRST MATING IN FEMALE HOUSE CRICKETS, *ACHETA DOMESTICUS* (ORTHOPTERA: GRYLLIDAE)

Scott K. Sakaluk[1]

Abstract.—The age at which females first become phonotactic to conspecific calling song, and the age at which females first mate were studied in the house cricket, *Acheta domesticus* L. (Orthoptera: Gryllidae). The average age at which virgin females first showed positive phonotaxis to tape recorded male calling song was 5.4 days after the last molt. In another group of adult female *A. domesticus,* the average age at which females first mated was 6.9 days, a significantly later age than that for phonotaxis. Early onset of phonotaxis may function to increase mate availability when females become sexually receptive.

Introduction

Formation of sexual pairs in crickets is facilitated by male calling songs which attract females (Alexander and Otte 1967). Species specificity of female cricket phonotaxis to the calling songs of conspecific males has been demonstrated repeatedly (e.g. Forrest 1980; Paul 1976; Popov and Shuvalov 1977; Shuvalov and Popov 1971, 1973; Ulagaraj and Walker 1973; Walker 1957; Zaretsky 1972). Although the pairing function of male calling songs is clear, scant evidence exists indicating a developmental link between female phonotaxis and the readiness of a female to copulate (Stout et al. 1976). Shuvalov and Popov (1971) found that only sexually mature female *Acheta domesticus* (Gryllidae: Gryllinae), 7–10 days after the imaginal molt, exhibited positive phonotaxis. Additionally, Stout et al. (1976) tested responsive and non-responsive female *A. domesticus* (determined by whether a female mounted a male during 30 min of confinement) for phonotaxis: the speed of responsive females in phonotactic locomotion was greater than non-responsive females, although this difference was not significant.

During the course of a study of *A. domesticus* reproductive behaviour

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(Sakaluk and Cade 1980; Sakaluk 1981), the onset of female phonotaxis and the age at which females first mate were quantified. I here report experimental evidence which indicates that females show positive phonotaxis at a significantly earlier age than that at which they first mate.

Methods of Study

Immature *A. domesticus,* purchased from Armstrong's Cricket Farm, Monroe, Louisiana, were housed in a fibreglass chamber containing ample food (Purina® Mouse Chow), cotton-plugged test tubes containing water, and layered egg cartons for cover. Late instar females were removed and held separately, thus ensuring virginity upon the imaginal molt. The nymphs were examined every day and adult females were considered 1 day old on the day they were found to have molted. Crickets were exposed throughout to a 12 h light : 12 h dark photoperiod opposite the ambient photoperiod and at 28 ± 2°C.

To determine the age at which females first mate, 1 day old virgin *A. domesticus* were numbered and observed for 15 consecutive days in a plastic mating arena (78 cm × 49 cm × 10 cm). A jar lid which contained crushed mouse chow, another which contained moistened vermiculite for oviposition, and 2 cotton-plugged test tubes containing water were placed in the arena. The number of females in the arena ranged from 15–20 depending on the molting frequency and the death of some females. The same number of sexually mature males was placed in the arena each day and observed for 2 h under red lights, 3 h into the dark portion of the photoperiod. Age at first mating was recorded for each female.

To determine the onset of positive phonotaxis to male calling song in female *A. domesticus,* a separate group of females was tested using tape-recorded *A. domesticus* song. One day old virgin females obtained from the same colony were housed in a separate terrarium without males. Trials were conducted 1 hour into the dark portion of the photoperiod in a circular arena (105 cm (diam) × 15 cm (ht)) constructed of Styrofoam®; this experiment immediately preceded the test for first mating. The arena contained 2 Phillips AD 0160/T8 loudspeakers embedded in the wall of the arena at a height of 3 cm and 2 red lights at 90° to the speakers. A Sanyo M2211 cassette tape recorder broadcast previously recorded *A. domesticus* calling song through 1 loudspeaker at 70 dB (A scale) as measured with a General Radio Sound Level Meter –1565B held 10 cm in front of the loudspeaker. This sound intensity was consistent with previous measurements of *A. domesticus* males calling in the laboratory. Recordings were made with a Uher 240 CR tape recorder and a Uher M640 microphone. In each trial, a single female was placed under an inverted plastic vial in the centre of the arena. After a 5 min period in which the female was allowed to become

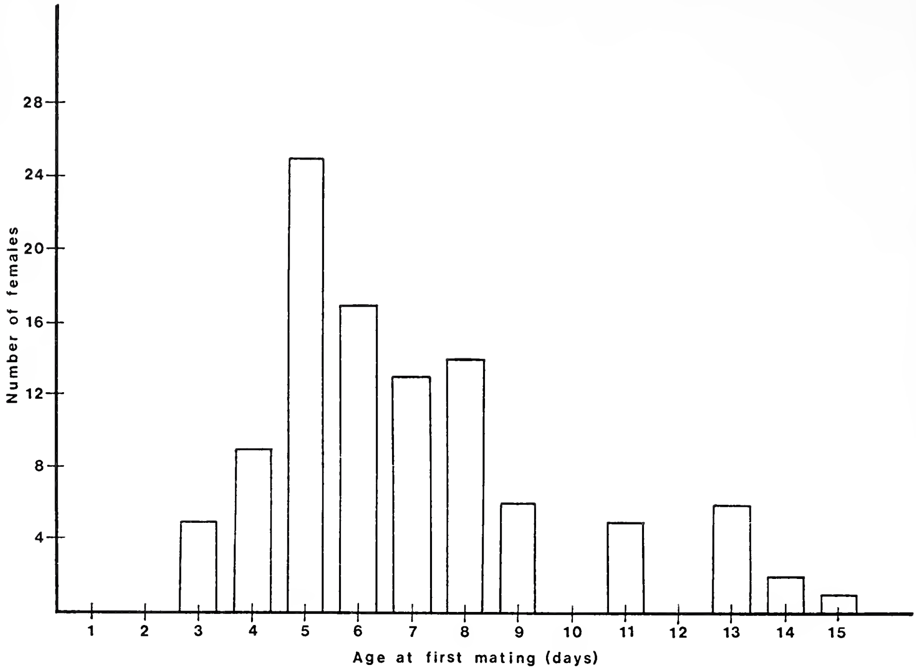

Fig. 1. The age at which female *A. domesticus* first mated.

quiescent, the vial was removed and broadcasting of taped song commenced. A trial lasted until a positive response was recorded, until 5 min had elapsed, or until the female left the arena. A positive response involved a female remaining in a marked area (15 cm × 11 cm) under the speaker and/or on the speaker for a total duration of 1 min of the 5 min trial. All females were tested once every day until a day of positive response was recorded, and 9 of the 28 females were tested for 15 consecutive days regardless of the age at which they first showed positive phonotaxis.

Results

Data on the age at which females first mated are in Fig. 1. Female *A. domesticus* mated for the first time at an average age of 6.9 days (N = 103; SD = 2.7 days). Data on the age at which females first showed positive phonotaxis to conspecific calling song are in Fig. 2. Females were first attracted to a loudspeaker broadcasting *A. domesticus* song at 5.4 days of adult age (N = 28; SD = 2.4 days). The mean number of positive phonotactic responses exhibited by the 9 females tested over 15 consecutive days was 7.8 (SD =2.2; range = 5–11). The mean ages at which females first mated and first became phonotactic are significantly different (t = 2.6; $P < 0.01$).

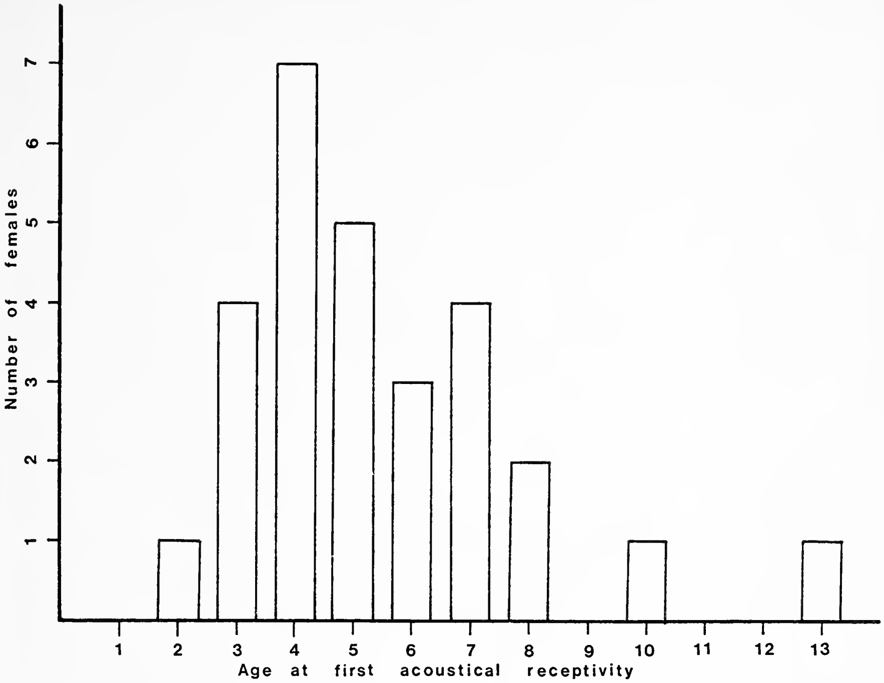

Fig. 2. The age at which female *A. domesticus* first showed a positive phonotactic response to conspecific calling song.

Discussion

The dominant carrier frequency of the male *A. domesticus* calling song is 4.6 kHz, with the maximum sensitivity of the cricket's tympanal ear falling within 4–7 kHz (Counter 1976). However, Shuvalov and Popov (1971) showed that up to 85% of female *A. domesticus,* less than 5 days of age after the imaginal molt, exhibited an escape response when exposed to artificially generated square pulse signals emitted at 4 kHz. This conflicts with our finding that 61% of female *A. domesticus* exhibited positive phonotaxis to broadcast male calling song within 5 days of age. The discrepancy in these results likely reflects the use of different source stimuli.

The close correspondence of onset of female phonotaxis with the age at which females first mated indicates that female phonotactic responsiveness and readiness to copulate in *A. domesticus* are developmentally linked. This is supported further by the similarity in shape of the frequency distributions. However, the onset of female phonotaxis occurred at a significantly earlier age than that at which females first mated. When phonotaxis precedes mating, selection may favour phonotaxis by non-receptive females since males will thus be present when mating is possible. Pair formation is not the only plausible result of female phonotaxis. In mole crickets (Forrest 1980; Ulagaraj and Walker 1973), field crickets (Cade 1979a), and katydids (G. K. Morris, pers. comm.), females may use the conspecific calling song as a cue for resource location.

Females tested for phonotaxis over 15 consecutive days exhibited, on the average, 8 phonotactic responses. Cade (1979b) found that when female field crickets were deprived of males (as was the case here), the frequency of positive phonotaxis was increased significantly. Nonetheless, female *A. domesticus* did not always respond subsequent to the first phonotactic response. It may be that sexually mature females that do not exhibit phonotaxis will not mate.

The age at which females first mate may correspond to when mature eggs are available for fertilization. No ovariole growth occurs in the last nymphal stadium, but begins to increase drastically at an adult age of 3 days in *A. domesticus* (Woodring et al. 1979). Therefore, adult females that mated before the availability of mature eggs might encounter reduced fitnesses due to time and energy expenditures. Also, adult crickets are soft-bodied for about 3 days after eclosing and females might risk physical damage if they mated before the cuticle hardened.

A different situation exists for field crickets, *Teleogryllus commodus* Walker, as females less than 24 h old will mate. Two females that were 4 and 5 h old were observed mating even though the cuticle was soft and the ovaries were immature. Eggs laid by these females were fertilized and yielded viable offspring (Loher and Edson 1973). Additionally, conspecific male calling song does not initiate running activity in female *T. commodus* 3 days of age after the imaginal molt. This suggests that a female is ready to mate before she can be attracted to the male calling song (Loher 1979). These differences clarify the need for further ontogenetical studies, before generalizations concerning the development of female cricket sexual responsiveness can be made.

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I thank Dr. William H. Cade for his guidance during this research project and writing of the manuscript. I also thank Paul Bell, Dr. Glen K. Morris, Dr. W. Gary Sprules, and an anonymous reviewer for comments on the manuscript. Financial support was provided by a Natural Sciences and Engineering Research Council grant to W. Cade (A6174) and an Ontario Graduate Scholarship to S.K.S. Page charges were met by the Department of Zoology, Erindale College at the University of Toronto. This study represents a portion of a thesis submitted to Brock University in partial fulfillment for the M.Sc. degree.

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LARVAL MORPHOLOGY AND PHYLOGENY OF *TRICHORDESTRA TACOMA* (STRECKER) (NOCTUIDAE)[1]

Tim L. McCabe and George L. Godfrey

Abstract.—The larva of *Trichordestra tacoma* (Strecker) (Lepidoptera; Noctuidae) has been misidentified in the past, resulting in a discrepancy in the phylogenetic placement of this species in separate works based on adults and on larvae. Both larva and adult prove to be similar to *T. rugosa* (Morr.) and *T. liquida* (Grote). The larva is described and illustrated, and a host list is presented.

Comparisons of two recent reclassifications of hadenine noctuids based on larvae (Godfrey 1972) and on a section of the adults (McCabe 1980) has yielded a discordance in the phylogenetic placement of *Mamestra tacoma* Strecker (1900). *M. tacoma* has been placed in *Polia* (McDunnough 1938), but recently the genus *Trichordestra* was erected for it and its relatives (McCabe 1980). *Trichordestra* presently includes eight nearctic species, the larvae of which are characterized by two inner mandibular teeth and a striped body pattern in addition to the characters Godfrey (1972) used in his group seven. The adult moths are best defined by three bandlike signa on the female bursa copulatrix.

One of us (TLM) cultured the larvae and discovered that specimens previously determined, by association, as "*Polia*" *tacoma* were actually another, as yet unidentified noctuid larva. True *T. tacoma* larvae have the two inner mandibular teeth so typical of other known *Trichordestra* larvae (Fig. 1). *T. tacoma* larvae were discovered to have two color phases: the typical phase is green and appears unstriped in life, although faint stripes are traceable in preserved larvae; a red color phase has prominent stripes and in this manner is more typical of the genus. Dyar (1904) may have described the green phase of *T. tacoma* larvae.

T. tacoma are related to *T. liquida* (Grote) on the basis of the paired, inner mandibular teeth with the tooth in the second inner ridge being weakly developed (broken off or worn down in some specimens of *T. tacoma*) (Fig.

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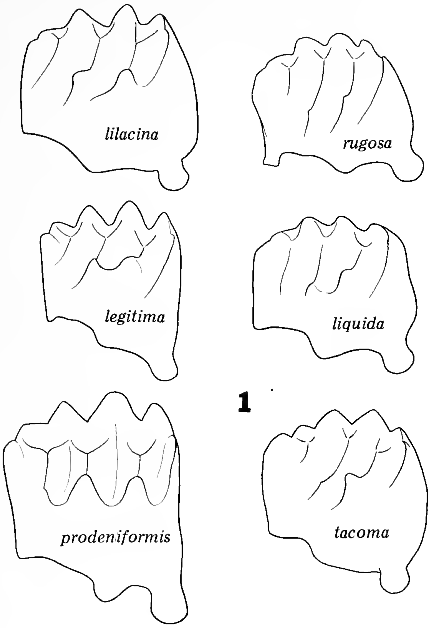

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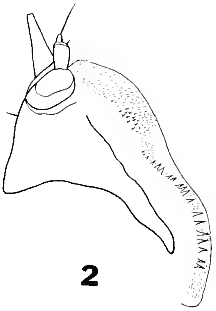

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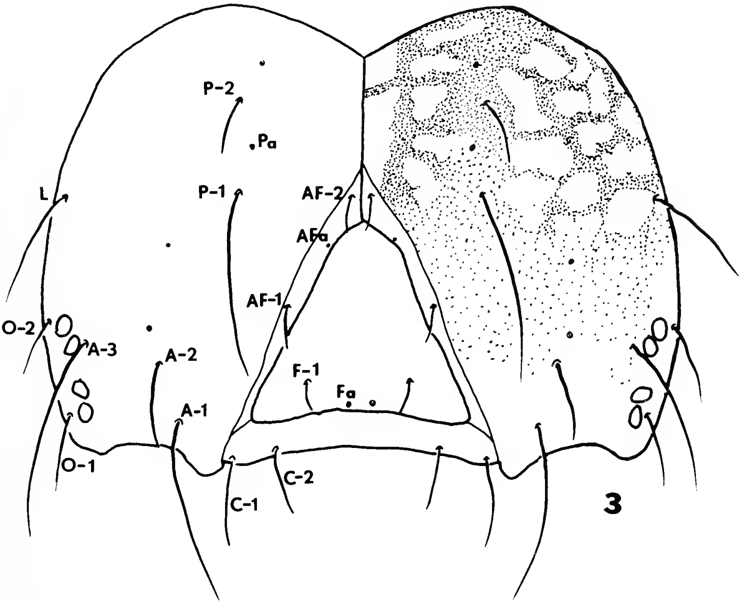

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Figs. 1–3. 1. Oral aspect of the left mandibles of the known larvae of *Trichordestra*. 2. Hypopharynx of the larva of *T. tacoma*. 3. Frontal aspect of the head capsule of *T. tacoma*.

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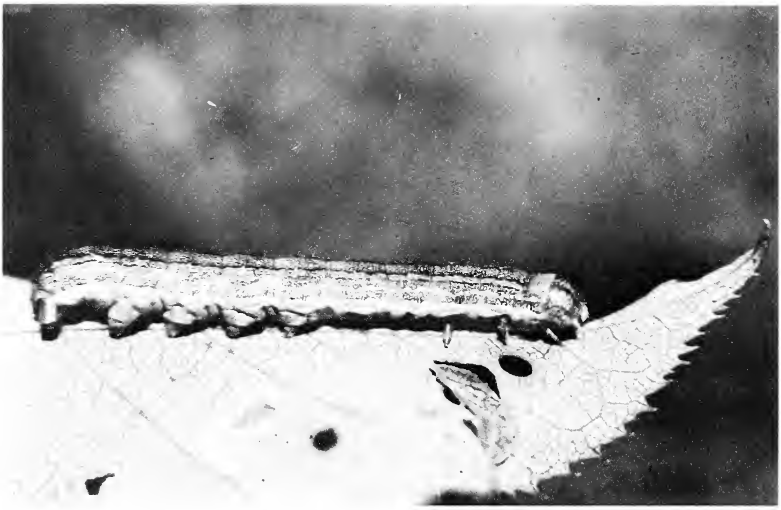

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Figs. 4, 5. 4. Green phase of living larva of *T. tacoma* from the Adirondack Mountains. 5. Red phase larva from the same locality.

1). *T. tacoma* and *T. rugosa* (Morr.) adults have an appendix bursa nearly as large as the bursa copulatrix in the females, asymmetrical valves in the males, and both lack male coremati. The adult male is also similar to *T. liquida* in their similar habitus, similar broad cuculli, and similar asymmetrical valves.

Confined first instar larvae of *T. tacoma* fed on *Apocynum androsaemifolium* L. (APOCYNACEAE), *Sambucus canadensis* L. (CAPRIFOLIACEAE), *Betula papyrifera* Marsh (CORYLACEAE), *Vaccinium myrtilloides* Michx. (ERICACEAE), and *Prunus virginiana* L. and *Spiraea latifolia* (Ait.) Borkh. (ROSACEAE). First instar larvae rejected *Carex* spikes (CYPERACEAE), *Abies balsamea* L. (PINACEAE), and *Viola selkirkii* Pursh (VIOLACEAE). Larvae from an early season female did very well on *Prunus* and were reared to maturity on it, however, larvae from a late-season female had older *Prunus* leaves and did poorly until switched to a non-woody host (*Apocynum*).

First instar larvae have prominent pinaculi, a weakly sclerotized prothoracic shield, and reduced prolegs on the third and fourth abdominal segments. The mature larva is described below.

General (Figs. 4, 5).—Head 2.9–3.0 mm wide; total length (fully expanded) 36 ± 6 mm (N = 14). Abdominal prolegs present on 3–6th and 10th segments.

Coloration (living material).—Green phase (Fig. 4): Soft yellow-green with pale middorsal line, a pair of slightly darker subdorsal bands on each side separated by a narrow pale line, then a pale lateral band which includes the top half of the spiracles followed below by a greenish white subspiracular band which includes the bottom half of the spiracles. Red phase (Fig. 5): Similar to preceding, but much darker, with prominent stripes and with the prevalent color a brownish red.

Head (Fig. 3).—Epicranial suture 0.94 mm long. Height of frons 0.96 mm. Top half of head with reticulate pattern near epicranial suture and between setae P-2 and L. Seta P-1 as long as frons is wide. Ocellar interspaces between Oc1–Oc2 .5 × diameter of Oc2; Oc2–Oc3 1.5 × Oc2; Oc3–Oc4 .5 × Oc3; Oc4–Oc5 2.5 × Oc4; Oc5–Oc6 3.0 × Oc5.

Mouthparts.—Hypopharyngeal complex (Fig. 2): With spinneret as long as labial palpi and apical seta combined (Lpg 1&2 and Lp2); distal region with fine spines; proximolateral region with a row of 19–27 spines. Mandible (Fig. 1): Two shallow inner teeth, 6 triangular outer teeth.

Body segments.—Prothorax: SD-2 and SD-1 lacking pinaculum; L1 and L2 share weakly developed pinaculum. Meso- and metathorax and abdominal segments without pinaculi. Crochets uniordinal, 16–26 on 3rd, 18–26 on 4th, 20–28 on 5th, 22–30 on 6th, and 28–32 on 10th proleg.

Material examined.—14 specimens, 10 kilometers east of Indian Lake, elev. 555 meters, lat. 43.45.30, long. 74.10.14, Hamilton County, New York, 19 June 1977 (12 specimens) and 23 July 1977 (2 specimens), from ova of females collected and determined by T. L. McCabe. All larvae, P1 ♀'s, and reared adults are labelled tlm 77-159a (1st ♀) and tlm 77-159 (2nd ♀). Larvae are deposited in the New York State Museum, the Illinois Natural History Survey, and the United States National Museum.

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DESCRIPTIONS, SYNONYMY AND SEX ASSOCIATIONS IN THE GENUS *EUCERCERIS* (HYMENOPTERA: PHILANTHIDAE)[1]

George R. Ferguson

Abstract.—*E. geboharti, E. melleoides* and *E. sculleni,* n. spp. are described from western North America. *E. barri* Scullen is removed from synonymy, and *E. cavagnaroi* Scullen is elevated from subspecies to species status. *Aphilanthops marginipennis* Cameron is removed from synonymy with *E. rubripes* Cresson and placed in synonymy with *E. canaliculata* (Say). The male of *E. brunnea* Scullen and the female of *E. melanovittata* Scullen are characterized. *E. menkei* Scullen is the female and a junior synonym of *E. melanosa* Scullen.

Since Scullen's (1968) revision of the genus *Eucerceris* much additional material has become available. A study of this material has permitted recognition of three previously undescribed species, some new sex associations, and new or revised synonymy involving other species. The results and conclusions presented here are a continuation of those in Ferguson (1981).

Eucerceris **geboharti** Ferguson, n. sp.
Figure 1

Female.—Length 12–13 mm; forewing 8–9 mm; mandible with broadly triangular tooth deflected inward, slightly recurved, weakly bicuspidate; ventral margin of mandible swollen and elbowed slightly distad of middle, apical margin of clypeal midsection with 2 rounded lobes medially, connected basally, angled outward from plane of face (Fig. 1); preapical setae arising from underside of apical lobes; disc of clypeal midsection convex; eyes diverging below; mesopleural tubercle present; subalar carina strongly produced laterally into a roundly triangular lobe, projecting beyond tegula when viewed from above; scutal punctures separated by 1 to 3 puncture diameters; scutellum and metanotum polished with a few scattered punctures; propodeal enclosure polished with a few scattered punctures and/or weak ridges, median groove linear; mesopleuron ridged between punctures, hypoepi-

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meron with separated punctures; metapleuron densely ridged; propodeum densely striatopunctate except immediately adjacent to enclosure; second submarginal cell of forewing petiolate anteriorly; punctures on anterior and posterior ridges of terga II–IV coarse, well separated, polished between; transverse depressions of terga II–IV with smaller punctures, closely but irregularly spaced; hypopygium flat, with transluscent area; pygidium subtriangular, narrowly rounded apically.

Male.—Length 10–11 mm; forewing 8–9 mm; mandible edentate with small membranous lobe on lower side slightly distad of midlength; clypeal margin with 3 rounded teeth of equal length; eyes slightly divergent below; clypeus sparsely punctate; lower face moderately punctate, upper face and vertex more or less contiguously punctate except punctures separated behind ocelli; subalar carina and punctation of thorax as in female; forewing with second submarginal cell sessile, marginal cell with a basoposterior pocket; fimbriae loosely clumped on sterna III and IV, that on III narrower than on IV; fimbria on sternum V denser, hairs shorter medially, somewhat irregular in length; pygidium narrowed apically, longer than basal width, distance between apicolateral teeth about ½ basal width, strongly incised inside each lateral tooth with middle lobe wider than distance to tooth.

Coloration.—Much like *Eucerceris bitruncata* Scullen with which it has been confused; scape, pedicel and basal 5 or 6 flagellar segments fulvous to red, remainder of flagellum black; ground color of head mostly red in female, mostly black in male, with several yellow marks; thorax with black background and numerous yellow markings, more abundant in male; legs variably yellow, fulvous and red; wing veins yellowish to light brown, membrane lightly yellow stained, lightly infuscated apically; tergum VI red in female, pygidium infuscate apically; pygidium of male yellow to ferruginous.

Holotype.—Female, Utah, [Garfield County], Boulder, VI-28-75 (J. Alcock); University of California, Davis.

Paratypes.—4 males, 4 females as follows: UTAH: 2 females, same data as holotype [UCD, OSU]; 2 males, 2 females, Garfield County, Boulder, 7,200 ft., June 5, 1966 (G. E. Bohart) [USU, OSU]; 1 male, Emery County, July 20, 1921 [OSU]; 1 male, Emery County, Aug. 23, 1921 (Grace O. Wiley) [OSU].

Other specimen.—1 male, UTAH; Sphinx, June 14, 1950 (G. F. Knowlton), heavily cyanided [USU].

The sternal fimbriae of the males of *E. geboharti* are very much like those of *Eucerceris provancheri* (Dalla Torre). The fimbria on sternum V is narrower, more compact and the hairs are of more uniform length in the latter species. The two broadly rounded median lobes of the apical clypeal margin are diagnostic in the female. The strongly expanded subalar carina in both sexes is unique in the genus. The mesopleural tubercle, unidentate mandible, diverging eyes, and sparse punctation of the female, and the weak clypeal teeth of the male place *E.* **geboharti**, n. sp. in the same species group with *Eucerceris barri* Scullen, *E. provancheri,* and *Eucerceris similis* Cresson.

Eucerceris **melleoides** Ferguson, n. sp.
Figure 2

Female.—Length 13 mm; forewing 10 mm; inner margin of mandible with blunt tooth slightly distad of midlength; clypeus with median domelike swelling, apicomedial margin with transverse, rectangular lamina beyond base of preapical setae, lamina as long as pedicel width and 3 times as wide as long, transverse apically, with poorly developed flanking tooth on each side (Fig. 2); clypeal punctures irregular, mostly well separated, remainder of head contiguously punctate; eyes diverging below; interocellar distance scarcely 2 lateral ocellus diameters and about half ocellocular distance; propodeal enclosure crossridged on anterior half, remainder polished; metapleuron finely ridged; scutellum polished on anterior half, remainder punctate; mesopleuron and propodeum contiguously punctate; mesopleural tubercle absent; second submarginal cell of forewing petiolate anteriorly; subalar carina not widened laterally; terga II–IV with dense, uniform, contiguous punctures in transverse depressions well differentiated from polished, more coarsely punctate anterior and posterior tergal ridges; sterna sparsely punctate; hypopygium flat, transluscent area distinct; pygidium narrowly suboval, twice as long as wide.

Male.—Length 12–14 mm; forewing 9–11 mm; mandible edentate; clypeal lip with 3 teeth of equal size; eyes slightly diverging below; ocelli and sculpture of head as in female; forewing with second submarginal cell sessile, marginal cell with basoposterior pocket; sculpture of thorax as in female; sterna III–IV with numerous hairs but not differentiated into fimbriae; fimbria on sternum V about twice as wide as distance between apices of pygidial teeth, hairs long, somewhat ragged at the tips, irregularly clumped; pygidium with narrow median lobe projecting slightly beyond lateral teeth, distance between median lobe and lateral tooth equal to or greater than width of lobe; sculpture of abdomen as in female.

Coloration.—Background color black, pale markings yellow; 3 spots on clypeus, 3 stripes on face, spot behind eye, pronotal ridge, metanotum, spot on mesopleuron, spot on propodeal side, narrowly interrupted transverse band on tergum I, narrow transverse band on posterior ridge of terga II–V, lateral spots on sternum IV, yellow; mandible red, fulvous at base; scape, pedicel and flagellomeres I–II red, remainder of flagellum black; coxae black, remainder of legs mostly red; anterior ⅓ of forewing infuscated, remainder of forewing and hindwing lightly smoky.

Holotype.—Female, Mexico, Coahuila, Los Pinos, 19 mi. SE Saltillo, IX-24-76, 6,800′ (J. A. Chemsak, J. Powell, A. and M. Michelbacher). University of California, Berkeley. [To be deposited on indefinite loan at the California Academy of Sciences, San Francisco.]

Paratypes.—4 males, all from Mexico, as follows: 1 male, same data as holotype [UCB]; 1 male, Hidalgo, Zimapan, VI-11/14-51, on flowers of *Eysenhardtia polystachya* (Ort.) (P. D. Hurd) [UCB]; 2 males, Nueva Leon, 40 mi. W Linares, 5,200 ft., Sept. 7, 1963 (Scullen and Bolinger) [OSU].

The long middle lobe of the pygidium separates the males of this species from all others in the genus except *E. melanosa* Scullen and *E. mellea* Scullen. *E. melanosa* has the fimbria on sternum V reduced to a pair of pointed tufts medially, whereas the fimbria is distinctly transverse in *mellea* and **melleoides**, n. sp. The female of **melleoides**, n. sp. is much like *mellea,* but the apical margin of the clypeus is trilobed medially in *mellea* whereas it is transverse in **melleoides**, n. sp. I have been unable to separate *mellea* and **melleoides**, n. sp. males except by color; *mellea* is a red and yellow species whereas **melleoides**, n. sp. is essentially a black and white species.

Eucerceris **sculleni** Ferguson, n. sp.

Figure 3

Eucerceris melanovittata, Scullen 1968:39, figs. 77a, b, d, f, females only, nec Scullen 1939.

Female.—Length 14–16 mm; forewing 10–12 mm; mandible large, thick, with blunt tooth having long axis subparallel to long axis of mandible; disc of clypeal midsection with large protuberance, bluntly rounded apically with apex closer to clypeofrontal suture than to apical clypeal margin and above a line drawn between tentorial pits; lateral clypeal teeth large, bluntly triangular, closer to each other than to eye margin; transverse lamella connected to underside of lateral teeth, in front of and below preapical setae, with a bluntly bidentate median elevation on lamella; clypeus and face densely punctate, punctures essentially contiguous in area below midocellus; interocellar distance about half ocellocular distance; eyes diverging below; mesopleural tubercle indistinct; scutal punctures dense anteriorly, separated by 1 to 2 puncture diameters across middle ⅓, surface polished; propodeal enclosure polished, weakly sculptured, a few foveae in midline and a few weak ridges anteriorly; subalar carina not laterally expanded; forewing with second submarginal cell petiolate anteriorly; anterior and posterior ridges of middle terga with large separated punctures, well differentiated from dense, small punctures in transverse depressions; pygidium twice as long as midwidth, narrowly rounded apically, slightly narrowed basally; hypopygium with large, evenly rounded transverse swelling posteriorly (Fig. 3) with transverse or broadly U-shaped carina at base, transluscent area absent.

Male.—Length 13–15 mm; forewing 10–11 mm; clypeal lip with strong teeth, midtooth slightly longer; eyes slightly diverging below; ocelli and punctation of head as in female; thorax punctured as in female except scutal punctures separated by less than 1 puncture diameter; forewing with second submarginal cell sessile, marginal cell with basoposterior pocket; sterna III–IV without fimbriae; sternum V with sharply rectangular fimbria, hairs very dense, uniform in length, fimbria about 3 times as wide as length of hairs; pygidium transversely swollen at apical ⅓ with lateral carinae converging from base to middle, subparallel over apical ½, median lobe not extending beyond lateral teeth; punctation of abdomen as in female.

Coloration.—Similar in color pattern to red marked specimens of *E. rubripes* Cresson; background color black, usually replaced in part by red; pale markings usually bright yellow; 3 spots on clypeus, 3 lines on face with middle one more or less reaching midocellus, spot behind eye, sometimes spots behind ocelli, pronotal collar and lobes, hypoepimeron, scutellum, metanotum, propodeal sides, spots behind mid and hind coxae, incised or interrupted band on tergum I, complete transverse band on posterior ridge of terga II–V, complete or partial transverse band on anterior ridge of terga II–V, transverse band or lateral spots on one or more of sterna II–IV, yellow; scape, pedicel and basal 2 to 4 flagellomeres reddish, remainder of flagellum black; legs red, coxae sometimes infuscated; forewing infuscate along anterior ⅓ and distal ⅔. Males colored like females except legs marked with yellow.

Holotype.—Female, Willcox, [Cochise County], Arizona, July 7, 1956 (A. D. Telford); University of Arizona, Tucson. [Deposited in the California Academy of Sciences, San Francisco.]

Paratypes.—16 males, 6 females, as follows: ARIZONA: 1 male, 2 females, same data as holotype [UAZ, OSU] [Note: one of these females [OSU] carries a *Eucerceris melanovittata* Scullen determination label and a yellow Plesiotype label affixed by Scullen.]; 1 male, Cochise County, 3 mi. SE Willcox, VIII-29-57, on *Cleome* sp. (W. F. Barr) [UID]; 1 male, Cochise County, Willcox, VIII-18-58 (P. D. Hurd) [UCB]; 2 males, Graham County, 12 mi. S Stafford, 4,250 ft., IX-14-62 (H. A. Scullen) [OSU]; 1 male, Navajo County, 1 mi. SW entr. Navajo Nat. Mon. VIII-2-67 (D. C. and K. A. Rentz) [UCB]; 1 male, Pima County, Baboquiviri Mts., near Kits Peak, VIII-7/9-1916, about 3,600 ft., [AMNH]; 2 males, Pima County, Baboquiviri Mts., VIII-15-1924, VIII-18-1924 (O. C. Poling) [CAS]; 1 male, Pima County, Nogales Springs, Whetstone Mtns., VIII-17-77, 4,400–4,600 ft. (Werner, Olson, Hetz) [UAZ]; 1 female, Pima County, 3 mi. SE Continental, VIII-26-76 (S. Kuba) [CDA]; 1 male, Pima County, Greaterville, X-8-80 (B. F. and J. L. Carr) [ALB]; 1 male, Santa Cruz County, 5 km N Nogales, VIII-17-79 (J. v. d. Vecht) [UCD]; 1 male, 1 female, Santa Cruz County, 5 mi. E Nogales, IX-1-70 (R. M. Bohart) [UCD]; COLORADO: 1 female, Costilla County, San Luis, VIII-11-76 (B. F. and J. L. Carr) [ALB]; NEW MEXICO; 1 male, Hidalgo County, Skeleton Cyn., VIII-12-65 (G. W. Forister) [UCR]; 2 males, Santa Fe County, Santa Fe, VII-14-34 (F. E. Lutz), IX-2-34 (P. E. Geier) [AMNH]; TEXAS: 1 female, Jeff Davis County, Davis Mts., IX-4-44 (F. Werner and W. Nutting) [MCZ]. [Note: This specimen carries a *Eucerceris melanovittata* Scullen determination label, a yellow Plesiotype label, and an orange "D" label, the latter indicating that the specimen was used for the illustration of *E. melanovittata* in Scullen (1968).]

Other specimen.—1 female, Mexico, Chihuahua, La Campana, IX-8-73 (W. J. Hanson, B. A. Haws) [USU].

The strongly swollen hypopygium separates the female of *E.* **sculleni**, n. sp. from all other species in the genus; otherwise it is very similar to *E. melanovittata* except for the larger size and partly red markings of the former. The sharply rectangular fimbria on sternum V and lack of fimbriae on sterna III and IV separate the males of *E.* **sculleni**, n. sp. from its congeners except for *E. melanovittata* and *E. sinuata* Scullen. *E. sinuata* has the anterior transverse ridges of the midterga finely punctate, similar to the punctures of the transverse depressions, whereas in the other two species the anterior transverse ridges are polished between well separated large punctures, the anterior ridges being similar to the posterior ridges. Males of *E.* **sculleni**, n. sp. are very similar to males of *E. melanovittata* morphologically. Males of **sculleni**, n. sp. are larger (13–15 mm) than males of *melanovittata* (11–13 mm), and the latter are black and white whereas in **sculleni**, n. sp. there are variable amounts of red and the pale markings are yellow. The scape and pedicel are red in **sculleni**, n. sp. but black or piceous in *melanovittata.*

E. **sculleni**, n. sp. has not been collected in the Portal area of Cochise County, Arizona, where *E. melanovittata* is relatively common. The specimen from the state of Chihuahua, Mexico, is black and white, but it has the strongly swollen hypopygium characteristic of *E.* **sculleni**, n. sp.

Eucerceris barri Scullen (Revised Status)

Eucerceris barri Scullen, 1968:19. [Female holotype, Jacob's Cabin, Hart Mtn., Lake County, Oregon; U.S. Natl. Mus. Nat. Hist., Washington, D.C.]
Eucerceris similis, Bohart and Grissell 1975:33, nec Cresson, in part; Bohart and Menke 1976:592, in part; Krombein 1979; 1740, in part.

Bohart and Grissell (1975) synonymized *Eucerceris barri* Scullen with *Eucerceris similis* Cresson presumably because of the similarity of the males of the two species. Bohart has recognized *barri* in subsequent determinations. Females of the two species are quite distinct in clypeal structure. *E. similis* has four teeth on the apicomedial margin of the clypeus with all teeth equally separated from each other. *E. barri* lacks the two median teeth, and the apicomedial emargination of the clypeus is bounded by a carina or rim which connects with the lateral teeth. Each lateral tooth is formed by a blunt, triangular expansion of the apical rim and the tooth is sometimes bicuspidate. In *E. similis* the preapical setae arise from the apical clypeal margin, whereas in *E. barri* they arise from underneath the apical rim.

Males of *barri* and *similis* are separable by differences in antennal coloration. In *similis* the flagellum is black or infuscate above and at least the apical 3 to 5 segments are black below. In *barri* the flagellum is fulvous to light brown below for its entire length and partly to entirely pale above. In about 75% of the male specimens of *barri* the pale facial maculations are fused above the antennal sockets and almost fused in the remainder. In *similis* the black stripes above the antennal sockets are of more or less uniform width with no strong tendency toward fusion of the pale stripes.

The pale markings of *barri* are whitish, whereas they are usually distinctly yellow in *similis.* The pale markings are much reduced in *barri* females, as the face and head are often completely black, the sterna are black, and the femora are black with an occasional apical pale spot.

Material examined.—87 males including 8 paratypes and a male collected with the holotype female; 29 females including the holotype and 4 paratypes. The California distribution data are given in detail since these records are the southern extension of the range of this predominantly northern species. County records are given for the remaining states with elevations when stated on the labels. CALIFORNIA: 1 female, Lassen County, 4 mi. S Ravendale, VIII-10-59 (J. A. Chemsak), paratype [UCB]; 2 males, Mono County, Crooked Creek Lab., White Mtns., 10,150 ft., VII-19-61 (G. L. Stage) [UCB]; 1 male, Mono County, Blanco's Corral, White Mtns., 10,150 ft., VIII-25-60 (P. D. Hurd) [UCB]; 3 males, Mono County, Cottonwood Cr., 9,300 ft., VII-10-61 (H. V. Daly) [UCB]. IDAHO: Camas, Cassia, Clark, Custer (5,899 ft.), Fremont, Jefferson, Jerome, Lemhi, Oneida and Teton Counties [UCD, UID, OSU, USU]. NEVADA: Lander and White Pine Counties [UCD, UID]. OREGON: Lake County [OSU, USNM]. UTAH: Rich County [USU]. WYOMING: Albany, Carbon (8,800 ft.), Natrona (7,000 ft.), Sublette, Sweetwater, Teton, Uinta (7,000 ft.) Counties and Yellowstone National Park [UCB, UCD, CSU, COR, NEB, OSU, USNM]. In addition, Scullen (1968) reported a male from Moffat County, Colorado.

Collection dates are July 2 to August 28 with the exception of one male collected in Lemhi County, Idaho, on June 21.

Eucerceris brunnea Scullen

Eucerceris brunnea Scullen, 1948:159. [Female holotype, Jacala, Hidalgo, Mexico; Mus. Comp. Zool. Cambridge, Massachusetts]; Scullen 1968:22; Bohart and Menke 1976:591.

Eucerceris velutina, Scullen 1948:160, males in part; Scullen 1968:69, males in part.

The males of *Eucerceris brunnea* Scullen have not heretofore been characterized. A series of specimens collected by H. E. Evans at Guadalajara Mexico, in 1959 and 1965 [COR, OSU, USNM] contained females of both *E. brunnea* and *Eucerceris velutina* Scullen together with a number of superficially similar males which had been determined as *E. velutina* by Scullen. It seemed probable that these males were not all conspecific, but that males of both *brunnea* and *velutina* were present. Although females of *brunnea* and *velutina* are easily separated by their markedly different clypeal structure, the two belong to the same species group on the basis of wing venation and other characters. A similarity in the males of the two species would therefore not be surprising.

Since surface sculpture is only weakly sexually dimorphic in the genus *Eucerceris,* characters based on sculpture are important clues in associating the opposite sexes of a species. It was found that there were substantial differences in surface sculpture between females of *brunnea* and *velutina,* and that the series of males collected at Guadalajara, Mexico, separated readily into two groups each of which corresponded in sculpture to one of the two species of females with no intergradation between the two.

Both sexes of *velutina* have the anterior and posterior transverse ridge of terga III–IV sharply differentiated in punctation from the transverse furrow of the same tergum. The transverse furrow is densely, contiguously punctate with small, mostly hexagonal punctures, whereas the transverse ridges are polished between large punctures mostly separated by one or more puncture diameters. Both sexes of *brunnea* have punctation similar to *velutina* on the posterior tergal ridge and in the transverse furrow of the same terga, but the anterior transverse ridge is punctured almost as densely as the furrow.

Males collected with *velutina* females in the absence of *brunnea* females, and males collected with *brunnea* females in the absence of *velutina* females show an identical pattern of tergal punctation.

The dense, black, "carpet-like," velvety pile on the scutum of males of *brunnea* and *velutina* is a highly unusual character state. Since *Eucerceris cavagnaroi* Scullen, *Eucerceris punctifrons* (Cameron), and *Eucerceris violaceipennis* Scullen belong to the same species group on the basis of female wing venation, I strongly suspect that the males of these latter three species, when found, will also possess this character.

Specimens examined.—The following records for *E. brunnea* Scullen are all from Mexico: CHIHUAHUA: 2 males, 1 female, Cuiteco, VIII-9-69 [UCD]; HIDALGO: 1 male, 28 mi. SW Jacato, 6,300 ft., VI-23-57 [OSU]; JALISCO: 7 males, 4 females, Guadalajara, VII-14-59 [COR], VII-17/28-65 [OSU, USNM]; MICHOACAN: 1 male, 1 female, 6 mi. NW Quiroga, VII-11-63 [UCD]. I have also seen the male holotype of *Eucerceris velutina* Scullen at the U.S. National Museum of Natural History, Washington. It is not at the California Academy of Sciences, San Francisco, as reported by Scullen (1968).

Eucerceris canaliculata (Say)

Aphilanthops marginipennis Cameron, 1890:105. [Male holotype, Atoyac, Veracruz, Mexico; Brit. Mus. (Nat. Hist.), London.] *New Synonymy.*

Aphilanthops marginipennis Cameron was incorrectly synonymized with *Eucerceris rubripes* Cresson by Scullen (1968) and should be added to the synonymy of *Eucerceris canaliculata* (Say) as given by Ferguson (1981). The type locality of *marginipennis* is outside the known range of *rubripes,* and the original description of *marginipennis* does not fit *rubripes.*

I have studied the holotype male of *marginipennis* which consists of a head and thorax without a gaster. Nevertheless, the available parts of the holotype taken together with Cameron's (1890) original description make identification possible. Cameron described the fimbriae on sterna III and IV as occupying the middle three-fourths of the sterna and stated that the hairs were nearly as long as the segments. He described the fimbria on sternum V as "stiff, comb-like, almost continuous," and the abdomen as mostly yellow except for the tergal depressions. This pattern of sternal fimbriae occurs only in *E. canaliculata* (Say) and *Eucerceris atrata* Scullen. *E. atrata* is a black and white species known only from elevations of 5,500 to 7,300 ft. in the state of San Luis Potosi, Mexico (Scullen 1968). *Eucerceris conata* Scullen has a very narrow, stiff fimbria on sternum V, but the mandible is rather strongly elbowed medially, quite different from the mandible of the holotype of *marginipennis,* and the distribution is similar to that of *rubripes.*

The holotype of *marginipennis* has a black scutum and extensive black markings on the thoracic pleura and propodeum. It is an example of the dark color form of southern Mexico and Guatemala described by Scullen (1968) as *Eucerceris zimapanensis* and previously synonymized with *E. canaliculata* by Ferguson (1981).

In my previous paper (Ferguson 1981) I neglected to give the reasons for deleting *Cerceris cameroni* Schulz from the synonymy of *Eucerceris canaliculata* (Say) as listed by Scullen (1951, 1968), Bohart and Menke (1976), and Krombein (1979). *Cerceris cameroni* was proposed by Schulz (1906) as a new name for the Indian species *Cerceris canaliculata* Cameron, nec Say, nec Perez, and is a synonym of *Cerceris bimaculata* Cameron according to Turner (1912). Bohart and Menke (1976) list *C. cameroni* Schulz in the synonymy of both *Eucerceris canaliculata* (Say) and *Cerceris bimaculata* Cameron, the latter being correct according to my interpretation.

Eucerceris cavagnaroi Scullen (New Status)

Eucerceris punctifrons cavagnaroi Scullen, 1968:53. [Female holotype, Volcan de San Salvador, El Salvador; Univ. of California, Davis]; Bohart and Menke 1976:592.

Scullen (1968) separated this taxon from *Eucerceris punctifrons* (Cameron) on the basis of color characters. Examination of the types of *E. punctifrons* and *E. cavagnaroi* shows that they are morphologically distinct species. In *E. cavagnaroi* the apical clypeal lip is very narrow, not or scarcely wider than the diameter of an antennal socket, and with a distinct emargination at the base of the lip on each side. In *E. punctifrons* the apical clypeal lip is wider than an antennal socket diameter and forms a shoulder on each side at its base at which point the width of the lip is about as wide as the width of the subantennal sclerite. The size of the apical clypeal lip in *punctifrons* is intermediate between the very narrow lip of *cavagnaroi* and the very wide lip of *Eucerceris velutina* Scullen, the lip being distinctly wider than the subantennal sclerite in the latter (Figs. 4–6).

Differences also exist in tergal and propodeal punctation. In *cavagnaroi* the anterior transverse tergal ridges of terga III–IV have dense punctures, almost as dense as those in the transverse tergal depressions, with virtually no interspaces of more than one puncture diameter. In *punctifrons* the anterior tergal ridges have numerous interspaces of more than one puncture diameter being somewhat intermediate between *cavagnaroi* and *velutina.* The transverse tergal depressions are rather broad in *cavagnaroi,* about 6 to 8 punctures in width, whereas they are quite narrow in *punctifrons,* being about 3 to 4 punctures in width. The propodeum of *cavagnaroi* is densely punctured with virtually no interspaces of more than one puncture diameter, whereas the propodeum of *punctifrons* has numerous interspaces of more than one puncture diameter.

Material examined.—Holotype female of *Eucerceris punctifrons cavagnaroi* Scullen [UCD]; holotype female of *Aphilanthops punctifrons* Cameron [BMNH]; 1 female of *E. cavagnaroi* Scullen, El Salvador, Santa Tecla, 638 m, 28-VI-1974 (C. G. Dean, B. M. 1974-366) [BMNH].

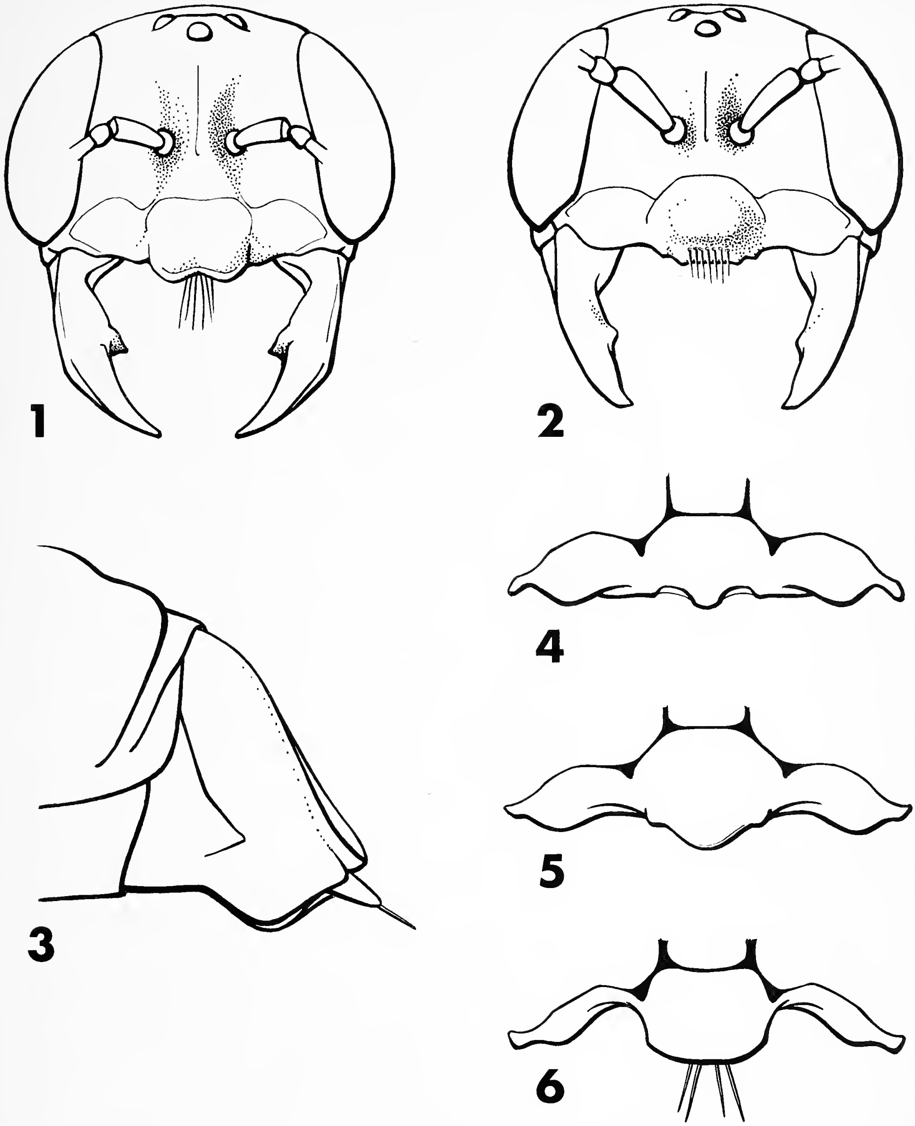
Eucerceris melanosa Scullen

Eucerceris melanosa Scullen, 1948:163. [Holotype male, Tehuacan, Puebla, Mexico; U.S. Natl. Mus. Nat. Hist., Washington]; Scullen 1968:38; Bohart and Menke 1976:591.

Eucerceris menkei Scullen, 1968:42. [Holotype female, 10 mi. NW Tamazulapan, Oaxaca, Mexico; Univ. of California, Davis]; Bohart and Menke 1976:591. *New Synonymy.*

Scullen (1968) suggested that *Eucerceris menkei* might be the female of *Eucerceris melanosa* Scullen. A male and female collected together in the state of Oaxaca, Mexico, were available to him [OSU]. In addition I have seen a male collected with two females in the state of Puebla, Mexico [UCB].

The two species are of similar size, color pattern and surface sculpture, and they are the only two species in south central Mexico for which opposite sexes have not been identified. These facts and observations taken together



Figs. 1–6. 1, 2. Head of female of *E.* **geboharti**, n. sp. (1) and *E.* **melleoides**, n. sp. (2); head width 3.1, 3.5 mm respectively. 3. Side view of terminal gastral segments of *E.* **sculleni**, n. sp. female; length of hypopygium 1.2 mm. 4–6. Clypeus of female *E. cavagnaroi* Scullen (4), *E. punctifrons* (Cameron) (5), and *E. velutina* Scullen (6); clypeal width 2.9, 2.9 and 3.2 mm respectively.

with the collection records leave no doubt that *melanosa* and *menkei* represent opposite sexes of the same species.

Specimens examined.—The following records are all from Mexico. HIDALGO: 1 female, Zimapan, VII-14-68 [UCD]; 1 male, 5 mi. W Pachuca, 7,900 ft. VIII-25-62 [OSU]; MEXICO D.F.: 1 male, 2,300 m, VIII-26-28 [COR]; OAXACA: 1 male, 1 female, 8 mi. SW Oaxaca, Monte Alban ruins, 6,000–6,500 ft., VIII-23-63 [OSU]; PUEBLA: 1 male, 2 females, 2 km E Tecamachalco, VII-4-74 [UCB]; 1 female, 275 km NE Chapulco, VIII-2-65 [COR]; 1 male paratype, 18 mi. W Tehuacan, 6,200 ft., IX-5-57 [OSU]; 1 male paratype, Cacaloapan, IV-26-62 [OSU]; QUERETARO: 1 male paratype, 41 mi. N Queretaro, 6,500 ft., IX-19-63 [OSU].

Eucerceris melanovittata Scullen

Eucerceris melanovittata Scullen, 1948:164. [Male holotype, 25 mi. E El Paso, Texas; Calif. Acad. of Sci., San Francisco]; Scullen 1968:39, males only; Bohart and Menke 1976:591; Krombein 1979:1739.

Scullen (1948) described *Eucerceris melanovittata* from males, and later (Scullen 1968) described what he thought was the female based on two specimens of a species described earlier in this paper as *Eucerceris sculleni.* The two males mentioned by Scullen (1968) as representing a darker form of *melanovittata* belong to the species described earlier in this paper as *Eucerceris melleoides.*

The true female of *E. melanovittata* was found among specimens carrying *Eucerceris arenaria* Scullen determination labels. Several females with associated males have also been identified in collections submitted for determination. *E. melanovittata* and *E. arenaria* are almost identical in size and coloration, both being black and white species. In males of *arenaria* the fimbria on sternum V is about ¾ as wide as the sternum, and the hairs are shorter medially; whereas in males of *melanovittata* this fimbria is narrower, sharply rectangular and the hairs are of even length. The females differ in several morphological characters as follows:

E. melanovittata	*E. arenaria*
(1) Clypeal elevation with apex above the middle	Clypeal elevation with apex below the middle
(2) Clypeal teeth with long axis directed forward	Clypeal teeth with long axis directed slightly outward
(3) Face below midocellus densely and regularly punctate	Face below midocellus irregularly punctate with many interspaces of one puncture diameter or more
(4) Hypopygium shagreened, without translucent area	Hypopygium with a transluscent area

(5) Propodeal enclosure smooth, weakly sculptured	Propodeal enclosure ridged over most of surface
(6) Mandible with single blunt tooth	Mandible bicuspidate, small tooth arising from base of larger tooth
(7) Subapical clypeal process separated from lateral teeth by width of process	Subapical clypeal process separated from lateral teeth by more than width of process
(8) Distance from lateral tooth to eye margin greater than distance between lateral teeth (ratio 1.5/1.1)	Distance from lateral tooth to eye margin slightly less than distance between lateral teeth (ratio 1.4/1.5)

Specimens examined.—I have studied the holotype male of *Eucerceris melanovittata* Scullen [CAS] and the holotype female of *Eucerceris arenaria* Scullen [CAS]. In addition I have seen 66 males and 32 females of *E. melanovittata* [AMNH, AZS, CAS, CDA, UCB, UCD, COR, UFL, OSU, PUC, USNM] with the following distribution: ARIZONA: Cochise, Graham, and Santa Cruz Counties; NEW MEXICO: Hidalgo, San Miguel and Torrance Counties; TEXAS: Brewster, Culberson, El Paso, Hudspeth, Jeff Davis and Presidio Counties. I have seen 1 male specimen from each of the states of Coahuila and Nueva Leon, Mexico.

Eucerceris pimarum Cockerell and Rohwer

Ferguson (1981), following previous authors, incorrectly cited Rohwer as the author of this species. Menke and Bohart (1979) pointed out that authorship of the species is Cockerell, T. D. A. and S. A. Rohwer 1908:326, *in* Rohwer, S. A. 1908. New philanthid wasps. Can. Entomol. 40:322–327.

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PERCHING BEHAVIOR OF *CANTHON VIRIDIS* (COLEOPTERA: SCARABAEIDAE) IN MARYLAND[1]

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Abstract.—*Canthon viridis* Beauv. is shown to perch on leaf surfaces near a food source (dung) before attempting consumption. It is hypothesized that predator pressure by staphylinids has contributed to the development of this behavior. Correlated with perching behavior in *C. viridis* is low population density, relative absence of diurnal beetle competitors, observed predation by *Staphylinus maculosus* Grav., the capability of feeding on old feces abandoned by staphylinid predators, and a long survival period without food.

Introduction

It has been known for quite a few years that numerous species of Scarabaeinae (Coleoptera: Scarabaeidae) can be found perching on vegetation above the forest floor (Ohaus 1900). Recent investigators have suggested that perching behavior may function to partition resources among competing species (Howden and Nealis 1978; Young 1978). All previous reports of this behavior, however, originate from tropical areas (Halffter and Matthews 1966; Howden and Young 1981). I report herein observations of perching by a species of Scarabaeinae in a north temperate (Maryland) forest and present a hypothesis relating to such behavior.

Observations

As part of a two-year study of the arthropods associated with dung in Maryland, pitfall traps baited with human feces were placed weekly in a 50 hectare oak-hickory forest 4 km NE of Clarksville, Howard County. On 14 May 1979, at 0900 hr, a trap on gently sloping terrain was freshly baited and then observed for one hour from a distance of three meters upslope. Five minutes after bait placement, one *Canthon viridis* Beauv. was observed flying in a zig-zag manner upslope at a height of approximately 15 cm. When the beetle was within one meter of the bait, it landed on a horizontal leaf

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surface 30 cm above the forest floor. For the next ten minutes it remained inactive, facing the bait. At the end of this period the beetle flew directly to the trap and was captured. No other scarabs were attracted to the bait during the one hour observation period. This same sequence of behaviors was also observed with single individuals of *C. viridis* in the same forest near fecal material on 12 June and 2 July 1979, and on 6 and 9 June 1980. During the two-year period of this study, no other scarabaeine species was observed perching on leaf surfaces in this forest.

Laboratory Experiments

Starvation.—During the period June–Sept. 1979, individuals of several dung beetle species were brought into the laboratory and maintained at ambient temperature (20–30°C) in 473 cc glass mason jars with a screen top and 4 cm of packed soil in the bottom. Individuals were exposed to cow or human dung for 48 hr, then removed to a fresh container and monitored daily for survival without food. Atomized water was routinely added to maintain suitable moisture conditions. Five individuals of *C. viridis* ($\bar{x}$ length = 5 mm) were processed in this manner and lived an average of 32 days (R = 27–36). Similar-sized species of *Aphodius* did not live as long under these conditions (*A. lividus,* $\bar{x}$ = 17 days, R = 11–20, n = 50; *A. ruricola,* $\bar{x}$ = 22 days, R = 12–25, n = 40).

Predation.—During the period June–Sept. 1979, individuals of *Staphylinus maculosus* Grav. ($\bar{x}$ length = 21 mm, n = 15) were brought into the laboratory and maintained under the same conditions as in the starvation experiments previously discussed. Food in this case, however, was small dung beetles placed alive in each cage every second day. On ten separate occasions, a single *C. viridis* was placed in a container with one *S. maculosus* (six different individuals) and was consumed on the average in 40 minutes (R = 15–85).

Discussion

In Maryland, *Canthon viridis* occurs uncommonly in forests at fecal material and even more rarely at carrion (pers. obs.). Usually no more than two individuals will co-occur at a specific food site. Other forest-inhabiting diurnal coprophagous scarabs are likewise quite rare, with the vast majority of the coprophagous scarab guild—such as species of *Aphodius, Ateuchus, Canthon, Copris, Geotrupes,* and *Onthophagus*—occurring at night.

Areas of the neotropics where perching in scarabaeines has been reported may contain many species displaying this behavior. At Rio Palenque, Ecuador, of 35 species of scarabaeines captured at human feces, 11 species also perched on leaf surfaces (Howden and Nealis 1978). In a feeding guild of this size, as the authors suggest, perching behavior may indeed be an important component of foraging strategies effecting resource partitioning. In a Maryland forest, however, where only one scarabaeine species sits on leaves during the day and other diurnally-active dung scarabs are rare or absent, resource partitioning among competing species does not appear to be related to perching behavior.

Daytime competition for dung in Maryland forests appears to occur primarily among the Diptera, with many predaceous Coleoptera usually in association. Some of the predatory beetles (Staphylinidae) are common, large (>15 mm), diurnally active, and capable of consuming small and medium-sized dung beetles. These predators include *Creophilus maxillosus* (L.), *Ontholestes cingulatus* (Grav.), and *Staphylinus maculosus.* Laboratory experiments show that at least *S. maculosus* can capture *Canthon viridis* quite easily and completely consume one individual in as little as 15 minutes.

Perching behavior in *C. viridis* may be correlated most closely with parameters associated with predation. One of those correlations may be between the age (and odoriferous nature) of dung and the presence of staphylinids and scarabs. Fresh fecal material in Maryland forests is quickly utilized by Diptera if produced during the day and by scarabs if produced at night. Occasionally, dung can be found in the forest that has not been completely utilized and is a week or more in age. Diptera and staphylinids will not be present on this old dung, but *C. viridis* may occasionally occur. In one experiment during July 1979, human feces left exposed on the forest floor and observed daily was still intact after 17 days, when the first *C. viridis* arrived and was captured. When the feces was collected after 21 days, two more *C. viridis* were obtained. Several small *Aphodius* and *Onthophagus* were also collected during the same period, but no staphylinids were obtained after the eighth day. This data is consistent with the hypothesis that *C. viridis* is minimizing predation by consuming food that is no longer attractive to predatory staphylinids.

Species of dung scarabs that are competitively superior to other dung beetles and have the highest population densities are usually unable to survive for long periods of time without food (Young, ms.). In a series of laboratory starvation experiments, *C. viridis* could survive for 32 days whereas several *Aphodius* species of similar size could survive for approximately 20 days without food. Diurnal species of *Aphodius* do not perch on leaves, can be among the earliest arrivals at fresh dung, and probably reduce predation pressure by burrowing immediately into dung and creating tunnels in the soil underneath. *Canthon* species, however, may perch on leaves, can also be among the earliest arrivals at fresh dung but may be among the last, and are exposed to predation during the formation of a dung-ball and its subsequent rolling away to a burial site. Although the capability of doing without food for long periods of time may be merely a response to low food availability, it may also allow individuals of *C. viridis* to choose the food site with the lowest possible level of potential predation.

The strategy of perching near food, before consumption is attempted, may be a technique for assessing the presence of predators. Although no direct information is available, research on dung beetles in Panama suggests that the detection of staphylinid predators may be of an olfactory nature. As discussed in Howden and Young (1981), at least one species of *Canthon* can detect the presence of another species of *Canthon* (that is competitively superior) at a food site and will not attempt to obtain food until the superior species departs. Detection of the allelochemic involved can occur at a distance of 15 cm or more. Some staphylinids are known to produce pheromones (Peschke 1978) and allelochemics (Schildknecht et al. 1976), and experimental demonstration of olfactory communication between *Canthon* species and potential staphylinid predators would not be a great surprise.

A number of criteria may need to be satisfied before a species such as *Canthon viridis* can use perching as part of a predator-assessment strategy. It should be able to detect the presence of predators, perhaps by olfactory cues, at a food site. It may employ the complementary strategy of arriving at food before and/or after potential predators arrive. It should be able to survive without food for a sufficient period to allow adequate search time for food sites without predators. And finally, perching on leaf surfaces should not increase the likelihood of predation. The first three criteria have been considered, but the final one requires some comment. *C. viridis,* like many of the leaf-sitting scarabaeines, is brightly colored (green) and shiny. This probably makes them particularly obvious to leaf-foraging visual predators such as birds and lizards. It has been suggested (Poulson 1980) that some species of *Canthon* in the tropics are distasteful to such predators and/or belong to a large mimetic complex. This has yet to be determined for *C. viridis,* in Maryland, but may function to minimize predation while sitting on leaves.

Conclusion

Given that the nature of the evidence is largely circumstantial and inferential, it still seems reasonable to suggest that a species such as *Canthon viridis,* which is so vulnerable to staphylinid predation, would have evolved a strategy for minimizing that predation. The hypothesis of predator assessment presented herein has the virtue of being testable. Although the project that produced these observations has been terminated, it is easy to envisage a series of laboratory olfactometer experiments with *C. viridis* that could demonstrate the presence or absence of staphylinid-detection capabilities. Also, manipulations in the field at dung involving removal and introduction procedures with predators and prey could give strong support to the hypothesis. Finally, detailed field observations where diurnal forest dung beetle populations are more abundant than in Maryland could also be corroborative.

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DESCRIPTIONS OF THE IMMATURE STAGES OF *MYNDUS CRUDUS* (HOMOPTERA: FULGOROIDEA: CIXIIDAE)[1]

Stephen W. Wilson and James H. Tsai

Abstract.—The 5 immature stages of *Myndus crudus* Van Duzee, an apparent vector of lethal yellowing disease of palms, are described and illustrated and a key for separating nymphal instars is provided. Features useful in distinguishing nymphal instars include the number of metatarsal segments (2 in first through third instars, 3 in fourth and fifth instars), the presence of a tooth on the profemora of fourth and fifth instars, and the increase in body size, wingpad size, and number of pits during nymphal development.

Myndus crudus Van Duzee has been recorded from Florida south to Venezuela and west to Panama, central Mexico, and the southern tip of Baja California (Kramer 1979). This planthopper has been implicated as a vector of lethal yellowing disease of coconut palms (*Cocos nucifera* L.) (Howard and Thomas 1980; Tsai 1980; Tsai and Thomas 1981).

The eggs of *M. crudus* are laid in moist soil adjacent to grass stolons or palm roots. The nymphs feed at the stem bases and roots of several species of grasses, sedges, and palms (Reinert 1977; Tsai et al. 1976; Tsai and Kirsch 1978). Both adults and nymphs are phloem feeders on coconut palm (Fisher and Tsai 1978). At least nine species of palms as well as several species of grasses are feeding hosts of *M. crudus* (Reinert 1977; Tsai 1978). Although *M. crudus* has been studied extensively in the laboratory and field (Reinert 1977, 1980; Tsai and Kirsch 1978), including laboratory rearing (Tsai et al. 1976; Tsai and Kirsch 1978), the eggs and nymphs of this species have not been illustrated or described. Tsai and Kirsch (1978) provided measurements of the eggs and nymphs but not detailed descriptions. Zenner and Lopez (1977) published measurements and figures of eggs and nymphs of *Haplaxius pallidus* Caldwell, a synonym of *M. crudus* (Kramer 1979).

There are few available descriptions of the immatures of any Cixiidae and none of any species of *Myndus.* Cumber (1952) described the immatures of *Oliarus atkinsoni* Myers, and Myers (1929) described the third, fourth, and fifth instars of *Mnemosyne cubana* Stål and the fifth instar of *Bothriocera*

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signoreti Stål. The fifth instar of *Oliarus placitus* Van Duzee is being described by Wilson (unpublished).

This paper includes descriptions of, and keys for separating, the five immature stages of *M. crudus.*

Materials and Methods

Specimens to be described were obtained from laboratory stock maintained by Tsai, and preserved in 70% ethyl alcohol. The description of each stage is based on 10 specimens. The first instar is described in detail, but only major changes from previous instars are described for subsequent instars. Comparative statements refer to previous instars (e.g., "darker"). Dimensions of eggs and nymphs are expressed in mm as mean ± SE. For nymphs, length was measured from tip of vertex to tip of abdomen; width was measured across the widest part of the body, usually the mesothoracic segment. Thoracic length was measured along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum; this measurement was included because total length measurements are affected by differences in head shape among specimens, and because the abdomen often becomes distended when preserved in ethyl alcohol. Specimens of each instar were cleared in 10% KOH in order to observe some structures (e.g., tergite of first abdominal segment).

Descriptions of Immature Stages

Egg (Fig. 1).—Length 0.54 ± 0.032; width 0.17 ± 0.030.

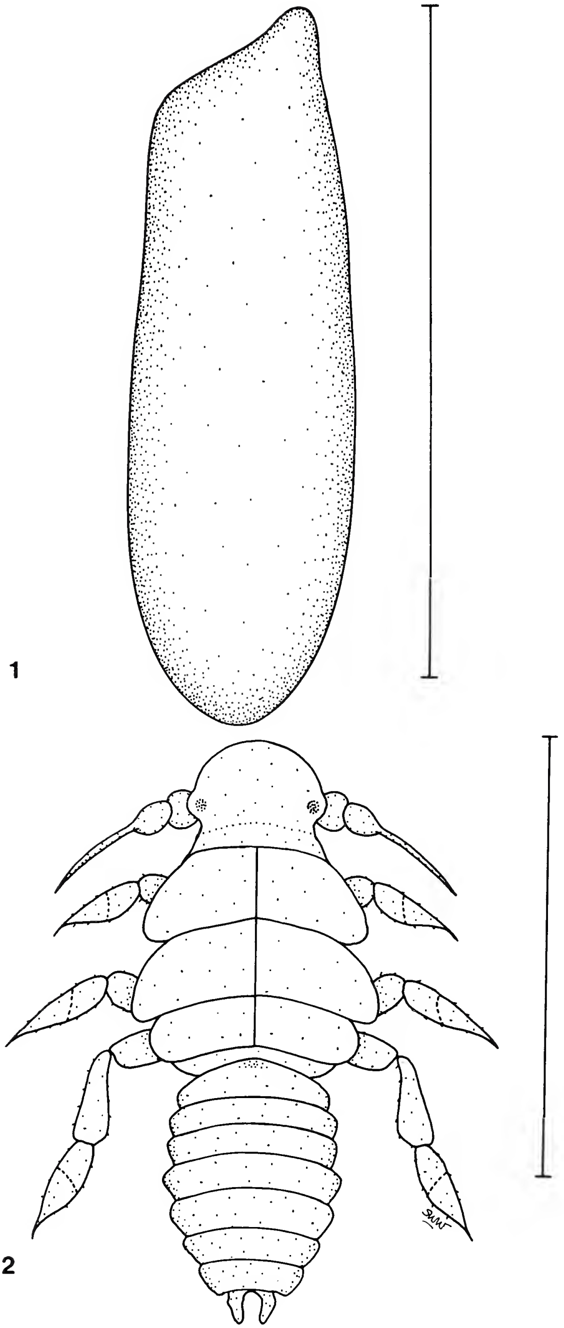
Eggs laid singly; elongate, subcylindrical; white; chorion translucent, smooth; anterior end asymmetrical and pointed, posterior end broadly rounded.

First Instar (Fig. 2).—Length 0.64 ± 0.088; thoracic length 0.24 ± 0.041; width 0.26 ± 0.041.

Form elongate, subcylindrical, slightly flattened dorsoventrally, widest along mesothorax. Vertex, frons, thoracic nota, and abdominal tergites with a few, shallow, indistinct pits.

Vertex broadly rounded anteriorly, widest in anterior ½, slightly narrowing posteriorly. Frons subquadrate, lateral margins slightly convex, dorsal margin highly convex, juncture with clypeus obscure. Clypeus narrowing distally. Beak 3-segmented, extending just beyond metacoxae; segment 1 obscured by clypeus, segments 2 and 3 subequal. Eyes reduced, barely visible in ventral view, red. Antennae 3-segmented; scape and pedicel cylindrical and subequal; flagellum bulbous basally, filamentous distally, bulbous portion subequal in size to pedicel.

Thoracic nota divided by a longitudinal mid-dorsal line into 3 pairs of plates. Pronotum longest medially; each plate subrectangular, anterior mar-



Figs. 1, 2. Immature stages of *M. crudus.* (1) Egg, (2) 1st Instar. Vertical bar = 0.5 mm.

gin almost straight to ca. level of lateral margin of eye then extending posterolaterally, lateral margin slightly convex, posterior margin slightly sinuate. Mesonotum with median length subequal to that of pronotum; each plate subrectangular, lateral margin convex, posterior margin broadly curved. Metanotum with median length ca. ⅔ that of mesonotum; each plate subrectangular, lateral margin convex. Pro- and mesocoxae posteromedially directed; metacoxae smaller, obscured by trochanters. Tarsi 2-segmented, divisions between segments very obscure; segment 1 somewhat wedge-shaped; segment 2 subconical, slightly curved, with a pair of slender apical claws.

Abdomen 9-segmented, subcylindrical, widest across segments 2 and 3; segment 9 elongate vertically, surrounding anus.

Second Instar (Fig. 3).—Length 1.01 ± 0.103; thoracic length 0.40 ± 0.054; width 0.40 ± 0.052.

Antennae with bulbous portion of flagellum ca. ⅔ length of pedicel.

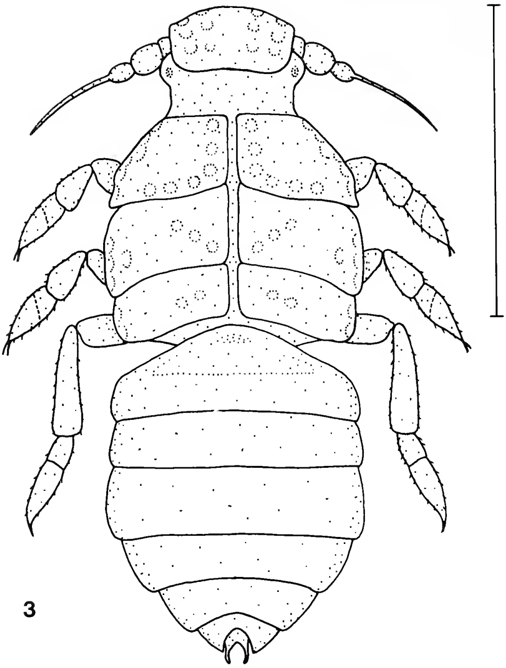
Pronotum with each plate bearing 10–15 shallow pits. Each plate of mesonotum bearing ca. 7 pits with 3 pits extending anterolaterally from posteromedial corner and 4 pits near lateral margin; posterolateral corners of plate slightly lobate. Each plate of metanotum bearing ca. 4 pits with 2 pits near medial border and 2 pits near lateral margin.

Third Instar (Fig. 4).—Length 1.29 ± 0.104; thoracic length 0.51 ± 0.048; width 0.55 ± 0.073.

Vertex somewhat less rounded anteriorly; pits in 2 irregular rows, more distinct; posterior and lateral margins distinct, slightly carinate, and sinuate. Frons with 2 irregular rows of pits bordering lateral margins; lateral margins almost straight, narrowing distally, juncture with clypeus distinct, ventral margin concave; juncture between anterodorsal postclypeus and posteroventral anteclypeus straight and apparent laterally. Antennae with bulbous portion of flagellum ca. ½ length of pedicel.

Pronotum with each plate bearing ca. 20 large, distinct pits. Each plate of mesonotum bearing 12–13 large, distinct pits with 1 pit in the anteromedial corner, an oblique row of 3–4 pits (usually 4) extending anterolaterally from posteromedial corner, 7–8 pits near lateral margin; posterior margin distinctly lobate in lateral ½. Each plate of metanotum bearing 7–8 pits with 1–2 pits near medial border, 2–3 pits ca. midway between medial and lateral margins and 2–3 pits near lateral margin.

Abdominal tergites of segments 1 and 2 reduced, not extending to lateral margins. The following number of pits on either side of midline of each segment: segment 3 with 2 pits on tergite, segments 4–5 each with 5 pits on tergite, segment 9 with 3 caudal pits. Tergites 6–8 each with a pair of enlarged subtriangular, dorsoposteriorly oriented waxpads in intermembranous area posterior to narrow tergite (waxpads probably present but indistinct in previous instars); each waxpad with a transverse row of 3 very small, obscure pits near anterodorsal margin.



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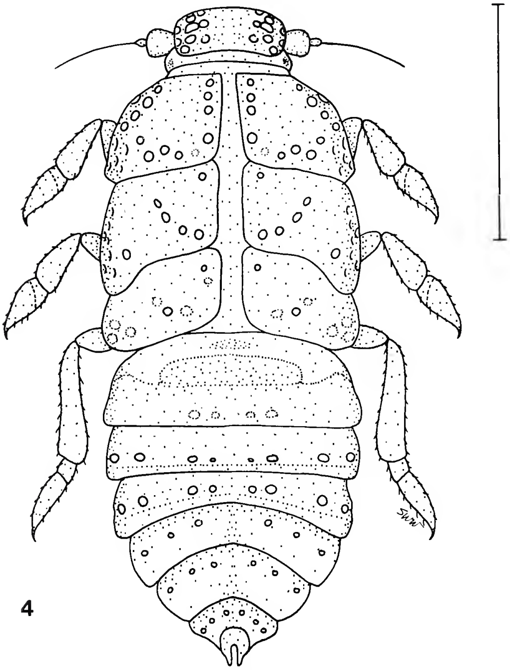

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Figs. 3, 4. Immature stages of *M. crudus.* (3) 2nd Instar, (4) 3rd Instar. Vertical bar = 0.5 mm.

Fourth Instar (Fig. 5).—Length 2.20 ± 0.162; thoracic length 0.81 ± 0.068; width 0.92 ± 0.074.

Vertex, frons, thoracic nota, and abdominal tergite light gray-brown; pits, intermembranous areas, clypeus, beak, antennae, legs, and sternum white.

Head with pits on vertex and frons more numerous. Antennae with scape reduced, ca. ⅓ length of pedicel, bulbous portion of flagellum ca. ⅓ length of pedicel.

Pronotum with each plate bearing 25–30 pits. Each plate of mesonotum bearing 22–24 pits with 1–2 pits in anteromedial corner, an oblique row of 5 pits extending anterolaterally from near posteromedial corner, and 13–15 pits near lateral margin and extending onto wingpad; each wingpad covering ca. ⅔–¾ of each metanotal plate laterally. Each plate of metanotum bearing 9–13 pits in the following arrangement: 3 pits near anteromedial border, 3–4 pits ca. midway between medial and lateral margins and 3–6 pits near lateral margin. Distal ⅔ of profemora with slender tooth on median aspect of ventral margin. Metatibiae with setae in longitudinal rows on ventral aspect (present in previous instars but not apparent); distal setae somewhat stout, almost toothlike or spinelike. Metatarsi 3-segmented, segments 1 and 2 cylindrical, segment 3 subconical, slightly curved and bearing a pair of slender apical claws; segment 3 slightly longer than segment 1, segment 2 ca. ⅔ length of segment 1.

Abdomen with each segment bearing the following number of pits on either side of midline: segment 2 with 1 pit on tergite near midline (obscure, not illustrated), segment 3 with 2 pits on tergite near midline and 1 pit near lateral margin, segments 4–5 each with a transverse row of 7 pits extending from near midline to lateral margin, segments 6–8 each with 2 pits on tergite near lateral margin, segment 9 with 4 caudal pits. Waxpads on segments 6–8 each with a transverse row of 4 very small pits near anterodorsal margin.

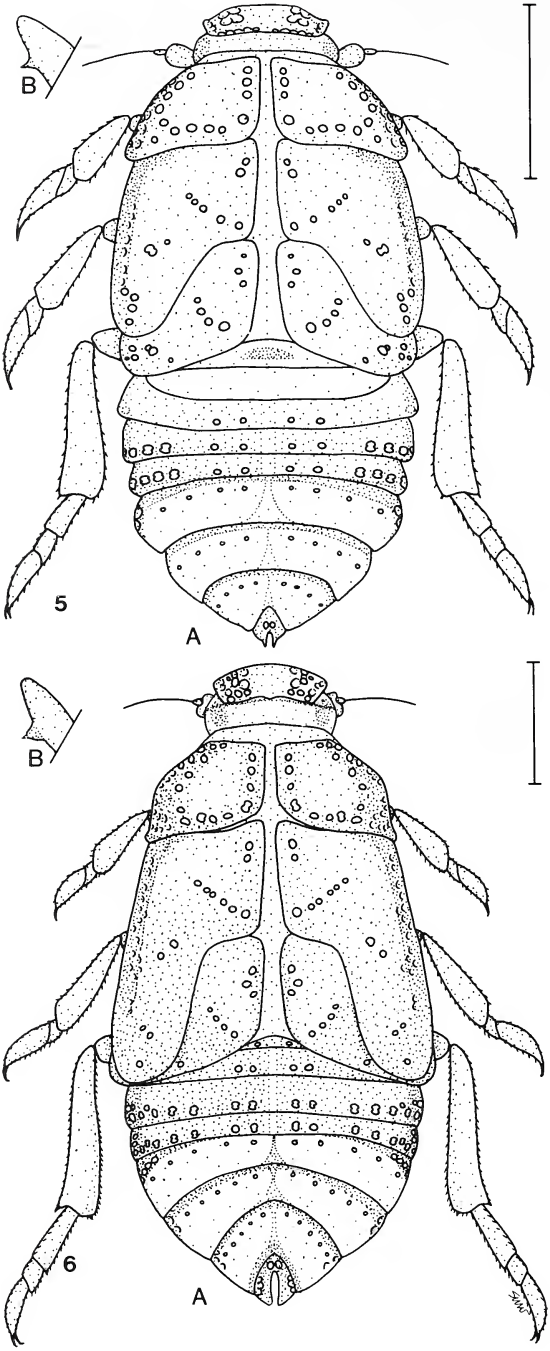
Fifth Instar (Fig. 6).—Length 2.68 ± 0.122; thoracic length 1.17 ± 0.059; width 1.31 ± 0.077.

Sclerotized portions of body darker.

Head with pits more numerous on vertex and frons.

Each pronotal plate bearing 31–33 pits. Mesonotal plates bearing 25–29 pits with 2 pits in anteromedial corner, an oblique row of 6 pits extending anterolaterally from near posteromedial corner, 17–21 pits on wingpad and near lateral margin of plate; wingpads extending to or beyond apex of metanotal wingpad. Each metanotal plate bearing 8 pits with 3 pits in anteromedial corner, an oblique row of 4 pits extending anterolaterally from near posteromedial margin, and 1 pit near region overlapped by mesonotal wingpad; wingpads extending almost to fourth tergite. Profemora with stouter ventral tooth.

Each abdominal segment bearing the following number of pits on either side of midline: segment 2 with 1 pit on tergite near midline; segment 3 with



Figs. 5, 6. Immature stages of *M. crudus*. A. Nymph, B. Distal end of profemur. (5) 4th Instar, (6) 5th Instar. Vertical bar = 0.5 mm.

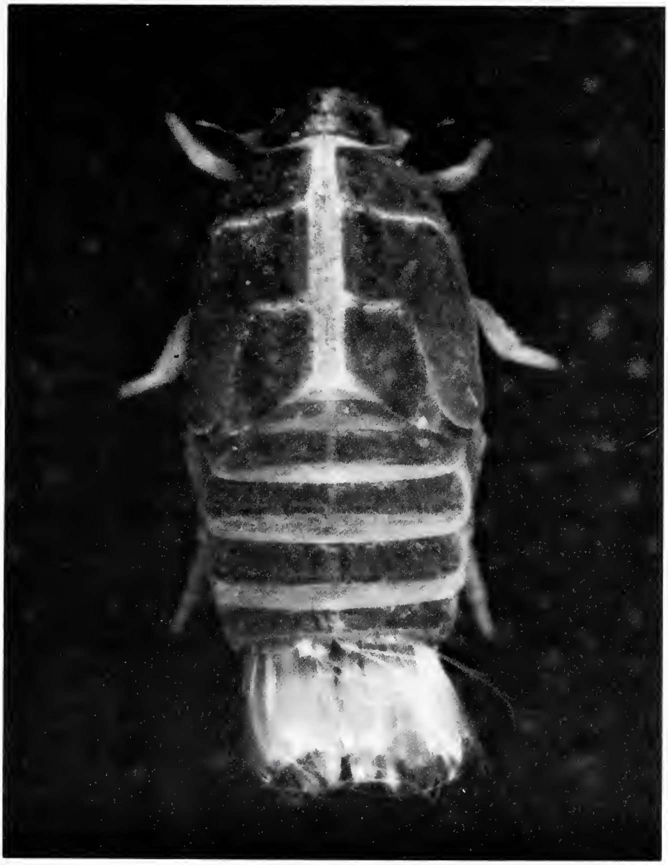


Fig. 7. *M. crudus* nymph with waxy exudate.

2 pits on tergite near midline (lateral pit present in previous instar absent in this instar); segment 4 with a transverse row of 10–11 pits on tergite; segment 5 with a transverse row of 10 pits on tergite; segment 6 with 4 pits on tergite laterally, segments 7–8 each with 2 pits on tergite laterally, segment 9 with 4 caudal pits. Waxpads on segments 6–8 each with a transverse row of 5 very small pits near anterodorsal margin. Waxy exudate present in this and earlier instars in living specimens (Fig. 7).

Key to the Nymphal Instars of *M. crudus*

1.	Metatarsi 2-segmented; profemora lacking tooth on ventral margin (Figs. 2–4)	2
–	Metatarsi 3-segmented; profemora bearing tooth on ventral margin (Figs. 5, 6)	4

2. Posterolateral corners of mesonotum distinctly lobate; mesonotum with more than 10 distinct pits on each side (Fig. 4) Third Instar
– Posterolateral corners of mesonotum not lobate or weakly so; mesonotum with fewer than 10 pits on each side, pits shallow and often indistinct (Figs. 2, 3) 3
3. Mesonotum with ca. 7 indistinct pits on each side; basal bulbous portion of antennal flagellum distinctly smaller than pedicel; thoracic length greater than 0.35 mm (Fig. 3) Second Instar
– Mesonotum apparently lacking pits; basal bulbous portion of antennal flagellum subequal to pedicel; thoracic length less than 0.30 mm (Fig. 2) First Instar
4. Mesonotal wingpads extending to apex of metanotal wingpads; mesonotum with an oblique row of 6 pits on each side extending anterolaterally from near posteromedial corner (Fig. 6) Fifth Instar
– Mesonotal wingpads not extending to apex of metanotal wingpads; mesonotum with an oblique row of 5 pits on each side extending anterolaterally from near posteromedial corner (Fig. 5) Fourth Instar

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UNIONICOLID MITES FROM CENTRAL NEW YORK

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Abstract.—Mites of the family Unionicolidae were collected from 110 freshwater bivalves in New York. Five species of adult mite were found. Of the dominant bivalves found in Conesus Lake, only *Lampsilis siliquoidea* (Barnes) contained adult mites. *Unionicola fossulata* (Koenike) infected 84.8% of this mussel and 75.3% of the nymphal and adult mites were found between the gills. There were 2.08 ± 0.12 mites per infected *L. siliquoidea.* At Spencer creek, *Unionicola arcuata* (Wolcott) and *Najadicola ingens* (Koenike) were found in *Alasmidonta undulata* (Say). *Unionicola formosa–ypsilophora* complex (Vidrine 1980) and *Unionicola tumida* (Wolcott) occurred in *Anodonta cataracta* (Say). In the case of *N. ingens* this is a new host record and the first published report of its occurrence in New York State. No nymphal or adult mites were found in 42 *Elliptio complanata* (Solander) from the two contrasting sites.

Introduction

Unionicolid mites parasitize freshwater mussels. The family has been studied by a number of workers in North America including Wolcott (1899), Mitchell (1955, 1957, 1965a), Cook (1974), and Vidrine (1977, 1979, 1980). In particular Mitchell (1965b) studied population densities and regulation of *Unionicola fossulata* (Koenike) in *Lampsilis siliquoidea* (Barnes), and Gordon, Swan and Paterson (1979) and Paterson and Macleod (1979) the biology of *Unionicola formosa* (Dana and Whelpley) in *Anodonta cataracta* (Say). *Najadicola ingens* (Koenike) has been studied by Humes and his co-workers (1950, 1951, 1952).

Materials and Methods

Collections were made using a hand net in shallow water and by SCUBA diving to reach a depth of 7.5 m the maximum at which bivalves occurred.

The mussel collections were examined as soon as possible on return to the laboratory. The number and location of the active mites within each mussel was noted and estimates were made of the numbers per host of eggs, prelarvae and nymphochrysalids. Prelarvae and nymphochrysalids were dis-

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sected from the mantle and gills respectively. Specimens of all stages were preserved in Koenike's fluid.

Results

Five common species of freshwater mussels were collected from two contrasting sites.

Conesus Lake is part of the St. Lawrence River system. It is situated south of Rochester and is the most westerly of the Finger Lakes system. A total of 88 mussels were collected made up as follows: 46 *L. siliquoidea,* 38 *Elliptio complanata* (Solander) and 4 *Anodonta grandis* (Say). The only adult mite found was *U. fossulata* in L. *siliquoidea. E. complanata* contained the developmental stages of a transient species but no nymphal or adult mites.

Spencer Creek the out-flow channel of Spencer Lake is situated in the town of Spencer, south of Ithaca and forms the northern part of the Susquehanna River system. A total of 22 mussels were collected, in running water of up to 1 m depth made up as follows: 11 *Alasmidonta undulata* (Say), 7 *A. cataracta* and 4 *E. complanata. N. ingens* and *U. arcuata* were found in *A. undulata.* Of the 7 specimens of *A. cataracta* 2 contained *U. tumida.* The other 5 contained a species of *Unionicola* closely resembling *U. formosa* (Dana and Whelpley) but the males have a discrete posterior border on coxal plate IV as in *Unionicola ypsilophora* (Bonz). They have been referred to as the *U. formosa–ypsilophora* complex by Vidrine (1980).

U. fossulata in L. siliquoidea.—In *L. siliquoidea* 39 out of the 46 specimens contained nymphal and adult stages of *U. fossulata,* a 84.8% level of parasitization by the active stages. In addition most contained unionicolid eggs and prelarvae in the mantle and nymphochrysalids in the gills.

A total of 81 nymphs and adults of *U. fossulata* were found in the infected specimens of *L. siliquoidea* averaging 2.08 ± 0.12 mites per mussel. These were made up as follows: 35 males, 41 females and 5 nymphs (Table 1). Of the infected mussels, 89.7% had a male, never more than 1 per mussel and 61.5% had 1 male and at least 1 female. If 1 adult mite was present it was

Table 1. Nymphs and adults of *Unionicola fossulata* infecting the mussel *Lampsilis siliquoidea.*

Mite	Total numbers	Mean number per infected host	Mean number per total number host
Males	35	0.90 ± 0.05	0.76 ± 0.06
Females	41	1.05 ± 0.13	0.89 ± 0.13
Nymphs	5	0.13 ± 0.05	0.11 ± 0.05
All stages	81	2.08 ± 0.12	1.76 ± 0.15

46 *L. siliquoidea* examined, 39 infected with active stages.

most frequently a male, if 2 mites were present they were normally male and female and when 3 adults occurred in the mussel, 1 male and 2 females were found.

The nymphal and adult mites of *L. siliquoidea* showed a preferred location with respect to the gill surface. Table 2 refers to these results. The site numbers are those used by Davids (1973). 75.3% of the mites occurred between the gills, 17.3% between the gills and the foot and only 2.5% were found between the outer gill surfaces and the mantle.

Measurements of the developmental stages indicated that 1 type of *Unionicola* was present in *E. complanata* and 4 types in *L. siliquoidea,* one of which is the same as that found in *E. complanata* (Jones, personal communication). Identification to species is not possible since detailed descriptions of most American unionicolid larvae are not yet available.

N. ingens in A. undulata.—N. ingens is an endobranchial parasitic mite of freshwater bivalves. It belongs to the family Unionicolidae Oudemans 1909 and is the only genus and species in the subfamily Najadicolinae Viets 1935.

N. ingens was found only in *A. undulata.* 11 specimens of this bivalve were collected, 8 were infected and a total of 15 adult *N. ingens* recovered.

The presence of *N. ingens* in *A. undulata* is a new host record. The present report is also the first published account of *N. ingens* being found in New York State although student project reports from "The International Field Workshop on Aquatic Invertebrates," 1978, St. Lawrence University, U.S.A, listed *N. ingens* in 7 specimens of *Strophitus undulatus* from Grannis Brook (St. Lawrence County, New York) as well as an unstated number of infected *Anodonta* sp. (Crowell, personal communication).

N. ingens has previously only been recorded within the gills of its hosts. In the present collection 7 out of a total of 15 mites were found inside the pericardial region of 6 specimens of *A. undulata.*

Discussion

The dominant bivalves in Conesus Lake are *L. siliquoidea, E. complanata* and *A. grandis* (Clarke and Berg 1959). The first 2 show an interesting comparison with regard to parasitism by unionicolid mites. Although both harbour immature resting stages, only *L. siliquoidea* had resident nymphal and adult mites. *E. complanata* accommodates the transforming developmental stages of a single species of unionicolid. Adult female mites must visit this mussel in order to lay eggs and then leave. *L. siliquoidea* appears to be the natural host for *U. fossulata* and the preferred host for other species of immature transient unionicolids in this lake. Mitchell (1955) working in Michigan, found four species occurred together in *L. siliquoidea* namely *U.*

Table 2. Distribution of *Unionicola fossulata* in infected *Lampsilis siliquoidea.*

Site in the mussel	Total numbers of active nymphs and adults at each site
I	1
II	29
III	14
IV	32
V	1
VI	4

Site numbers are those used by Davids (1973).

fossulata, U. abnormipes, U. serrata and *U. aculeata* of which only the latter was transient.

Adult mites were most frequently found between the gills and to a lesser extent between the gills and the foot, which agrees with the work of Mitchell and Pitchford (1953) for *U. ypsilophora,* Mitchell (1965b) for *U. fossulata* and Davids (1973) but is in contrast to the findings of Gordon, Swan and Paterson (1979) who worked on *U. formosa.* The latter workers frequently found mites on the outer surface of the gills.

Although seasonal collections were not made both Mitchell (1965b) and Gordon, Swan and Paterson (1979) found there were no significant seasonal changes in the total number of mites in all stages or in the percentage infection. The present results agree closely with the findings of Mitchell (1965b).

A number of authors previously described *N. ingens* as rare or infrequent but it has now been recorded from 16 states in North America, from Canada and recently from Thailand (Vidrine, personal communication). New York State can now be added to this list.

The new host reported here further supports the view of Vidrine and Bereza (1977) that *N. ingens,* unlike the majority of unionicolids, lacks host specificity and parasitizes a broad spectrum of mussel genera.

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PREDATORS, PARASITES, AND ASSOCIATES OF *ANTHOPHORA ABRUPTA* SAY (HYMENOPTERA: ANTHOPHORIDAE)[1]

Beth B. Norden and Aubrey G. Scarbrough

Abstract.—Predators, parasites, and associates of the gregariously nesting solitary bee, *Anthophora abrupta* Say (Hymenoptera: Anthophoridae), were studied in Baltimore County, Maryland during 1976–1979. Adult bees were preyed on by barn swallows (*Hirundo rustica* L.) and parasitized by conopid flies (*Physocephala marginata* Say). Immature stages were parasitized by *Chrysis* sp., *Ganperdea apivora* (Aldrich), *Hornia minutipennis* Riley, and *Monodontomerus mandibularis* Gahan. Juvenile mortality was high (about 57%), and may have been contributed to by 10 species of fungi (Eumycota) infesting 50% of the bee cells. Fifteen non-parasitic insect species also nested at the study site and possibly competed with *A. abrupta* for nesting space.

Introduction

Anthophora abrupta Say is a solitary bee that nests gregariously in clay embankments or adobe structures. Each nesting female typically digs a horizontal tunnel into the soil, then constructs and provisions a series of 6–8 cells. Each lipid-lined cell contains one egg laid on the semi-solid provision, and is sealed with an earthen cap (Norden 1979). In this study, predators, parasites, and inquiline associates of *A. abrupta* were recorded.

Materials and Methods

During 1976–1979, bees were observed as they nested in the adobe walls of a farm shed in Owings Mills, Baltimore County, Maryland. Associates of *A. abrupta* were monitored daily during the 1977 and 1978 seasons. Any dead adult bees found at the site were collected in vials and returned to the laboratory for examination. At the end of nesting in 1978, 600 bee cells were also taken to the lab where they were opened and inspected.

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[1] This paper is derived from research conducted in partial fulfillment of requirements for the Master of Science degree in the Department of Biological Sciences, Towson State University, Towson, Maryland.

Results and Discussion

Barn swallows (*Hirundo rustica* L.) were observed capturing adult female bees as they flew above the shed on 23–30 May 1977. Swallows were not observed foraging on bees after 30 May and it was suspected that the emergence of worker bumblebees affected this behavior. Three bumblebee species (*Bombus bimaculatus* Cress., *Bombus nevadensis* Cress., and *Bombus perplexus* Cress.) that closely resemble *A. abrupta* also nested at the site. In contrast to *A. abrupta,* bumblebees inflict painful stings and Batesian mimicry may have discouraged the swallows from preying on bees after 30 May.

It has been noted that gregarious nesters, especially Anthophoridae, are frequently attacked by parasites (Callan 1977). In this study, five parasitic insect species were found and are considered briefly below.

1) *Chrysis* sp. (Hymenoptera: Chrysididae): These metallic green cuckoo wasps were abundant at the site (15 May–10 Sept.), and frequently were seen entering bee tunnels. Three sealed cells contained body fragments of adult *Chrysis,* but no immature stages were found. Most cuckoo wasps are external parasites of bee prepupae (Borror and DeLong 1971).

2) *Ganperdea apivora* (Aldrich) (Diptera: Anthomyiidae): The holotype and allotype of this parasitic fly were obtained from *A. abrupta* cells collected in Missouri in 1877 (Steyskal 1967). Adult flies were very common at the study site between 3 May and 19 July. Their occurrence corresponded closely to that of adult bees (13 May–15 July). *Ganperdea* flew close to the wall or crawled along its surface, frequently entering bee nests. Oviposition probably occurred while the cell was still being provisioned. One bee cell containing six fly pupae was found to have been partially provisioned, then filled with loose clay particles. Five sealed cells opened in the lab contained an average of 5.6 ± 0.5 fly pupae but no remnants of bee larvae. Bee eggs were probably killed and the provision consumed by *G. apivora* larvae.

3) *Hornia minutipennis* Riley (Coleoptera: Meloidae): Riley described this beetle from specimens also obtained from *A. abrupta* cells in Missouri in 1877. During this study, four *H. minutipennis* were found within sealed *A. abrupta* cells (April 1977 and 1978). One specimen was also removed from a spider web in the shed on 14 June 1977. Rau (1930) reported that female beetles laid their eggs in the cells in which they were reared. When the eggs hatched, the mobile triangulins (first instar larvae) crawled out from the bee cells and attached themselves to passing adult *A. abrupta.* They were then carried by adults into cells where they fed on bee eggs and cell provisions. Only adult meloids were found in this study, and all appeared to have consumed the provision but not the cell lining (see Norden et al. 1980).

4) *Monodontomerus mandibularis* Gahan (Hymenoptera: Torymidae): These minute metallic green wasps were abundant at the wall from May to October. They mated at the wall following emergence, and then females

entered *A. abrupta* nests. Bee cells (n = 8) contained 25.5 ± 4.5 wasp larvae which consumed bee prepupae, leaving only the prepupal skins. Evidence of more than one generation per season was provided in the laboratory where adult wasps continued to emerge during September.

5) *Physocephala marginata* Say (Diptera: Conopidae): One conopid fly emerged from a dead adult female *A. abrupta* on 8 July 1977, and another was collected as it flew in front of the shed on 23 June 1978. Conopids insert their eggs into bee abdomens during flight (Askew 1971). Bees remained active as fly larvae fed on their abdominal contents, and pupation of the conopid did not occur until after the death of the host bee.

Also noteworthy was the emergence of 64 *Pediobius williamsoni* (Girault) from the body of a dead female *A. abrupta* collected on 27 June 1976. These wasps were probably parasitoids of a conopid parasitizing the bee (E. E. Grissell, pers. comm.).

Bees may also have succumbed to fungal infections. Examination of cells (n = 600) in the laboratory revealed that 343 (57.4%) were infested by fungi (Eumycota). Of these, 50.2% were completely filled with fungal mycelia which had destroyed brood and provisions, while 7.2% contained living prepupae with fungal growth limited to cell caps. Fungi were identified as follows:

Order Eurotiales
  Sporothrix sp.
Order Moniliales
  Aspergillus niger van Tiegh.
  Cladosporium sp.
  Fusarium sp.
  Paecilomyces sp.
  Sporodesmium sp.
Order Mucorales
  Mortierella sp.
  Mucor sp.
  Rhizopus sp.
Order Sphaeriales
  Kernia sp.

Fusarium is known to be a faculative parasite of bees (Batra et al. 1973), however, we could not determine whether this or other fungi were responsible for larval death. Bees killed by other causes might later have become infested by saprophytic fungi.

Whatever the causes of death, we found a juvenile mortality rate of about 57%. *Anthophora linsleyi* Timberlake exhibited a similarly high mortality rate (about 50%), while maintaining a stable population (Linsley and

MacSwain 1942). Apparently, *A. abrupta* also produced sufficient cells to offset this high juvenile loss since the population did not appear to change significantly during this study.

In addition to those organisms directly effecting *A. abrupta,* we also found several non-parasitic insect species in close proximity to active bee nests. These associates may compete with *A. abrupta* for nesting space, as they were found inhabiting old nest cavities. They included:

- Anthophoridae
  - *Anthophora bomboides* Kirby
- Apidae
  - *Bombus bimaculatus* Cress.
  - *Bombus nevadensis* Cress.
  - *Bombus perplexus* Cress.
- Eumenidae
  - *Ancistrocerus unifasciatus* (Saus.)
  - *Stenodynerus* sp.
  - *Symmorphus* sp.
- Megachilidae
  - *Megachile latimanus* Say
  - *Osmia lignaria* Say
  - *Prochelostoma philadelphi* (Robt.)
- Pompilidae
  - *Agenioideus humilis* (Cress.)
- Sphecidae
  - *Crossocerus* sp.
  - *Trypoxylon clavatum* Say
  - *Trypoxylon kolazyi* Kohl.
- Vespidae
  - *Polistes fuscatus* F.

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ENTOMOLOGY IN THE PEOPLE'S REPUBLIC OF CHINA[1]

James H. Tsai

Introduction

China is one of the oldest civilizations in the world. The span of Chinese history is the evolution from half-million-year old Peking-Man to 20th Cen-

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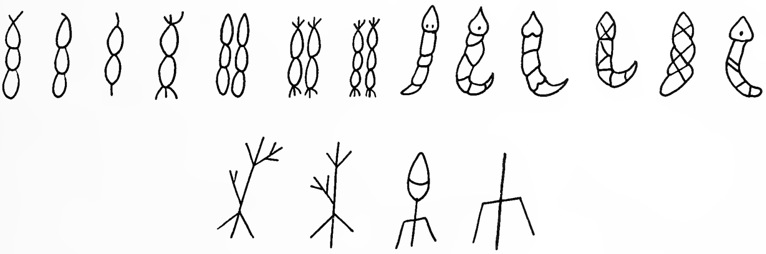
tury technologists. The earliest evidence of Chinese civilization and science development provided by a series of archaeological findings is set at more than 5,000 years ago. Under successive dynasties Chinese achievements in literature, philosophy, art, and certain fields of science are among the highest in the world. However, the advent of Western technologies at the turn of 19th Century had profound consequences for traditional China. In order to accommodate with the outside world, China has gone through drastic changes in political, economic, and scientific systems. As with other sciences in China, entomology has evolved and reached to a level of glorious attainment in the history. It would be highly inappropriate for anyone to discuss the current entomology in The People's Republic of China (PRC) without knowing the history of Chinese entomology.

I. Development of Entomological Studies

A. Historical Overview of China's Entomology

a. Study of beneficial insects.—Silkworm (*Bombyx mori* L.) (Lepidoptera: Bombycidae): Sericulture and silk technology date back to the period of Agriculture ca. 4,500–7,000 years ago, as evidenced by the recent discovery of a Neolithic relic site in Zhejiang Province (Map 1), where the silk material along with rice seeds unearthed were determined by C^{14} dating method to be 4,728 ± 100 years old (Anonymous 1980; Chou 1980). The silk technology advanced further in Yin Dynasty (16th–11th Century B.C.) as the silk cloth unearthed from the Yin tombs revealed both flat and in relief patterns. During this period, the tortoiseshells used as paper were found inscribed with the idiograms denoting the characters silk, silkworm and mulberry tree respectively (Chou 1980). The mass planting of mulberry and indoor rearing of silkworm were recorded in the Xia Dynasty (1711 B.C.) (Anonymous 1980; Chou 1980). By the 9th Century, as a result of continuous breeding and rearing of the silkworm, many books on the bionomics of this insect had been published. The technique for storing the eggs of silkworm in low temperatures was developed in the 4th Century A.D. The domesticated silk-



worm, *B. mori* is thought to be evolved from the wild species *B. mandarina* (Moore) (Chou 1980). The silk road was built 138–126 B.C. in Han Dynasty, but the records showed that the technology of sericulture was not introduced in Turkey until the 6th Century A.D. It was introduced into Korea as early as the 12th Century B.C. Because of geographical barriers its introduction into Japan came as late as the 2nd Century A.D.

Other silk producing insects have also been utilized in China since the 12th Century B.C. The breeding of the other silkworms, *Antherea pernyi* Guerin started in the 1st Century A.D.; and *Semia cynthia pryeri* Butler, and *Eriogyma pyretorum* (Westw.) in the 17th Century A.D.

Honeybee (*Apis cerana* Fab.) (Hymenoptera: Apidae): The history of apiculture is as old as sericulture in China. The tortoiseshells found in the Yin tombs bore the inscriptions of the idiograms of bee (Chou 1980).

The commercial breeding and the teaching of beekeeping prospered 1,800 years ago (Anonymous 1980). The uses of beeswax for candles and pills were known in the 7th Century A.D. Several monographs dealing with bee morphology, biology, rearing techniques, social behavior, control of natural enemies, honey extraction, and apiary management were published during the period of 1273–1817 A.D.

Wax insect (*Ericerus pela* Chav.) (Homoptera: Coccidae): The wax of this scale insect was first utilized in China in 1300 B.C. In the next two centuries, a great deal of information on its host ranges, distribution, biology, and methods of extracting wax was published.

Lac (*Laccifer lacca* Kern) (Homoptera: Lacciferidae): During the 3rd Century A.D., the Chinese were first to describe methods of distributing the immatures of *L. lacca* on the tree in order to produce the lac which was used for dye, lacquer, and medicine (Anonymous 1980; Chou 1980).

Gall insect (*Melaphis chinensis* Walsh.) (Homoptera: Eriosomatidae): As early as the 1st Century B.C. the leaf galls produced by *M. chinensis* were used for extracting tannin which has been used in dye and medicine (Anonymous 1980; Chou 1980).

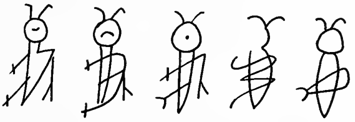
Insects as medicine: From 31 B.C. to 1578 A.D. a total of 73 species of insects had been listed in Chinese medical publication entitled "Compendium Materia Medica." Several common insects are currently used in Chinese medicine: the exuviae of cicadas are used against fever. Tannin extracted from the leaf galls of *M. chinensis* is an astringent compound. Cantharadin from the blister beetles, *Lytta caraganae* Pallas, *Myabris phalerata* Pallas, and *Epicauta* spp., is used as a cure for ulcers and as a abortion agent. The egg cases of mantid are used for curing impotence. Silkworms infected with muscardine fungus, *Metarrhizium anisopliae* Metsch, are used as a cure for palpitation. Lepidopterous larvae parasitized by *Cordyces* sp. fungus are used as a cough medicine, and the bee sting is used for treating arthritis (Anonymous 1980; Chou 1980).

Edible insects: Historical records showed that men ate the larvae and pupae of bees and wasps, the nymphs of cicadas, and the immatures of ants in 1200 B.C. Locusts as food were recorded in 23 A.D. Currently the pupae of silkworm and giant silkworm and the predaceous diving beetles (*Cybister* spp.) are still being used as food by some people in China.

Insects used for other purpose: Insects have become the main theme in numerous poems and paintings throughout Chinese history. May beetles and buprestids were used as ornamentals in the 11th Century A.D. During 618–905 A.D., cicadas and crickets were bred for song contests. Since then several species of crickets (*Scapsipedus aspersus* (Walker), *Homoeogryllus japonicus* (Haän), *Gryllus testaceus* Walker, and *Brachytrupes portentosus* L.) were bred for fighting contests. As a consequence there were at least five monographs dealing with cricket identification, food preference, biology, fighting techniques, and artificial rearing techniques published during 1265–1884 A.D.

b. Study of agricultural pests.—China has been an agricultural society for more than 5,000 years. Undoubtedly, China has a long history of fighting against various agricultural pests. A book written in the 11th Century B.C., entitled "Book of Poems" which dealt with a number of agricultural subjects described the decree issued by the ancient ruler to mobilize peasants in insect control, and to recommend insect control with fire. A pest control officer was officially installed in Zhou Dynasty (ca. 240 B.C.). During this period a series of control measures were employed such as the use of heat, lime, plant ashes and insecticidal plants (Chou 1980).

Locusts (*Locusta migratoria* L.): The locust problem has plagued Chinese agriculture for as long as Chinese history is dated. Probably it has evolved with the cultivated crops, mainly Gramineae, for about 6,000 years. The earliest evidence of locust and man association was found in the Yin Dynasty. The tortoiseshells found in the Yin tombs have a number of idiograms representing the character "locust." The first antilocust decree was issued in 29 A.D. (Chou 1980). During the period of 707 B.C. to 1911 A.D., between 538 and 800 locust outbreaks were recorded (Anonymous 1977a; Chou 1980). Since the 17th Century A.D. a number of publications have appeared concerning the breeding sites, host ranges, morphology, biol-



ogy, ecology, gregarious and migratory behaviors, and control measures of this insect.

Lepidopterous insects: Stemborers (*Diatraea verosata* Walker, *D. shariinensis* Eguchi, *Chilo simplex* Butler) are currently considered to be the second most important pests of graminaceous crops. Between 718 B.C. and 1911 A.D. about 50 serious outbreaks were recorded (Chou 1980). Army worm (*Leucania separata* Walk.) had 49 outbreaks between 500–1700 A.D.

Other insects such as wild silkworm (*Bombyx mandarina* Moore), mulberry geometrid, (*Hemerophila atrilineata* Butler), angoumois grain moth (*Sitotroga cerealella* Oliv.), black mulberry beetle (*Chrysochus chinensis* Baly.), wheat midge (*Sitodiplosis mosellana* Gehin), and the cricket (*Gryllus* spp.) were reported for a number of outbreaks during the period of 26–1839 A.D.

c. Insect control measures.—Physical control: The manual control of insects was first described 1,800 years ago, the control of silver fish *Ctenolepisma* (*Lepisma*) *vilosa* (Fabricius) was recorded 2,000 years ago. The use of fire to control insects was recorded about 240 B.C. (Anonymous 1979).

Cultural control: Weeding and deep plowing were employed to control insects in 239 B.C. Varying dates of planting and harvesting which played an important role in reducing the insect pests were reported during 528–549 A.D. Other practices such as crop rotation, irrigation, and the use of resistant variety were also recorded in the history.

Biological control: This practice has been used in China since 304 A.D. The classic example is the use of predaceous ants (*Oecophylla smaragdina* F.) to control a number of citrus pests such as leaf beetles, curculioes, scarabaeus beetles, and stink bugs (Anonymous 1980). The use of ducks to control pests in paddy field dates back to the period of 1611–1672 A.D. The decree was issued by the ruler of Late Han Dynasty (948–980 A.D.) to protect such insect predators as birds and frogs.

Chemical control: The use of plant ashes and lime to control the household insects has been known for over 3,000 years. Mercury used for flea control and the treatment of wheat seeds with arsenic for control of underground insects were reported 2,000 years ago. Other organic compounds such as aluminum and copper for flea control and sulfur for control of ornamental insects were reported 1,000–1,500 years ago (Anonymous 1980; Chou 1980).

The use of a variety of insecticidal plants including *Zingiber mioga,* and *Illicium lanceolatum* to control medical and storage insects was recorded 3,000 years ago. Other plants with insecticidal activities were: *Aconitum lycactorum, A. fischeri, Daphne genkwa, Chaenomeles sinensis, Ligusticum sinensis, Artemisia scoparia, Incarvillea sinensis, Celastrus* sp., *Croton* sp., *Ruta* sp., *Stemona* sp., *Xanthium* sp., *Spirodela* sp., *Gleditsia* sp. They were used during 1000 B.C. to 1700 A.D. (Chou 1980).

d. Study of insect morphology and biology.—The earliest record of studying insect morphology came in 250 B.C. when the Chinese described the exoskeleton and endoskeleton of the insects. The morphological characteristics of the planthopper, *Lycorma delicatula* white, and the louse fly, *Hyppobosca capensis* Olfers were described in detail in 1116 and 1578 A.D. respectively (Anonymous 1980; Chou 1980). At the same time, the phenomenon of metamorphosis in mantids was reported. Later the metamorphosis of Lepidoptera (butterflies and moths) and caddisflies was reported in 300 and 739 A.D. respectively. The parthenogenesis of insect was recorded in 600 B.C. Color mimicry was first described in the 1st Century A.D.

The relationship between the prey and predator was first studied in 502 A.D. with sphecid wasps (including the members of Eumenidae, Sphecidae, Trypoxylidae) carrying the borer larvae to their nests as food for their young (Anonymous 1977a; Chou 1980). During the 7th Century it was reported that not only the borer larvae but also spiders were used as food for the young, and that the eggs of wasps were deposited on the prey. Others reported that tachinid flies parasitized on the silkworms in the 15th Century A.D. (Chou 1980).

B. The Influence of Western Industrial Revolution in the 19th and 20th Centuries

Although China has a glorious ancient history of science and civilization, it was only at the turn of the 19th Century that the study of entomology as part of plant protection was initiated as a modern scientific discipline. China is a country built on agriculture, and will probably remain an agricultural nation from some time to come. This is basically due to the fact that the country covers an area of 9,6000,000 km^2 (=3,706,000 mi^2), and the current population is about 1 billion. Two-thirds of the total area is mountainous or semidesert; only 11% of the land is arable. Nearly 90% of the population is concentrated on the fertile plains and deltas of the east which accounts for $^1/_6$ of the land. Geographically speaking, the country is in the Temperate Zone with the exceptions of the southern portions of the country including Yunan, Guangdong, and Guangxi Provinces which are within the Tropics. Therefore, agriculture which provides enough foods and clothes has become the major theme for every dynasty in Chinese history.

The industrial revolution and Western expansionism of the 19th Century has brought China a series of military and political humiliations. Realizing the inability of the old agricultural system in dealing either with internal difficulties or with foreign encroachments, China started a series of reforms in a society structured by about 5,000 years of civilization. Since then, China has been repeatedly subjected to political, economic and intellectual chaos and revolutions in order to accommodate with the modern world. Like most other disciplines of science, entomology, in the broader field of plant protection, has gone through many phases of changes. A systematic study of entomological science started in 1911. During the period of 1922–1924, a Bureau of Entomology was first established in Jiangsu and Zhejiang Provinces. The entomologists in these two organizations engaged in the systematic study of the major agricultural pests, and medical insects in southern China. The first "Year Book of the Bureau of Entomology" and "Insects and Plant Diseases" were both published by the Bureau of Entomology in Zhejiang Province. Meanwhile they also had trained several scores of entomologists who were later assigned to other provinces. Immediately after 1924, an Entomological Institute similar to the Bureau of Entomology was formally established in Hunan, Jiangxi, Guangdong, and Sichuan Provinces. Several universities and colleges had established a Department of Plant Pathology and Entomology, or Division of Entomology. At the same time, formal teaching and research in entomology were instituted in the colleges and universities. The prestigious Chinese Academy of Sciences (CAS) was formed in 1930. Courses in entomology were included in the curriculum of the Department of Agricultural Zoology in the comprehensive universities and agricultural colleges.

Plant protection science in general suffered a lot from the impact of World War I, and internally, China was all but shattered in the era of warlords. Then came World War II. Most of the research institutes and universities were forced to evacuate to the interior during the war, and very little progress was made in the field of entomology during the 1940's. In spite of the difficult situation during the war, a number of institutions maintained or re-established a Department of Plant Pathology and Entomology usually in their Colleges of Agriculture. Students in their junior and senior years would specialize in either entomology or plant pathology, even though their degree was awarded by the same department. Only Beijing University and Qinghua University had established an independent Department of Entomology in their College of Agriculture during the period 1945–1949.

C. The Era of 1950's

After the founding of the People's Republic of China in 1949, the country enjoyed steady growth for a decade. The leaders of PRC had transformed a weak and backward China into a strong and modern state. The progress of Chinese economy and science in the years of rehabilitation following 1949 was very impressive. In 1953, the "First Five-Year Plan" was initiated in PRC with emphasis on national defense and heavy industry. The economy was basically still agrarian, with a small modern industry concentrated in the northeast and east coast. Even though agriculture produced a greater share of the GNP in this period, it still received little investment from the state. Progress continued until the experiments of the "Great Leap Forward"

(1958–1960) which featured backyard steel plants plunged China into a depression in the early 1960's.

Several outstanding accomplishments can be cited in this golden period. In 1949, there were 450 million people in PRC with an average of less than two years of education per capita. In a decade, the school enrollments quadrupled reaching 100 million and the average number of years of education rose to 3.5 years per capita. Enrollment in primary school was compulsory, therefore it became universal, and junior high enrollment was nearly universal in the cities and surrounding rural areas. The senior high and college enrollments were rather restricted due to lack of facilities and there was extreme competition for admission to these two levels. The Western schooling in China taking roots in this period was mainly due to the earlier influences of foreigners such as American, British, German, French and Japanese in China before the liberation, and the influence of more than 30,000 Chinese educated abroad. Immediately after the liberation, education was totally taken out of foreign hands.

In 1954, higher education was reorganized and modelled on the Soviet system, which emphasized science and technology and the topical specialization of institutions. As a consequence, separate Departments of Plant Pathology and Departments of Entomology were combined into one Department of Plant Protection. There were only two major courses in entomology taught at college: General Entomology and Agricultural Entomology. The former included morphology, anatomy, physiology, life history, ecology and taxonomy. Under this system, no elective courses were offered at colleges and the credit system was also abolished. The comprehensive universities became the main sources to train college faculty. The graduate program was also reorganized on the Soviet model. Roughly 16,000 students were trained by Chinese institutions at the graduate level during 1955–1965. In the same period, approximately 3,000 other Chinese students were trained at the graduate level in USSR and Eastern European nations.

The Institute of Entomology was first established in 1950 under the administration of CAS followed by the establishment of an Institute of Entomology in several localities under the administration of different city and provincial governments. Similarly, the Institute of Plant Protection was also established in several places under the jurisdiction of the Chinese Academy of Agricultural Sciences (CAAS) as well as city and provincial governments. Besides the expansion of various research institutions as mentioned above, there were noted accomplishments in the educational field. Courses in entomology and plant protection were offered in the Biology Department of the comprehensive universities and the College of Forestry respectively. In Central Government, the Bureau of Plant Protection was formed under the Ministry of Agriculture. Consequently, the Plant Protection and Inspection Stations functioned under various city and provincial governments. Plant Quarantine

Stations were set up at the major ports by the Foreign Trade Department. At the same time, medical entomology received a great deal of attention; several research institutes of medical entomology were brought into the picture by the Health Department.

During the period 1953–1957, most of the China's trained entomologists were brought into the CAS, and its affiliated research institutes. The CAS served as the focal point for planning and conducting research on a national scale. The Institute of Entomology served as the center of all entomological activities throughout the land. By decree of Mao Zedong, all scientific research had to point toward practical application. Therefore, the entomological publications during this era dealt, by and large, with applied research. Nonetheless, some basic research of high quality was published by Chinese entomologists trained abroad.

The first issue of "Acta Entomologica Sinica" and that of "Bulletin of Entomological Society of China" were published in 1951 by the Entomological Society of China. The latter was renamed "Kunchong Zhishi" (="Knowledge of Insects") in 1955. A total of 10 volumes of "Journal of Economic Entomology" was published in the 1950's. The Entomological Society of China grew from 861 members in 1954 to 1,068 in 1958 with 22 branches throughout the country (Yueh 1958). By 1963, the number of institutions of higher learning had doubled to 400 as compared to 1949, with the enrollment up from 117,000 to 819,000 (Cheng 1963). Both undergraduate and graduate training in entomology were offered by most of the 50 comprehensive universities and agricultural institutes. A monograph on the standardization of entomological nomenclature was published in 1956 containing a comprehensive list of the names of insects in Chinese and in Latin names (Anonymous 1956).

D. Pre-Cultural Revolution Period (1960–1966)

In 1962, the Plant Protection Society of China was installed and its official publication "Acta Phytophylacica Sinica" was issued subsequently. The following year a sister journal entitled "Zhiwu Baohu" (="Plant Protection") was published to accommodate the influx of manuscripts submitted to the society. During the period of 1962–1965, the Beijing Agricultural University and Nanjing Agricultural College were designated as two "Key" institutions by the Ministry of Education, specifically to train the college faculty and researchers in the field of plant protection. The college curriculum was five years with the additional year devoted to studying such entomological courses as taxonomy, physiology, toxicology, ecology, and forecasting. In the last year, the students were allowed to either specialize in plant pathology or entomology. But this 5-year college curriculum was reduced to four years a year before the onset of Cultural Revolution.

The average number of school years reached 5.5 per capita in the pre-Cultural Revolution period. As a consequence, a flood of graduates entered the labor markets seeking the city and industrial jobs, and met with disappointment. Meanwhile, the gaps between the better educated and the less educated, and the cities and the rural areas continued to widen. The leadership in PRC considered that these trends were very unhealthy. Thus the government instituted the initial program of sending millions of youths down to the country-side (Xiafang) in order to alleviate the tension and to increase the manpower in rural areas.

E. Cultural Revolution Period (1966–1976)

In subsequent years, the full scale Cultural Revolution was carried out which resulted in major changes in Chinese education and virtually all sectors of Chinese society. The "Xiafang" movement was intensified as millions of young people who had been enrolled in the school were sent to the rural areas in order to emphasize learning through practice. Text books and curricula were designed to emphasize the needs of the area in which each institution is located, especially if the subject is agriculture production. All middle school graduates were required to work in the factories or on farms for at least 2 years before applying for a recommendation to attend colleges. Higher education was especially a prime target of attack, colleges and universities were completely closed for a period of about five years. From 1966 to 1978 graduate school training was indeed nonexistent. At the onset of Cultural Revolution there were 100 research institutes, but that was reduced to only 40 in 1976. By this time, China had only 1.2 million scientists, engineers and technicians, less than 1% of the total population. When schools reopened in 1970, the students were recruited for colleges solely on the basis of applicant's political record and family-class background instead of academic excellence. In the early 1970's, college curricula were redesigned to meet needs of production, they were shortened to three or two years, from five years previously. Similarly the primary and secondary school curricula were also reduced from six to five years each. No school records were kept during the cultural revolution period.

It should, however, be noted that a great deal of applied research was carried out during this period (Guyer 1977), and that some of the students even though they were not selected on the base of academic excellence, were indeed intellectually talented. Most of the practical publications that appeared in this period were prepared by and credited to the editorial committee instead of individual researchers. The editorial committee consisted of producers, scientists, and administrators. Thus information in the publication met practical needs and was technically sound, and the measures recommended were also administratively feasible (Chiang 1977a).

The achievements in agriculture were impressive. The PRC was able to attain a self-sufficiency in foods even though its population was enormous and growing. During this period, the policy called for self-reliance at all levels, from the top of government to small communes. The chief reason for the success is in the intensive and efficient use of land through multiple cropping and intercropping along with good water and soil management practices, and resistant variety development. But multiple cropping and intercropping systems led to complicated plant protection methods.

F. Post Cultural Revolution Era

Since 1976, educational policy has returned to a pre-Cultural Revolution era committed to academic excellence. The examination system has been reintroduced in the schools. High school graduates are no longer required to work before entering the colleges. Because of a shortage of colleges and universities, the competition in entrance examination remains very keen. Thus only those who are well qualified academically as well as politically, will be admitted to the colleges. To date, college curricula have been lengthened to four years. In 1977 four modernization programs were initiated, they include agriculture, industry, defense, and science and technology. It was since further affirmed that top investment priority is given to the modernization of agriculture and science and technology (Reardon-Anderson 1978). The training in the secondary schools is heavily oriented toward the natural sciences and mathematics. Foreign languages begins in the primary schools and continues through middle school. The research activities for faculty and student are now evident, and research facilities are being rapidly procured and upgraded.

The current higher education in PRC can best be characterized as follows: Since 1949, education is considered to be a major governmental responsibility and a public enterprise. As in many socialist states, a private educational system is practically non-existent in PRC. The struggle for technological development and modernization in education is seen as a vital factor to enable China to establish and maintain a position of importance in the world. It is clear that science and technology are perceived as the fundamental features of the modern education. However, the emphasis is placed on applied science and technology rather than basic sciences.

II. Development of Control Methods

In the 1950's chemical control played the predominant role in China's struggle against such insect pests as migratory locusts, corn borers, sugar cane borers, rice stem borers, wheat midges, armyworms, cotton bollworms, pine caterpillars, mites, spiders, and medical insects. During the period of

1953–1957, a total of 170,000 tons of insecticides was used on the cultivated land, and about 6 million hectares of crops which covered 70% of infested areas were treated for locust control by aerial dusting. In 1958 alone, an average of 14.7 kg of indigenous insecticides per hectare was used on various crops (Chiu 1959). Benzene hexachloride (BHC), DDT, and other organic phosphorous compounds such as DDVP, malathion, Dipterex and Demeton were the main pesticides used for control of major pests throughout China.

The use of native plant and mineral products as a supplement to the imported insecticides was actively encouraged in 1958, about 500 native products were made into 10 million tons of insecticides and fungicides (Chiu 1959). Two *Derris* spp. containing 13.5 and 10% rotenone and one nicotine-bearing species, *Anabasis aphylla* were found and utilized (Cheng 1963).

The successful examples of using biological control were numerous in the 1950's. The use of parasitic wasps, *Trichogramma* spp. for sugarcane borer control in Guangdong and Guangxi Provinces was highly successful. By 1959, nearly 5,500 hectares of sugarcane plantations were under this control program as compared to 480 hectares in the previous year. As a result of biological control, the sugarcane yield increased by about ⅓ (Pu et al. 1956). Another noteworthy development in biological control was the rearing techniques for *Trichogramma* spp. and their biology study. It was found that the wasps reared on the eggs of pine caterpillar and ricinus silkworm were larger in size, more active, with a higher fecundity, and higher ♀ : ♂ ratio than those raised on angoumois grain moth, *Sitotroga cerealella* Oliv. The eggs of the hosts could be stored up to 2–3 months at 4°–0°C respectively without ill effect on parasite rearing. The adult wasps fed on a honey diet lived 8.6 times longer and produced 14.7 times more than those reared on distilled water.

Other examples of biological control were equally successful including the use of *Dibrachys cavus* Wilk. against the pink bollworm, the tachinid fly, *Zenillia roseanae* B. B. against the rice leaf roller, the rice swarming caterpillar and the European corn borer (Yang 1958), the lady beetles, *Rodolia cardinalis* Mulsant and *R. rufopilosa* Mulsant against cottony cushion scales (Chiu 1959). The muscardine fungus, *Beauveria bassiana* was reported to be used against the soybean pod borer, the sweet potato weevil, and the pine caterpillar (Hsu et al. 1959; Lin 1956).

In addition to chemical and biological control measures, other means of insect control were reportedly employed with limited success. Early or late sowing and transplanting of rice resulted in less borer damages (Chiu 1959). Similarly, late sowing of wheat was reported to reduce the damage by wheat stem maggot, *Meromyza saltatrix* L. in Shaanxi Province. The removal of the weed, *Leersia hexandra* Swartz from the paddy fields was an effective control of the rice gall-midge, *Pachydiplosis oryzae* Wood-Mason and the planthopper, *Nilaparvata lugens* Stål. The method of drowning the rice borer, *Tryporyza* (=*Schoenobius*) *incertulas* (Walker) was practiced over a large area (Chiu 1959).

In the 1950's the age-old problem of migratory locust, *Locusta migratoria manilensis* was effectively controlled by sophisticated environmental control techniques. The problems were managed through installation of reservoirs and drainage systems, transformation of water-logged areas, reclamation of wastelands along the coast, and elimination of particular breeding habitats such as lake shore, flooded plain, coastal areas, and river flooded areas (Ma 1958, 1962). An excellent example is that in a decade (1950–1960), a total of 15,492 km of irrigation systems were built. As a consequence, 39,000 hectares were under flood control, and 370,500 hectares were placed under irrigation system in Shangdong Province alone (Guyer 1977).

The system of monitoring and forecasting insect population became an integral part of pest management in China (Anonymous 1977a, b, 1979b): the program started in 1951 and by 1958 a total of 678 insect monitoring and forecasting stations was in operation throughout the nation, with 700,000 farmers participating in the program (Su 1959). These stations were mostly limited to short-range forecasting of insect outbreaks in large rural areas. However, the information obtained from the study of population dynamics of migratory locusts made long range forecasting possible.

The pests of major crops and their control measures are cited below.

1. Rice insects: China is the world's largest producer of many food crops including rice, sweet potatoes, sorghum, soybeans, millets, barley, peanuts, and tea. Of the 124 million hectares of rice land in Asia, about 35 million hectares of rice were planted in China. The grain production in PRC was estimated at 255 and 140 million metric tons in 1974 and 1981, respectively (Kelman and Cook 1977; Anonymous 1982). About 80% of the rice is of indica varieties; they are developed for certain qualities including high yield, fast growth under high fertility, early maturity, and short stems. Since rice is the dominant crop in China, pests are considered as important production-limiting factors. Pest problems are more serious in the south than central and northern China. Of the total 114 species of rice pests damaging the rice during either the growing or post harvest seasons, the rice paddy borer, *Tryporyza incertulas* (Walker); purplish stem borer, *Sesamia inferens* Walker; rice stem borer, *Chilo suppressalis* Walker; green rice leafhopper, *Nephotettix cincticeps* Uhler; brown planthopper, *Nilaparvata lugens* Stål; white-backed planthopper, *Sogatella furcifera* Horvath; rice leaf roller, *Cnaphalocrocis medinalis* Guenee; rice skipper, *Parnara guttata* Bremer and Grey; rice weevil, *Echinocnemus squameus* Billb.; the planthopper, *Laodelphax striatellus* Fallen; rice leafminer, *Hydrellia griseola* Fallen; rice thrip, *Chloethrips oryzae* Williams, *Haplothrips aculeotus* Fab.; and rice green caterpillar, *Naranga aenescens* Moore; are the major ones (Anonymous 1977, 1978a, 1979a).

The use of chemical control was solely based on its effectiveness, safety and economy. The time to use insecticide was determined through the monitoring and forecasting system. The monitoring procedures and determining economic thresholds for various rice pests were described in recent reports (Anonymous 1977b; Chiang 1977b).

Cultural controls played an important part in pest control; they included the use of resistant varieties, removal of alternate hosts, planting trap crops, alternation of planting dates, and flooding of rice fields. Biological control agents such as *Trichogramma* spp., *Bacillus thuringiensis* Berliner, ducks, and frogs were used considerably for pest control. Light traps were used not only as a monitoring device, but also for insect control. In addition to the individual control measures, the integrated pest management program was most frequently used in crop protection (Anonymous 1977b, 1979b).

2. Cotton insects: China is the third largest cotton producing nation in the world with annual production at 11.1 million 480-lb. bales in 1981 (Anonymous 1982). The cotton producing areas include 19°–45° north latitudes and 75°–124° east longitudes (Anonymous 1979b) which cover Zhejiang, Hubei, Sichuan, Anhui, Jiangsu, Shanxi, Shaanxi, Hunan, Yunnan, Guizhou, Guangdong, Guangxi, Shangdong provinces (Kung 1975). Eight species of insect and one spider mite were recognized as important pests: cotton aphid, *Aphis gossypii* Glover; cutworms, *Agrotis ypsilon* Rott., *A. tokionis* Butler; green plant bugs, *Lygus lucorum* Meyer-Dur., *Adelphocoris suturalis* Jak.; pink bollworm, *Pectinophora gossypiella* Saunders; cotton bollworm, *Heliothis armigera* Hubner; cotton leafhopper, *Empoasca biguttula* Ishida; and two spotted spider mite, *Tetranychus urticae* Koch (Anonymous 1977b, 1979b). Monitoring and forecasting procedures for the above pests were widely used like those described for rice culture (Anonymous 1977b; Chiang 1977a, b). The measure used to control these pests included integrated pest control, good cultural practices, biological control, and chemical control (Anonymous 1977b, 1979a, b). The biological agents used in integrated control were *Chrysopa septempunctata* L. and five species of lady beetles for control of cotton aphids, *Dibrachys cavus* Walker for control of pink bollworm, *Trichogramma confusum* Viggiani, *T. dendrolimi* Matsumura as well as *B. thuringiensis* for control of cotton bollworm (Anonymous 1977b, 1979b).

3. Wheat insects: Wheat is the second largest grain crop in China, the production in 1981 was estimated at 54.2 million tons (Anonymous 1982). Nearly 120 species of wheat pests consisting of 46 families and 11 orders were reported (Anonymous 1977b). Among these, the wheat aphids, *Macrosiphum avenae* Fab.; *Rhopalosiphum maidis* Fitch; *Schizaphis graminum* Rondani; wheat armyworm, *Mythimna separata* Walker; wheat midges, *Sitodiplosis mosellana* Gehin and *Contarinia tritici* Kirby; wheat stem maggots, *Meromyza saltatrix* L. and *Oscinella pusilla* Meigen; wheat shoot mag-

got, *Nanna truncata* Fan.; grubs, *Hototrichia titanus* Reitt, *H. diomphalia* Bates, *H. serobiculata* Brenske, *Anomala cuprea* Hope; mole crickets, *Gryllotalpa africana* Palisot de Beauvois and *G. unispina* Saussure; wireworms, *Agriotes patrualis* Frivalsky, *Pleonomus canaliculatus* Faldermann and *Melanotus caudex* Lewis were considered as major pests (Anonymous 1972, 1974, 1979b). Monitoring and forecasting procedures for wheat aphids, wheat midges and army worms as well as underground pests were developed (Anonymous 1979b; Chiang 1977b), and the control measures for wheat insects were similar to those mentioned above.

4. Soybean insects: Soybean is grown throughout China with annual production at 7.9 million metric tons in 1981 (Anonymous 1982). The main production area is in the northeastern part of the country. A dozen species of insects are considered as major pests: soybean pod borer, *Leguminivora* (*Grapholitha*) *glycinivorella* Matsumura; soybean borer, *Maruca testulalis* Geyer; pea-pod borer, *Etiella zinckenella* Treitschke; soybean leafroller, *Heaylepta indicata* Fah.; bean hawk moth, *Clanis bilineata* Walker; soybean tussock moth, *Dasychira locuple* Walker; bean blister beetle, *Epicauta gorhami* Marseul; scarabaeid beetles, *Holotrichia gebleri* Faldermann, *H. diomphala* Bates, *Anomala corpulenta* Motsch, and *Maladera orientalis* Motsch; bean shoot aphid, *Aphis craccivora* Koch; bean leafroller, *Matsumuraeses phaseoli* Matsumura; bean weevil, *Xylinophorus mongolicus* Faust (Anonymous 1977b, 1979b). Control measures for the pod borer are: cultural control, resistant variety, chemical control, and biological control (Anonymous 1979b). For controlling other lepidopterous pests, the most commonly used methods are light traps, chemical control, cultural control and biological control (Anonymous 1977b, 1979b).

5. Other crops: Important pests of citrus fruits, deciduous fruits, vegetables, stored products and structures, man and animals and their control methods were discussed in detail by earlier reports (Anonymous 1977b, 1979b; Guyer 1977; Williams 1979).

Other achievements in applied entomology during this period are listed below.

1) Insecticide and its use: Scientists in PRC were very concerned about the undesirable side effects of various pesticides on human health and the environment. Therefore the emphasis of pest control was placed on integrated pest control in 1970's. Insecticides were carefully chosen and used only if justified. Mostly pesticides were used as a part of integrated pest management program. In this period, the consideration was given to the production of highly effective insecticides of low toxicity, nonpersistance, and low cost. Many organophosphorus insecticides were produced industrially. The most commonly used were trichlorfon, dichlorvos, dimethoate, phosmet, fenitrothion, phosphamidon, and malathion. Trichlorfon was used against the cotton pink bollworm, bollworm, rice planthopper and thrips,

and cabbage worms. Dichlorvos was used to control soybean pod borer, cabbage root maggot, cotton pink bollworm, cotton aphid, and other species of aphids, housefly, mosquito, and citrus longicorn beetles. Dimethoate was used for control of the citrus leafminer, leafrollers, mites, rice greenleafhopper, rice thrips, rice paddy borer, and cotton aphid. Phosmet was used to control the tea scale and citrus leafminer. Fenitrothion was used for rice paddy borer, rice leafhopper and planthopper (Anonymous 1977b, 1979b; Guyer 1977).

2) Biological control agent and its use: It was the government policy that all research must be directly applied to the real needs of people. Biological control fits very well in this concept and has received substantial support from the government. It has become the main feature of the integrated pest management program. The most widely researched and used biological control agents included *Trichogramma* spp., *Anastatus* sp., *Rodolia* spp., *Dibrachys cavus, Chrysopa* spp., *Bacillus thuringiensis* and *Beauveria bassiana.* By 1974, a total of 12 species of *Trichogramma* was reported in China including *T. australicum* Girault, *T. closterae* Pang et Chen, *T. dendrolimi* Matsumura, *T. evanescens* Westwood, *T. euproctidis* Girault, *T. ivelae* Pang et Chen, *T. japonicum* Ashmead (Anonymous 1978b), *T. leucaniae* Pang et Chen, *T. lingulatum* Pang et Chen, *T. ostriniae* Pang et Chen, *T. raoi* Nagaraja, and *T. sericini* Pang et Chen. Among these, only four species were widely used in 26 provinces and regions of PRC, they included *T. confusum* Riggiani (=*T. australicum*), *T. dendrolimi, T. japonicum* and *T. ostriniae* for control of such pests as *Ostrinia furnacalis* Guenee, *Chilo sacchariphagas* Bojer, *C. infuscatellus* Snellen, *Argyroploce schistaceana* Snellen, *Dendrolimus* spp. and *Heliothis armigera* Hb. with parasitization 70–80% (Anonymous 1978b, 1979b; Guyer 1977). *Anastatus* sp. was first used to control litchi stinkbug, *Tessaratoma papillosa* Drury in 1960's. It was reported that the parasitization could reach to 80–90% (Anonymous 1979b; Huang et al. 1974). Their use has been extended to another 11 species of lepidopterous insects and the eggs of several species of Hemiptera and Lepidoptera (Anonymous 1978b). *Dibrachys cavus* was successfully used for control of the overwintering population of the pink bollworm, *Pectinophora gossypiella* Saunders with parasitization over 80%. Four species of *Chrysopa* (*C. septempunctata* Wesmael, *C. sinica* Tjeder, *C. carnea* Stephens, *C. boninensis* Okamoto) were commonly used for control of *Aphis gossypii* Glover, *Tetranychus urticae* Koch, and the egg stage of *Heliothis armigera* and *Ostrinia furnacalis* (Anonymous 1979b).

The establishment of the introduced *Rodolia cardinalis* Mulsant in southern China had effectively controlled the cottony cushion scale, *Icerya purchasi* Moskell in the citrus groves. Another species of lady beetles *R. rufopilosa* Mulsant was also successfully used for control of *I. purchasi* in south China (Anonymous 1979b).

In the decade of 1966–1976, a total of 17 varieties of *Bacillus thuringiensis* Berliner including 12 distinct serotypes was isolated and characterized by the researchers at the Institute of Zoology, Academia Sinica in Beijing (Guyer 1977). The bacteria were mainly used to control the immatures of Lepidoptera. There were more than 70 pest species listed with variable results ranging from 30 to 100% kill. They were effectively used against such insects as *Cnaphalocrocis medinalis* Guen, *Paranara guttata* Br., *Tryporyza incertulas* Walk., *Plutella xylostella* (L.), *Artogeia rapae* (L.), *Ostrinia furnacalis* Guenee, *Dendrolimus punctatus* and *Heliothis armigera* Hubn. (Anonymous 1979b). During the period of 1973–1977, about 1,100 metric tons of microbial materials were used on about 12,800 hectares of cotton (Guyer 1977).

The use of *Beauveria bassiana* Vuill as a biological control agent was introduced in 1971, in four years it was expanded to nearly 57,720 hectares (Guyer 1977). This agent was especially effective against European corn borer, *O. furnacalis* in the field with 80–90% kill (Hsiu et al. 1973). The granular preparations of *Beauveria* were often used in combination with B. t., Trichogramma and/or chemicals in the integrated control programs.

3) Integrated pest management: The practice of integrated pest control (IPC) or integrated pest management (IPM) began in the 1950's in China. It became intensified and popularized during the Cultural Revolution as it was in line with the teaching of Chairman Mao who advocated that man conquer nature. Thus IPM received top priority and strong governmental support. The plant protection systems in PRC were largely based on IPC techniques. Several integrated approaches were used in this highly successful plant protection system. First, the scientists in PRC developed an efficient monitoring and forecasting system which was set up at four levels including provincial, county, commune and brigade. The provincial forecasting center operated by the Academy studied the population dynamics, economic damage thresholds of the pests, and the impact on natural enemy. All substations reported to the provincial center. The county forecasting station determined the time of occurrence of the pests, and advised the commune and brigade what and when to carry out control operations. The commune forecasting station operated at the farm level that consists of 5 to 15 brigade forecasting stations. The commune forecasting station monitored the start of insect activities in the spring as determined by light-trap catches, or monitored the insect populations at the overwintering sites. The brigade forecasting station monitored the target fields and relayed information to the commune (Chiang 1977b). The system served as a guide to timing chemical applications. The insecticides were only used if proved economical, effective and safe. Secondly, cultural control is considered of vital importance in Chinese plant protection system which emphasized prevention. This practice emphasized the reduction in pest populations during the period between two crops. The application of the biological and ecological information of the pest is essential

in this approach. There were several measures commonly used in the cultural control including the use of light-traps for monitoring and mass trapping, crop rotation, sanitation, regulation of planting and harvesting dates, the use of a trap crop and bait trap. Thirdly, biological control was used successfully and widely among pests of many crops including forest trees. This approach is ranked second after cultural control at the production level. The detailed biological control elements were described in the aforementioned sections.

Other methods of insect control such as the use of resistant variety, sex pheromones, hormones and various insect traps were also used to a considerable extent in the integrated management schemes during the Cultural Revolution period. For details readers should refer to the earlier publications (Anonymous 1977b, 1979b; Guyer 1977).

III. Current Educational and Research Organizations in PRC

Since 1976, drastic shifts in policy have occurred. The new ideology emphasized the four modernizations. The development of education and research in science and technology became the national goal. New policies are quickly implemented at every level.

A. Institutes of Higher Education

Currently PRC is restoring many higher institutions that were closed down during the Cultural Revolution period, and establishing new institutions. The number of institutions of higher learning is about 600 as compared to 430 in 1966. The secondary schools and colleges and universities are divided into "key institutions" and "non-key institutions." The former are designated as priority institutions for development and receive generous appropriation of funds and attention, as well as enjoying higher prestige. They are run by the Ministry of Education (MOE), the Ministry of Agriculture (MOA) or the Ministry of Forestry (MOF). Generally speaking, the brightest and best of the freshmen will go to key institutions. A total of 94 colleges and universities has been designated as "key" institutions. A list of them which offer courses in biological sciences or entomology is given in Table 1.

The basic structure of higher education in PRC has not changed much since the early 1950's when China patterned herself after the USSR. Most Chinese institutions of higher education remain highly specialized in certain fields.

1) Comprehensive universities: About 30 institutions of higher education are in this category whose curricula include both basic and applied sciences and the liberal arts. A number of well known institutions is listed in Table 1.

2) Agricultural colleges and universities: As mentioned before, basically

Table 1. Key universities and agricultural institutions in PRC.

Name[a]	Governing[b] body	Characterisitic
*Anhui Agricultural College	MOA	Agricultural
*Beijing Agricultural College	Beijing City	Agricultural
Beijing Agricultural University	MOA	Comprehensive
Beijing Forestry College	MOF	Forestry
Beijing Normal College	MOE	Comprehensive
Beijing University	MOE	Comprehensive
Central China Agricultural College	MOA	Agricultural
Central China University	MOE	Agricultural
Chinese People's University	MOE	Comprehensive
Chonqing University	MOE	Comprehensive
Fudan University	MOE	Comprehensive
*Fujian Agricultural College	PG	Agricultural
Gansu Agricultural University	PG	Agricultural
*Guangxi Agricultural College	PG	Agricultural
*Guizhou Agricultural College	PG	Agricultural
*Hebei Agricultural University	PG	Agricultural
*Henan Agricultural College	PG	Agricultural
*Hunan Agricultural College	PG	Agricultural
*Hunan University	MOE	Comprehensive
*Jiangsu Agricultural College	PG	Agricultural
Jianxi Agricultural University	MOA	Agricultural
*Jilin Agricultural College	MOA	Agricultural
Jilin University	MOE	Comprehensive
Jinan University	MOE	Comprehensive
Lanzhou University	MOE	Comprehensive
*Liaoning University	MOE	Comprehensive
Nanjing Agricultural College	MOA	Agricultural
Nanjing Forest Industry College	MOF	Forestry
Nanjing University	MOE	Comprehensive
Nankai University	MOE	Comprehensive
*Nei Monggol Agricultural College	MOA	Agricultural and Animal Husbandry
Nei Monggol University	MOE	Comprehensive
*Ningxia Agricultural College	MOA	Agricultural
Northwest University	MOE	Comprehensive
Northwestern College of Agriculture	MOA	Agricultural
*Qinghai Industrial & Agricultural College	MOA	Agricultural
Qinghua University	MOE	Comprehensive
*Shangdong Agricultural College	PG	Agricultural
Shangdong University	MOE	Comprehensive
Shanghai Agricultural College	Shanghai City	Agricultural
Shanghai Normal University	MOE	Comprehensive
*Shanxi Agricultural University	PG	Agricultural
*Shenyang Agricultural College	PG	Agricultural
*Sichuan Agricultural College	PG	Agricultural
Sichuan University	MOE	Comprehensive
South China Agricultural College	MOA	Agricultural

Table 1. Continued.

Name[a]	Governing[b] body	Characteristic
*Southwestern Agricultural College	MOA	Agricultural
Southwest University	MOA	Agricultural
Tianjin University	MOE	Comprehensive
Tongji University	MOE	Comprehensive
Wuhan University	MOE	Comprehensive
Xiamen University	MOE	Comprehensive
Xian Jiaotong University	MOE	Comprehensive
Xiangtan University	MOE	Comprehensive
*Xinjiang Bayi Agricultural College	Autonomous Region	Agricultural
Xinjiang University	MOE	Comprehensive
*Xinjiang Shihetze Agricultural College	MOA	Agricultural
Yenan University	MOE	Comprehensive
Yunnan Forestry College	MOF	Forestry
Yunnan University	MOE	Comprehensive
*Zhejiang Agricultural University	PG	Agricultural
Zhejiang University	CAS	Comprehensive
Zhongshan University	MOE	Comprehensive

[a] * = non-key institutions; without * = key institution.

[b] MOE = Ministry of Education; MOA = Ministry of Agriculture; MOF = Ministry of Forestry; CAS = Chinese Academy of Sciences; PG = Provincial Government.

the PRC has an agricultural economy. Virtually all cultivable land is used for crops, and the intensive cultural techniques have already secured high yields. To increase the yields any further requires better technology. Thus, agricultural colleges and universities play an important role in this effort. There are approximately 90 agricultural schools throughout China, and they are mostly operated by the Ministry of Agriculture, the Ministry of Agricultural Machinery, or Provincial Bureaus of Agriculture. Nearly all provinces, autonomous regions and special municipalities have one agricultural college with the exception of Xizang autonomous region (see map). A list of well known agricultural colleges which deal with teaching and research in plant protection is given in Table 1.

3) Other specialized institutions of higher education: Other institutions of higher education can be categorized based on the nature of their curriculum. They include: (a) polytechnic colleges and universities, (b) normal colleges, (c) medical colleges, (d) science universities, (e) machine-building colleges, (f) shipbuilding colleges, (g) aeronautics colleges, (h) electronic and telecommunication colleges, (i) light industry colleges, (j) construction colleges, (k) transportation colleges, (l) mining and metallurgy colleges, (m) chemical and petroleum engineering colleges, (n) electric power college, (o) geology col-

leges, (p) meteorology colleges, (q) oceanography colleges, (r) other nontechnical colleges.

B. Institutes of Research

Currently PRC is attempting to upgrade the levels of professional researchers as well as training future generations of professionals. Entomological research in PRC takes place under the auspices of the Chinese Academy of Sciences, and the Ministry of Agriculture. The former is in charge of formulating science policy, conducting basic research, and running several universities. Therefore, it is considered as a prestigious organization. There are over 100 research institutes, five universities, and four libraries under the jurisdiction of CAS. The primary emphasis of research institutes is in basic research. However, CAS is also involved in teaching at its five universities and training researchers at the graduate levels. The research institutes of CAS dealing with agricultural production or plant protection are listed as follows: In Beijing: Institute of Chemistry, Institute of Microbiology, Institute of Genetics, Institute of Zoology, Institute of Botany; In Shanghai: Institute of Biochemistry, Institute of Cell Biology, Institute of Plant Physiology, Institute of Entomology; In Sichuan Province: Institute of Biology;

In Yunnan Province: Institute of Zoology, Institute of Botany, Institute of Tropical Plants; In Guangdong Province: Institute of Botany; In Liaoning Province: Institute of Forestry and Pedology; In Hubei Province: Institute of Virology, Institute of Botany; In Xinjiang Autonomous Region: Institute of Chemistry, Institute of Biology, Pedology and Deserts; In Hebei Province: Luancheng Institute of Agriculture Modernization; In Heilungjiang Province: Institute of Agriculture Modernization; In Hunan Province: Taoyuan Institute of Agriculture Modernization. The universities administered by CAS are: In Anhui Province: University of Science and Technology of China; In Beijing: School of Graduate Study, University of Science and Technology of China; In Zhejiang Province: Zhejiang University; In Sichuan Province: Chengdu University of Science and Technology; In Heilungjiang Province: Harbin University of Science and Technology.

The Ministry of Agriculture manages its own institutes numbering several hundred. The primary emphasis is conducting applied research. In general the research institutes are under the jurisdiction of the provincial Academy of Agriculture. The academies coordinate the activities of their subordinate research institutes. Nearly every province or autonomous region has a provincial academy of agriculture.

C. Undergraduate and Graduate Education

Currently, the undergraduate curriculum is a four-year curriculum with the requirement of 140 credit hours. However, some universities and colleges have reinstated a five-year curriculum. The students are selected almost exclusively on the basis of a nationally standardized entrance examination. The entrance examination is held simultaneously for a 3-day period at the various testing centers throughout the nation. As of July 1982, all participants are required to take three basic subjects including Chinese, politics, and mathematics. In addition, students majoring in science and technology are required to take tests in biology, physics and chemistry, and those majoring in social science and humanities are tested in history and geography. The third test is the foreign language test, all examinees are given one of the seven choices: English, French, German, Japanese, Russian, Spanish or Arabic. The total points that the examinee majoring in science scores out of 600 possible points determines the outcome. However, the score on the foreign language test is not counted in calculating the overall point total, it is only used for considering student's candidacy by the prospective college (Barendsen 1979; Hsu 1979). The passing score varies in different areas. The acceptance total score for the resident student in Beijing area for 1980 was 370 points at 500 possible points, where for students in other provinces the cutoff total score was 348 points. Because of limited capabilities and short resources, it is estimated that among the 12 million high school graduates, only about 300,000 students are able to enter the colleges. Current total undergraduate enrollments in China stand at about 1.2 to 1.5 million. The goal set for 1985 is at 3 million (Abelson 1979). Graduate enrollments will be increased to 200,000 by 1990. The faculty and student ratio is at 1:3. This enables close contact between students and professors. Thus the relationship, as traditional in China, becomes lifelong.

During the four years, all undergraduates majoring in plant protection are required to take courses in: foreign language, general physics, organic chemistry, inorganic chemistry, advanced mathematics, general botany, plant physiology, agricultural meteorology, philosophy, plant protection, political economics, plant pathology, agricultural plant pathology, general entomology, agricultural entomology, plant immunology, monitoring and forecasting, biostatistics, mycology, plant bacteriology, plant virology, research techniques, plant biochemistry, insect taxonomy, insect ecology, integrated pest control, insect morphology, plant quarantine, insect physiology and insect toxicology. The following courses are offered by some colleges: crop cultivation, cultivation techniques, plant breeding, soil and fertilizer, fruit tree cultivation, vegetable production, agricultural machinery, agricultural economics. The equipment and facilities in teaching laboratories and the libraries are generally adequate in most institutions. More expansion and improvement are underway. Some newly restored teaching laboratories have been equal to or superior to comparable institutions in the U.S.

Graduate programs were restored in the fall of 1978. Similarly, recruitment into graduate programs is on the basis of both preliminary and subject matter examinations. The former consists of four basic tests in politics, foreign language, a basic subject, and one of the specialized subjects. The preliminary examination is a nationally standardized test. The latter consists of foreign language, basic subject, specialized subject. The last tests are conducted by each graduate school. As a result, only one in six college graduates is able to pass the test. From this test program it is apparent that the leaders in PRC realize the importance of foreign languages as a tool in learning advanced science and technology. In 1979 approximately 19,000 graduate students selected from the 200,000 college graduates were enrolled in over 200 colleges and universities as well as 150 research institutes of the CAS and CAAS.

The graduate curriculum ranges from 2 to 4 years depending on various institutions. Because this program is still at its infant stage, it is somewhat flexible, with more emphasis placed on research, rather than the research and course work normally required in other countries.

Since the restoration of graduate study programs in 1978, the leaders in PRC also have realized the need to award the academic degrees which would help stimulate national interest in scientific research, raise academic standards, and facilitate international academic exchanges. Subsequently, the regulations governing the award of three academic degrees (Bachelor, Master and Doctor) were approved by the National People's Congress in February 1979. The measures further provide the State Council of PRC with a vehicle to establish an academic degrees committee. The bachelor degree is awarded by 458 colleges and universities authorized by the State Council, whereas master and doctor degrees are awarded by the academic degrees committee. Candidates enrolled in the institutions of higher learning and research institutes as well as those who can pass the qualifying examination and satisfy examiners in an oral examination or a written thesis are eligible for postgraduate degrees. The same regulations also apply to foreign students studying in PRC. Provisions are also made to award honorary degrees to outstanding scholars residing at home and abroad.

In 1980, the State Council approved the designation of the additional universities as key national institutions of higher education: (Northwest University, Southwest University, Central China University, South China University and Shenyang University), serving the needs of all regions. It is worth noting that these newest key universities have formally separated the Department of Plant Protection into a Department of Entomology and a Department of Plant Pathology. They are charged with the responsibility of training college faculty and researchers for the respective regions, whereas other colleges of agriculture still retain the Department of Plant Protection with the responsibility of training plant protection specialists in the fields.

The impact of the Cultural Revolution on China's education is profound. China not only has lost a generation of college graduates, but also a generation of students at other levels as well. Therefore, the tasks of modernization of a large educational system are enormous and complex. Currently, PRC produces about 200,000 college graduates per year. The newly initiated educational exchange programs with the Western countries, and the government funded overseas study programs are of current priority to the Chinese government. From January 1978 to November 1979, a total of 2,230 students and scholars was sent overseas including 1,600 researchers and scholars, 180 graduate students, and 450 undergraduates. Among these, 1,800 students were majoring in natural sciences, the rest in social study and linguistics. There were 500 individuals in the U.S., 500 in U.K., 200 in France, 200 in F.R. Germany and 100 in Japan. China's aim in sending students and scholars overseas for 1980 was 10–20,000. It was estimated that about 6,000 Chinese students and scholars were studying at the U.S. universities at the end of 1981.

Conclusions

China has an ancient history of science and civilization. Unfortunately, China has been repeatedly subjected to socio-economical, political, and intellectual chaos and revolutions in her search for accommodation with the modern world since the turn of the 19th Century. The process of transforming a traditionally agricultural society into a modern, industrial state has not been an easy one. After 1948, a decade of remarkable progress had been made on the unification of the country, self-sufficiency, fostering education and research. In the last two decades there have been advances, but progress has been variable. This was due in large part to repeated changes in ideology. One of the ideological changes with profound effect on education and research was the Cultural Revolution. As a result, China has lost a generation of educators and researchers. To implement the four modernizations and to make up for ground lost during this period are enormous and complex tasks which would require a vast infusion of foreign technical assistance and the creation of domestically exceptional capabilities. Hence, there are ample opportunities for foreign scientists to cooperate with Chinese counterparts.

During the Cultural Revolution, basic research in plant protection was greatly disrupted, but some applied research flourished. In some aspects of plant protection, the Chinese are indeed ahead of Western nations and are probably in a better position than any other nation to provide alternatives to chemical control of a number of agricultural pests. Many common pests in the PRC have been effectively managed and controlled by the use of integrated pest management measures involving cultural control, biological control, as well as some chemical methods. The success of IPM programs in China is attributed to the widespread enthusiasm for IPM shared by the farmers, scientists and administrators, and, to the application of the ecological principles essential to its development. The insect control measures developed in China are simple, effective and economical. Therefore, they could be used in other parts of the world where crop production and protection are carried out mostly by small farmers with little modern technology.

To increase grain production in meeting the need of population growth in China and to boost its already high per unit area yields pose a great challenge to Chinese scientists. Basic research and modern technology will undoubtedly play an important role in developing modern plant protection techniques in the years ahead. However, Chinese scientists should be aware of the impact of modern technology on the future plant production and protection, such example as the impact of the green revolution on plant protection in tropical and subtropical areas (Smith 1972). Also, they should be aware of the fact that once truly committed to modernization, they will face no end of changes, pressures and socio-economic problems. China is known to be well endowed with many important minerals and energy resources. Oil reserves are estimated at least three times as large as those of the U.S. It has tremendous resources of talented, industrious and moral people. It is to be hoped that their national goals will soon be realized.

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EFFECTS OF TWO INSECT GROWTH REGULATORS (HYDROPRENE AND R-20458) ON THE FOLLICULAR EPITHELIUM AND THE OOCYTES OF THE RICE WEEVIL, *SITOPHILUS ORYZAE* (L.) (COLEOPTERA: CURCULIONIDAE)

J. M. Mkhize[1] and A. P. Gupta

Abstract.—Effects of two insect growth regulators (IGRs) (hydroprene and R-20458) on the follicular epithelium and the oocytes of the rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae) were studied. Comparative histological studies of the treated and untreated ovarioles revealed that there were no apparent differences in the development and structure of the oocytes in the germarium and in the anterior part of the vitellarium. The IGRs, however, affected the penultimate oocytes and perhaps the basal oocytes, because the latter ovulated prematurely. Treated penultimate oocytes were atrophied, because they lacked yolk and karyospheres; in addition, follicular epithelium was not retracted from the surface of the oolemma. Untreated penultimate oocytes on the other hand, were larger due to the accumulation of yolk and they had karyospheres; the follicular epithelium was retracted from the egg membrane, leaving a space that had materials, which possibly are blood proteins. A fine brush-like border (microvilli) was observed on the side of the oolemma facing the follicular epithelium.

Introduction

Laboratory evaluation of IGRs as protectants against pests of stored products have shown considerable promise (Metwally et al. 1972; Bhatnager-Thomas 1973; Strong and Diekman 1973; Williams and Amos 1974; McGregor and Kramer 1975; Loschiavo 1976; and Amos and Williams 1977). It has also been demonstrated that treatment of certain species of insects with IGRs induces permanent ovarial abnormalities that lead to female sterility (Metwally and Landa 1972; Metwally et al. 1972; Rohdendorf and Sehnal 1973; Lanzrein 1974; Patterson 1974; Das and Gupta 1977; Masner et al. 1979; and Deb and Chakravorty 1981).

The purpose of this work was to find out whether hydroprene and R-20458 will induce ovarial abnormalities that might cause sterility in the female weevil.

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Materials and Methods

Several IGRs were screened for their effects, and hydroprene (ethyl(2E,4E)-3,7,11-trimethyl-2,4-dodecadienoate) and R-20458 (6,7-epoxy-3,7-dimethyl-1-(*p*-ethylphenoxy)-2-octene) were selected because they were more effective than others against *S. oryzae*. Of these two, hydroprene was more effective (Mkhize and Gupta 1980; Gupta and Mkhize 1982).

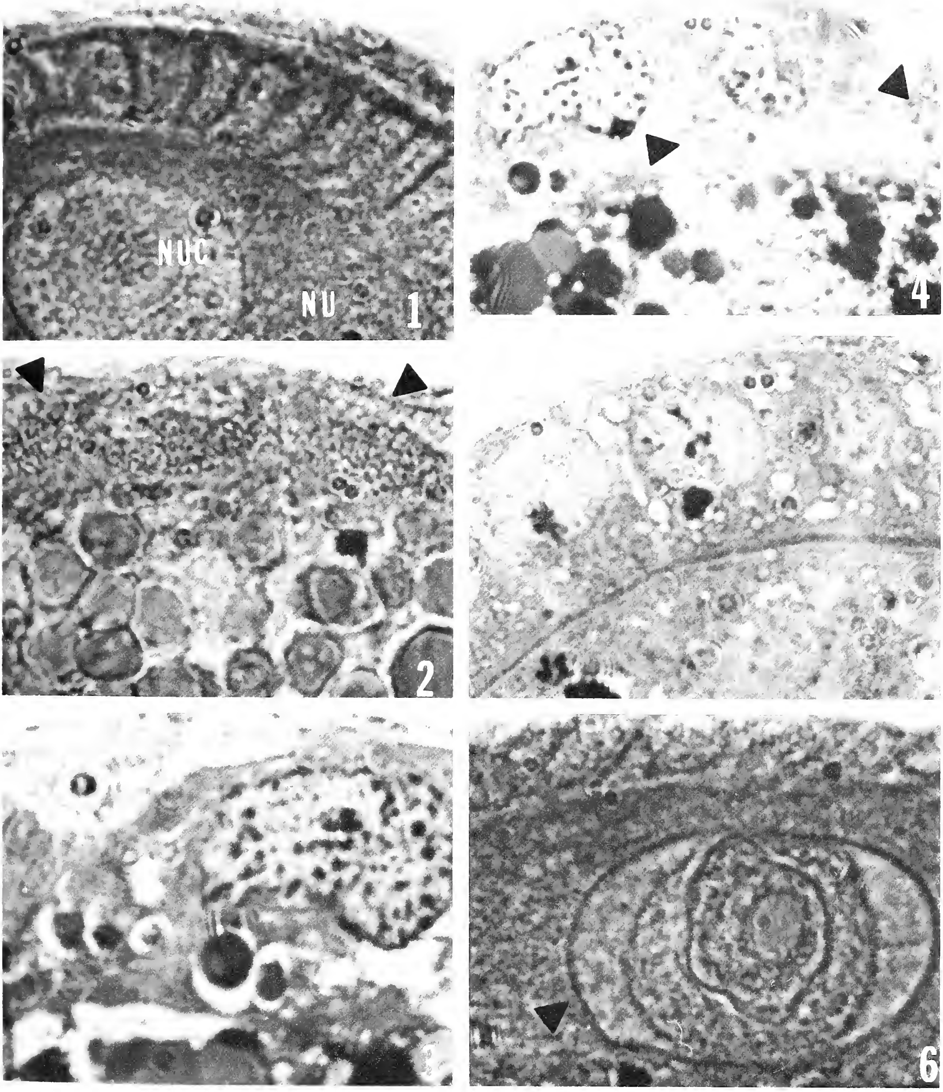
Ovaries of rice weevils, which emerged from either IGR-treated wheat (see Gupta and Mkhize 1982) or topical applications, were removed in saline solution and fixed in two successive changes of Bouin's fluid. The tissues were then dehydrated in ethanol series, cleared in xylene and embedded in paraffin wax. Longitudinal sections, each 5-μm thick, were stained in hematoxylin and eosin and mounted in permount. Histology of treated and untreated ovaries was compared in order to discover morphological abnormalities induced by IGR treatment.

For making ultrathin sections, treated and untreated ovaries were separately dissected in physiological saline solution and fixed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.2) for four hr. After rinsing the ovaries in a buffer, they were placed in 1% solution of osmium tetroxide for two hr. The ovaries were again rinsed in a buffer and then dehydrated in acetone as follows: they were placed in 30%, 70%, and 95% acetone for 20 min in each concentration; then in three changes of 100% acetone for 20 min/change. They were embedded in Epon 812. One μm-thick cross sections were made by Sorvall MT-2 ultramicrotome. The sections were stained for one min, and mounted in immersion oil. The sections were then sealed with permount. Light micrographs of cross sections of both treated and untreated oocytes were made and compared in order to observe abnormalities owing to IGR treatment.

Results

Examination of treated and untreated ovarioles revealed that the germarium and the anterior region of the vitellarium showed no apparent structural or developmental differences between the oocytes in the treated and untreated ovarioles. Differences, however, were observed in the penultimate oocytes and the follicular epithelium around them. In the anterior region of the vitellarium, the cells of the follicular epithelium were columnal in shape and had elongated nuclei (Fig. 1). The cell boundaries were distinct and the cytoplasm appeared strongly basophilic, probably indicative of synthetic processes taking place in these cells.

The follicular epithelium around untreated penultimate oocytes had cells that appeared slightly flattened, with small, elongated nuclei, indicating that these cells were in a transitional stage from cuboidal to squamous type of cells (Fig. 2). The epithelium also showed mitotic divisions (Fig. 3) and the nuclear chromatin material seemed to be evenly dispersed. Figure 4 shows



Figs. 1–6. 1. X-section of treated, young oocyte, showing columnar epithelium. NU =nucleus of oocyte; NUC = Nucleolus. ×3,500. 2, 3. X-sections of untreated penultimate oocytes, showing squamous follicular epithelium (arrow head) (Fig. 2, ×3,040) and mitotic figure (Fig. 3, ×2,945). 4. X-section of an untreated penultimate oocyte engaged in vitellogenesis. Note space between oolemma and follicular epithelium and inter-cellular space in the follicular epithelium (arrow head). ×2,945. 5. X-section of a treated penultimate oocyte. Note absence of intercellular space in the follicular epithelium and between the latter and the oolemma. ×3,040. 6. X-section of an untreated oocyte engaged in vitellogenesis, showing a germinal vesicle (arrow head). ×3,420.

the follicular epithelium of an untreated penultimatic oocyte actively engaged in vitellogenesis. This epithelium was retracted from the surface of the egg membrane (oolemma) creating a space between the two interfaces. In addition, there were intercellular spaces in the epithelium itself. These spaces contained material that was less granular than that in the oocyte. Focusing up and down over the space between the follicular epithelium and the oolemma sometimes revealed brush-like border on the oolemma. Retraction of the follicular epithelium from the oolemma enables hemolymph proteins to pass into the oocyte, supposedly by pinocytosis. By contrast, the follicular epithelium in a treated penultimate oocyte was not retracted from the oolemma (Fig. 5) and no intercellular spaces were present. The follicular cells were roundish with spherical nuclei. No mitosis was observed.

Untreated young oocytes in the anterior region of the vitellarium in both treated and untreated oocytes had centrally located nuclei (Fig. 1), with evenly distributed chromatin material. Mature untreated oocytes engaged in vitellogenesis showed germinal vesicle (=the enlarged oocyte nucleus due to accumulation of vesicular fluid) (Fig. 6) and karyosphere (the clumped chromatin material of the nucleus), both of which were not observed in treated oocytes.

Discussion

The follicular epithelium plays an important role in vitellogenesis. The synthesis of enzymes necessary for the uptake of nutrients from the hemolymph (De Loof and Lagasse 1970), proteins (King and Burnett 1959; Zalokar 1960; Beir 1962, 1963b) and of adsorbents that link blood proteins to the outer surface of the oocyte (Roth and Porter 1964; Anderson and Telfer 1970; Anderson 1971) is reported to occur in the follicular epithelium. The facts that the follicular epithelium in the IGR-treated ovarioles were not retracted from the oolemma, showed no mitosis, and the cells were roundish, suggest abnormalities that prevent successful completion of vitellogenesis. Retraction of the follicular epithelium from the oolemma enables hemolymph proteins to pass into the oocyte by pinocytosis (Beir 1962, 1963a; Kessel and Beams 1963; Telfer and Melius 1963; Roth and Porter 1964; Stay 1965; Hopkins and King 1966; De Loof and Lagasse 1970). Clearly, the IGRs in this study blocked retraction of the oolemma and thus vitellogenesis.

In most cases, during vitellogenesis the development of the oocyte nucleus is arrested at meiotic prophase and that just before vitellogensis takes place, both the nucleus and the cytoplasm become very basophilic and rich in RNA (Bonhag 1958; Mahowald 1972; De Robertes et al. 1975; Ambrose and Easty 1978). According to Schlottman and Bonhag (1956) and Gupta and Riley (1967) at about this time, the nucleus attains maximal size due to accumulation of vesicular fluid and is known as germinal vesicle, whose chromatin material is clumped and is called karyosphere (Chandley 1966). The absence of the germinal vesicle and the karyosphere in the treated oocyte confirms the disruption of vitellogenesis. As a result of the abnormalities discussed in the foregoing, the ovarioles in the IGR-treated weevils remain atrophied, and consequently no F_1 progeny is produced.

Acknowledgments

We are grateful to Zoecon Corporation and Stauffer Chemical Co. for gifts of the IGRs. This report is the New Jersey Agricultural Experiment Station Publication No. D-08112-24-82, supported by State Funds and by U.S. Hatch Act Funds. The secretarial assistance of Evelyn Weinmann is appreciated.

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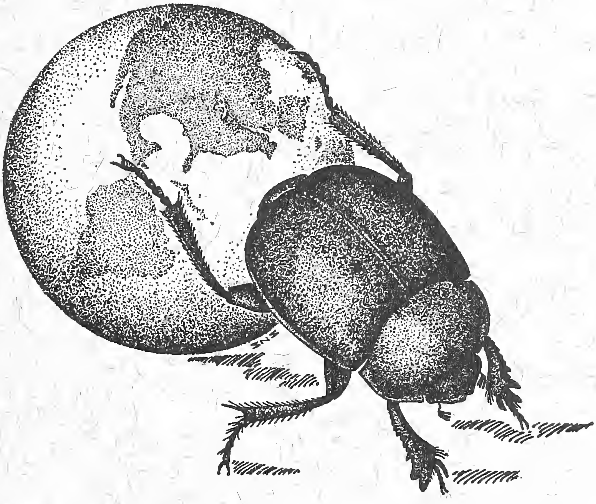

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NEW YORK ENTOMOLOGICAL SOCIETY
XC(4), 1982, pp. 220–228

VEGETATIVE GROWTH AND YIELD RESPONSE OF EGGPLANT TO VARYING FIRST GENERATION COLORADO POTATO BEETLE DENSITIES

Suzanne Cotty and James H. Lashomb

Abstract.—Varying densities (0, 8, 15, 23 or 30) of newly eclosed first generation Colorado potato beetle *Leptinotarsa decemlineata* larvae were maintained on eggplant to describe their effects on vegetative growth, flowering and yield. Significant depression of height and leaf area was detected 5–6 weeks post-infestation only for 30 larvae/plant. However, all densities temporarily disrupted flower production. Densities above 8 larvae/plant temporarily reduced yield. Beetles were excluded in all treatments during the second generation during which the plants compensated for early yield losses. Total yield for the season was the same in all treatments.

In New Jersey normal production of the solanaceous crops, eggplant (*Solanum melangena* L.), potato (*S. tuberosum* L.) and tomato (*Lycopersicon esculentum* Mill.) is currently complicated by insecticide resistant populations of the Colorado potato beetle (CPB) (*Leptinotarsa decemlineata* Say). In these crops there are no suitable alternatives to insecticides for maintaining the beetle below an economic threshold. For potato, Logan and Casagrande (1980) developed a physiological time model to predict yield losses on cv 'Superior' and Hare (1980) concluded that cv 'Katahdin' yield reductions were greatest during emergence and oviposition of summer adults. For tomato, cv 'Chico Grande' yield was negatively correlated with increasing plant damage (Shalk and Stoner 1979). There are no published results regarding yield losses caused by any insect on eggplant. In Japan, Fugi and Itagi (1954) showed that mechanical defoliation of eggplant disrupted fruit set. Saito and Ito (1973) demonstrated that artificial defoliation of eggplant retarded flower development and the resulting flowers had smaller sepals, petals, anthers and ovaries with smaller styles. Also, the reduced flowers were shed at a higher rate than normal ones. Neither Japanese study reported which cultivar was used or related defoliation intensity to yield.

S. melongena has an indeterminant growth habit, for after initial foliar development, flower production begins and continues until frost. There are always more flowers produced than fruit (Bailey 1891; Smith 1931; Eguchi

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et al. 1958; Prasad and Prakash 1968; Saito and Ito 1973; Free 1975; and Mohideen et al. 1977). When there is more than one flower in an inflorescence only the distal one is perfect and sets fruit. The remaining flowers are shed (Bailey 1891).

The purpose of this study was to determine the effect of varying larval densities of first generation CPB on vegetative growth, flowering and yield of eggplant.

Methods

We germinated 'Harris Special Highbush' seeds in flats in the greenhouse 8 weeks prior to planting in 1980. The plants were field conditioned for 5 days before transplanting on May 20, 1980 in rows with a 2.7 m spacing. A 10-10-10 NPK solution was applied at planting and again 1 month later with 30% ammonium nitrate crystals. Chlorthal (13.5 kg/ha) was applied 1 week after planting for weed control. Thereafter the plants were irrigated and cultivated regularly.

Twenty-three days post-planting we inoculated the plants with 0, 8, 15, 23, or 30 CPB eggs/plant. After eclosion we maintained larval density by adding similar aged larvae. The larval densities were selected based on a preliminary study in 1979 where we inoculated the plants with 0, 15, 30 or 60 larvae/plant. Plants with 60 larvae were soon defoliated, so in 1980 we used 30 larvae as our maximum density/plant. Each density was replicated on 12 plants in groups of 4 in 3 different sub-plots using a completely randomized design. Larvae were maintained on the plants until pupation. After 21 days the few remaining larvae were removed to maintain uniformity of feeding effects. Adults were not allowed to feed on any plants during the study. We used fenvalerate (276 g AI per hectare weekly) to maintain the 0 density during the larval feeding period. After larval feeding terminated all plants were sprayed to prevent adult feeding and oviposition.

Beginning with inoculation of the plants and weekly thereafter the following data were collected from each plant: height, leaf area, flower number and fruit number. To determine leaf area we established 3 leaf size classes: small, medium and large. We then sampled 20 leaves from each size class and measured their area with a photoplanimeter (LICOR-3000, LAMBDA Instruments, Lincoln, Nebraska). The mean values 62 cm^2, 250 cm^2, and 427 cm^2 were used to make cardboard templates for each leaf size class. Leaves on each plant were then classified as to size using the template and summed. Fruit were harvested upon maturity which was subjectively determined to be 454 g and having a shiny purple skin. The data were analyzed using a completely randomized Analysis of Variance to test the effects due to differing densities on each variable each week. Testing for differences between means of each variable was done using the least significant difference test (Cochran and Cox 1957).

Results

In 1979 the control plants produced only 60% of the normal yield of the cultivar which may have affected the relative differences between treatments. Therefore only the 1980 results are presented here. Each variable is discussed individually.

Plant height.—The shape of the plant height curve was very similar among the treatment levels, but at the higher larval densities, a slight delay in height occurred (Fig. 1). Height differences among treatments were not evident until week 5 (week number refers to time post-CPB inoculation). At this time, only mean plant height for the 30 larvae/plant treatment was less than the controls ($P \leq 0.05$). By week 6, the mean height for this treatment had dropped to 23% less than the controls ($P \leq 0.05$). Effects due to feeding could be expected to occur during weeks 5 and 6, since the larvae were in the fourth and most destructive instar (Tamaki and Butt 1978) and they tend to feed in the apical portion of the plant. After week 6, mean height of 30 larvae/plant was the same as the controls. Plant heights in the lower 3 larval densities were not different from the controls during the season.

Leaf area.—During weeks 1–4, there were no differences in mean leaf area between treatments (Fig. 2). By week 5, the effects of feeding became evident in the 8, 15, and 30 larvae/plant treatments, when compared to the controls. The leaf areas were 22%, 21%, and 25% less than the controls, respectively ($P \leq 0.05$) which might be attributed not only to an actual leaf loss, but also to a delay in the production of new leaves. This period is followed by a transition in which no differences in leaf area occurred among treatments. From week 10 to the end of the season, the mean leaf area of the 30 larvae/plant treatment ranged from 18 to 34% higher than the leaf area of the controls ($P \leq 0.05$). This difference appears to be a response to injury in which the heavier defoliated plants compensate for depressed leaf area. Throughout the season, mean leaf area of the 8, 15, and 23 larvae/plant treatments were generally intermediate to the controls and the 30 larvae/plant treatments. Differences in mean leaf area were not significant between treatments at the end of the season.

Flower production.—Flowering began 27 days after planting (4 days post CPB inoculation) and continued throughout the season (Fig. 3). The first 4 week flower production for all treatments was the same. By week 5, however all the treated plants (8, 15, 23, and 30 larvae/plant) produced 49, 79, 57, and 52% fewer flowers than the controls, respectively ($P \leq 0.05$). This depression of flower production continued through week 7, with the treated plants producing from 14 to 81% fewer flowers than the controls ($P \leq 0.05$). A transition then occurred during weeks 8 and 9 when the treated plants began producing more flowers than the controls and recovered to a level equal to the controls. From weeks 10 through 12, flower production in the

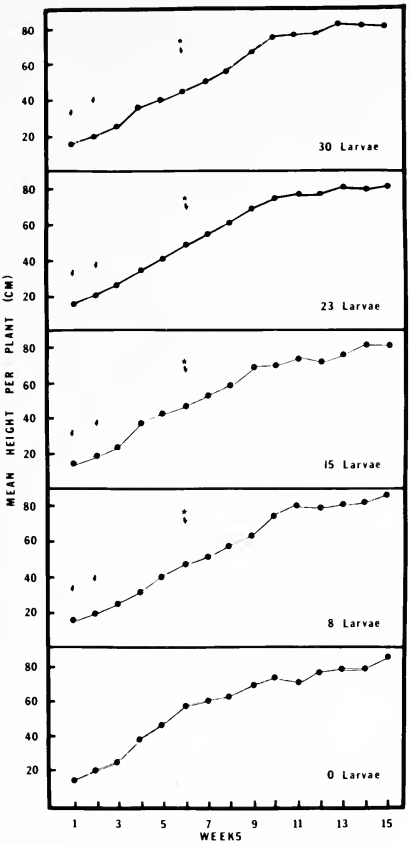

Fig. 1. Weekly mean height increment curves of eggplant inoculated with different densities of Colorado potato beetle in 1980. Arrows indicate inoculation dates and the starred arrow indicates termination of larval feeding. The following are Least Significant Difference Tests of mean height differences due to differing densities of larval feeding (Cochran and Cox 1957). For a given week treatments with the same letter are not significantly different, $P \leq 0.05$. Week 1 is 23 days post-planting.

	Larval density/plant				
Weeks	0	8	15	23	30
1–4	N.S.	N.S.	N.S.	N.S.	N.S.
5–6	a	ab	ab	ab	b
7–15	N.S.	N.S.	N.S.	N.S.	N.S.

treated plants ranged from 18 to 71% greater than the controls, but not in any pattern that could be attributed to larval density levels ($P \leq 0.05$). During the last 3 weeks of the season, there were no differences in flower production among treatments.

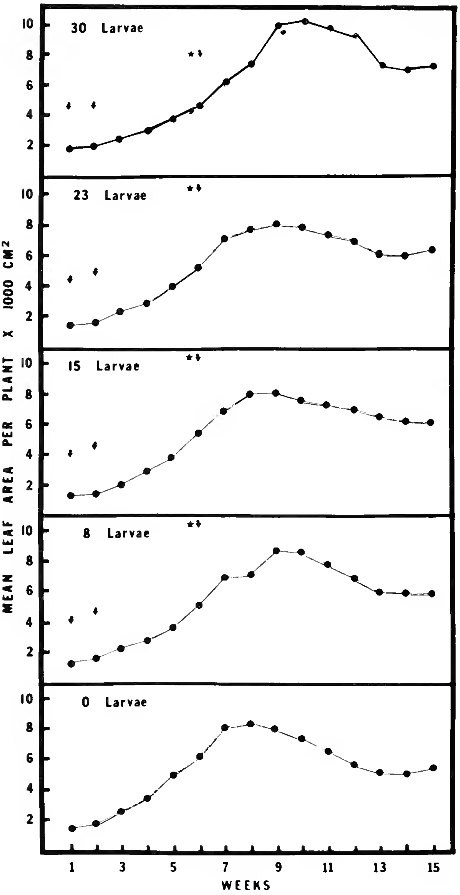

Fig. 2. Weekly mean leaf area of eggplant inoculated with different densities of Colorado potato beetle larvae in 1980. Arrows indicate inoculation dates and the starred arrow indicates termination of larval feeding. The following are Least Significant Difference Tests of mean leaf area differences due to larval feeding (Cochran and Cox 1957). For a given week treatments with the same letter are not significantly different, $P \leq 0.05$. Week 1 is 23 days post-planting.

	Larval density/plant				
Week	0	8	15	23	30
1–4	N.S.	N.S.	N.S.	N.S.	N.S.
5	a	b	b	ab	b
6	a	ab	ab	ab	b
7	a	a	ab	ab	b
8–9	N.S.	N.S.	N.S.	N.S.	N.S.
10	b	ab	b	ab	a
11–15	b	ab	ab	ab	a

Fruit production.—The first fruits were harvested 62 days after planting. Mean fruit weight (478 g ± 6.9 g) were similar among density treatments. From weeks 7 through 10, the controls yielded 56% more fruit than the treated plants ($P \leq 0.05$) (Fig. 3). During weeks 11 through 13, the treated plants produced between 23 and 65% more fruit than the controls ($P \leq 0.05$). Then a transition period ensued, when no yield differences occurred among treatments. After the transition the 8, 23, and 30 larvae/plant treatments yielded an average of 52% more fruit than the controls ($P \leq 0.05$). There were no significant differences in aggregate yield relative to treatment for the season, for each treatment produced an average of 10.5 fruit, the expected yield per plant for the cultivar.

Damaged fruit must also be considered in yield evaluations. The outer skin must be free from any scars or discoloration to be marketable (U.S.D.A. 1955). The controls and the 15 larvae/plant treatments had 14% damaged fruit, whereas the 8 larvae/plant treatments had 7% damaged fruit. These figures represent all fruit damage, since insect injury in this study was not distinguishable from other types of mechanical injury.

Discussion

For the vegetative and fruit growth variables, the same general pattern emerges. For the first 4 weeks there was an equal growth rate among all treatments including the controls. Then vegetative growth was disrupted in response to late larval feeding. Defoliation causes a decrease in photosynthate production, which decreases the amount of carbohydrate available for stem, leaf, and flower production (Wang et al. 1977). The differences which occurred between the partially defoliated plants and the controls early in the season apparently were caused by reduced carbohydrate supply. In our experiment the treatments depressed plant height, leaf and flower production during weeks 5, 6, and 7. These weeks correspond to the time when the larvae were in 4th instar and the week immediately following termination of feeding.

Following this delay, treated plants compensated for the earlier reduced growth rate and resumed normal growth. A transition phase then occurred, in which no treatment differences were found. The treated plants actually surpassed the controls in their production of leaves, flowers, and fruits. The shift of peak flower production was also due to plant compensation. Above 8 larvae/plant peak flowering was depressed and fruit production was retarded. Fuji and Itagi (1954) observed that the fruit-setting cycle of eggplant was disrupted as a result of defoliation. Also, Saito and Ito (1973) stated that defoliation caused an increase in the production of short-styled flowers. These inferior flower forms have a high abortive rate, which may account for the early delay in fruit production experienced in the higher density treatments.

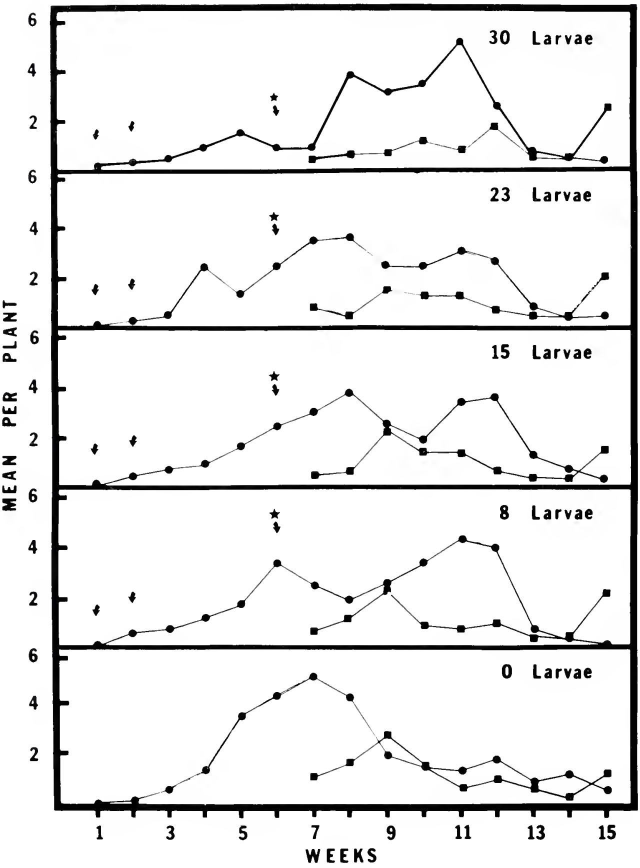

Fig. 3. Weekly mean flowers and fruit of eggplant inoculated with different densities of Colorado potato beetle larvae in 1980. Arrows indicated inoculation dates and starred arrows indicate termination of larval feeding. The following are Least Significant Difference Tests of mean flowers and fruit difference due to larval feeding (Cochran and Cox 1957). Within a week treatments with the same letter are not significantly different, $P \leq 0.05$. Week 1 is 23 days post-planting. Circles indicate flowers and squares indicate fruit.

	Mean flowers/plant Larval density/plant				
Week	0	8	15	23	30
1–4	N.S.	N.S.	N.S.	N.S.	N.S.
5	a	b	b	b	b
6	a	ab	bc	bc	c
7	a	cd	bc	ab	d
8	a	b	a	ab	a
9	N.S.	N.S.	N.S.	N.S.	N.S.
10	b	a	ab	ab	a

During 1980 the highest market price for eggplant coincided with the first two harvests, after which the market value declined during midseason and recovered slightly in the last weeks (New Jersey Department of Agriculture 1981). In this study, aggregate yield was the same for all treatments because late in the season the plants compensated for yield lost earlier in the season when eggplant value was again high. Therefore, no dollar losses were incurred. This study represents only the response of eggplant to first generation CPB feeding. Clearly, an interaction exists between first and second generation CPB feeding. Studies were planned to examine defoliation effects by both beetle generations in adjacent plots, but they were terminated due to a large immigration of CPB adults from neighboring fields which completely defoliated the plants.

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←

11	b	ab	ab	ab	a
12	b	a	a	ab	ab
13–15	N.S.	N.S.	N.S.	N.S.	N.S.

	Mean fruit/plant				
Week	0	8	15	23	30
6	N.S.	N.S.	N.S.	N.S.	N.S.
7	a	ab	b	a	b
8	a	ab	b	b	b
9	a	ab	ab	b	c
10	a	b	ab	ab	ab
11	b	b	a	a	ab
12	b	ab	b	b	a
13	ab	b	ab	ab	a
14	N.S.	N.S.	N.S.	N.S.	N.S.
15	b	a	ab	a	a

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PHENOLOGY OF EMERGENCE OF THE SPOTTED TENTIFORM LEAFMINER, *PHYLLONORYCTER CRATAEGELLA* (LEPIDOPTERA: GRACILLARIIDAE) AND ITS PARASITOIDS IN NEW YORK

Parker Gambino and Daniel J. Sullivan, S.J.

Abstract.—A phenological emergence study was carried out in Ulster and Orange counties, New York, using the overwintering generation of the spotted tentiform leafminer, *Phyllonorycter crataegella* Clemens and its parasitoids, *Sympiesis marylandensis* Girault, *Sympiesis conica* (Provancher) (Hymenoptera: Eulophidae) and *Apanteles ornigis* Weed (Hymenoptera: Braconidae). *S. marylandensis* was found to emerge concurrently with *P. crataegella,* followed in order by *S. conica* and *A. ornigis. S. conica* also hyperparasitized *A. ornigis* and thus served a dual role in this system.

Introduction

The spotted tentiform leafminer, *Phyllonorycter crataegella* Clemens is a pest of apple trees in the Northeastern United States. It is assumed to be an induced pest, resulting from the suppression of its natural controlling factors due to the use of pesticides intended for other orchard pests. Although the larvae of *P. crataegella* do not directly affect the fruit, the stress they place on the tree can result in reduced yield. High levels of infestation have been implicated in early fruit drop as well. The long term effects of *P. crataegella* upon the host tree are unknown. Recent outbreaks of *P. crataegella* in the Northeast, as recorded by Prokopy et al. (1980) and Weires et al. (1980), have caused concern among growers in the mid-Hudson valley and elsewhere. The appearance of organophosphate-tolerant strains (Weires 1977) has intensified this concern.

Integrated pest management programs, which are gaining acceptance among apple growers, consist of using various pest control techniques while minimizing both adverse environmental effects and farming expenditures. The timing of insecticide applications is a crucial part of this strategy. Since the insecticides affect benefical insects as well as pests, it is important to know at what stages these various insects will be most greatly affected by these treatments and when these vulnerable stages will be present in the orchard to be sprayed. Studies of basic insect biology and phenology serve to improve

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the efficiency of insecticide use by adding to the information which can be incorporated into an integrated pest management program.

In the mid-Hudson valley, 3 species of wasps commonly parasitize *P. crataegella*: *Sympiesis marylandensis* Girault, *Sympiesis conica* (Provancher), and *Apanteles ornigis* Weed. Since these wasps are potential control agents for this moth, their preservation would be a significant factor to be taken into consideration by growers wishing to synchronize or reduce pesticide applications. By knowing the phenological relationships between the various stages of *P. crataegella* and its parasitoids, data gained from procedures used to monitor flights of adult moths could also serve to predict the emergence of the adult parasitoids. The goal of the present study is to determine these phenological relationships.

Biology of the host, Phyllonorycter crataegella.—In the mid-Hudson valley, *P. crataegella* is trivoltine. Pupae overwinter in fallen leaves and adults emerge in the spring. The eggs are laid on the undersides of newly sprouted leaves; upon hatching, the larvae enter the leaves and begin feeding on the spongy mesophyll layer. The first 3 larval instars puncture the plant cells with their sharp mouthparts and feed on the liquids which drain from the cells. These stages are known as sap feeders. Fourth and fifth instar larvae have chewing mouthparts and take bites from the palisade layer of cells, causing a white spotted appearance of the leaf when viewed from above. Silk strands attached to the sides of the mine draw the walls of the mine inward, causing the upper leaf surface to bulge. Pupation occurs within the mine. Prior to eclosion, the pupa pokes its head through the underside of the leaf; the adult emerges, leaving behind the extruding pupal exuvium. The second and third generations follow the same basic pattern. Approximate periods of adult emergence in the mid-Hudson valley, which vary according to the weather conditions, are: April, for the overwintering generation; late June, for the first generation; mid-August, for the second generation.

Emergence of the overwintering generation is fairly well synchronized, but later in the season, individual larvae develop at widely differing rates. As a result, compared to the overwintering generation, the adult flight of the first generation is more spread out in time. By July, all of the life stages are present simultaneoulsy in an orchard. The final flight in August is even more poorly synchronized. Chemical control efforts for this moth have been concentrated in the spring, not only to "nip it in the bud," but also because this is the time when it is assured that those moths present will be in the same or similar stages of development.

Biology of Sympiesis marylandensis *and* Sympiesis conica.—*Sympiesis marylandensis* and *Sympiesis conica* are quite similar in their life histories and habits regarding *P. crataegella* on apple, and details presented here pertain to both species unless otherwise noted. While a *Sympiesis* individual may overwinter as a larva within the mine of the consumed host, the more common situation is overwintering in the pupal stage. After eclosion within the mine, the adult chews a small hole in the leaf and exits.

Behavior of the adults after emergence is not well known. According to Beckham et al. (1950), oviposition by the *Sympiesis* species occurs on hosts in the tissue-feeding stages. Evidence presented by Askew (1979) suggests that in other representatives of the genus *Sympiesis,* adult females may also affect mortality of their *Phyllonorycter* hosts by feeding on the early sap-feeding stages.

A *Sympiesis* larva feeds as an ectoparasite and usually consumes the host, preventing it from reaching the pupal stage. The wasp larva pupates after voiding a small characteristic meconium and extruding a short thread through the anus which serves to anchor it within the mine. In the area of study, at least 3 generations per year occur when *P. crataegella* serves as host.

Biology of Apanteles ornigis.—*Apanteles ornigis* is an endoparasitoid of *P. crataegella* larvae. As in the *Sympiesis* species, the tissue-feeding stages of *P. crataegella* are selected for oviposition by *A. ornigis* females. Although Pottinger and LeRoux (1971) report that overwintering by *A. ornigis* may occur naked in mines of *P. blancardella,* my observations are in agreement with those of Beckham et al. (1950), who found *A. ornigis* overwintering only within a cocoon. *A. ornigis* is the only species of the parasitoid complex of *P. crataegella* which constructs a cocoon; it is an elongate white oval which is attached by a silk thread at each end to the walls of the mine. The actual overwintering stage was undetermined, since it was concealed within the cocoon. Upon eclosion, the adult makes a circular incision so that one end of the cocoon opens as a flap. To emerge from the leaf mine, a small hole is chewed through the leaf epidermis.

Materials and Methods

During the apple growing season of 1979, several orchards in Ulster County and Orange County, New York, were surveyed in order to locate infestations of *Phyllonorycter crataegella* and to determine which parasitoids were attacking it. The presence of *P. crataegella* was apparent to the naked eye, the apple leaves showing the typical spotted mines where moth larvae were present. To locate populations of parasitoids, mined leaves were dissected. Pupating parasitoids were placed individually in #3 gelatin capsules, so that emerging adults could be identified.

The following sites in Ulster County were selected as locations for the collection of data: Turkey Hill plot, MacIntosh Farm plot and Home plot, VanDuser Orchards, Wallkill; DiStefano Orchards, Modena; E. Wright Orchards, New Paltz; Haetzler Orchards, Wallkill; and Gerken Orchards, Wallkill. Data were also collected from Finelli Orchards in Savilton, Orange

County. All collections were made from orchards in commercial production, receiving regular spray programs.

Only the Finelli Orchards site showed a sizeable population of *A. ornigis,* and a separate set of rearings was carried out using material from this site; description of this rearing experiment will appear near the end of this section.

Since the host moths and all of the parasitoids overwinter within the fallen apple leaves, collections of live insect material could be made by gathering leaves from the ground during the winter. Leaves from the various test sites were collected during one of two field trips, the first in December 1979 and the second in March 1980. Infested leaves were placed into rearing chambers made from empty one gallon translucent plastic jugs. The top of each jug was removed and replaced with a clear plastic specimen jar. Although the juncture of the jug and the jar was not airtight, the space between the two was too narrow to allow any of the insects under study to escape.

In an attempt to keep conditions within the rearing chambers as similar as possible to conditions in the orchards of origin, chambers were held out of doors on the porch of the Gambino residence, Bronx, New York. There they received afternoon sun and were sheltered from precipitation. A wooden enclosure, open on top, protected them from wind disturbance, but allowed light to reach the plastic jars at the tops of the chambers.

Insects emerging from the leaves in a chamber were attracted to the light at the top and gathered in the clear jar. All adults were collected on a daily basis, using an aspirator. After recording the date and chamber number, the insects were identified and placed individually in #3 gelatin capsules for future reference.

For the Finelli orchard, in addition to the procedure described, a more intensive rearing experiment was conducted. Infested leaves were gathered in March 1980, and leaves bearing *P. crataegella* mines were dissected until 100 healthy occupants were found. Health was judged from the appearance of the pupa; if it was not crushed or dented, and showed no signs of fungus growth, then it was selected. In the case of an *A. ornigis* cocoon, it was impossible to determine the actual condition of the inhabitant, so the outward appearance of the cocoon was used as a guide.

Insects were placed individually into #3 gelatin capsules and held indoors. The capsules were kept near a window, and thus were exposed to a natural photoperiod. Room temperature was approximately 70°F. As insects emerged, a record was made of the date, species of insect, and whether emergence was from an *Apanteles* cocoon or a naked pupa.

Determination of *P. crataegella* was made by Dr. Don Davis, Smithsonian Institution, Washington, D.C. Determinations of the 2 *Sympiesis* species were made by Dr. E. E. Grissell, U.S. National Museum, Washington, D.C., and the determination of *A. ornigis* was made by Dr. Paul Marsh, also of the U.S. National Museum.

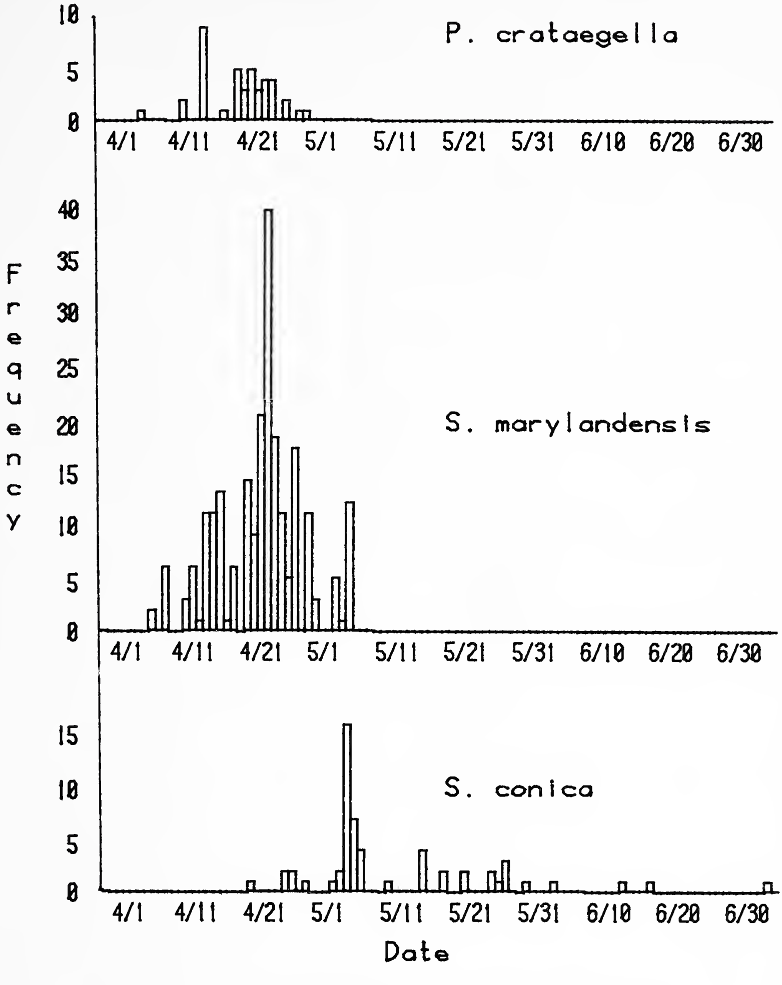

Fig. 1. Rearing chamber emergence frequencies of overwintering insects.

Results

The data gathered from the rearing chambers, pertaining to the emergence of *P. crataegella, S. marylandensis* and *S. conica* are combined and presented in Fig. 1, while Table 1 lists significant emergence dates for these 3 species. Due to the low number of individuals recovered, *Apanteles ornigis* (3) and other unidentified hymenopterous species (6) were not included in the presentation of rearing chamber data.

Data from the separate rearing of insects from the Finelli orchard are presented in Table 2. Of the 100 pupae or cocoons isolated in capsules, 82

Table 1. Rearing chamber emergence dates of *P. crataegella, S. marylandensis* and *S. conica.*

	Dates of emergence			
	N	First	Last	Median
P. crataegella	41	3 April	27 April	18 April
S. marylandensis	230	3 April	2 May	20 April
S. conica	56	18 April	2 July	3 May

yielded adult insects; the 18 mortalities did not receive further consideration. In addition to the 4 species which are the main concern of this study, an unidentified fifth species, recovered only as an *A. ornigis* hyperparasite, was also present in the Finelli orchard. Data concerning the occurrence of this unidentified species are included in Table 2, but are not subject to further analysis.

Discussion

The rearing chamber data (Fig. 1) show that *P. crataegella* adults appeared in April, with most (34/41 or 83%) emerging between 12 April and 22 April inclusive. With a larger sample, it is likely that recordings would have been made in late March and early May. During this time, the first leaves of the apple trees were also appearing, so that the behavior of the moths was well synchronized with phenological events of the host plant; young leaves were available to serve as oviposition sites.

Like *P. crataegella, S. marylandensis* emerged primarily during April. This species is recorded by Beckham et al. (1950) as an ectoparasitoid of *P. crataegella* fourth and fifth instars. At the very least, there would be 2 weeks between *S. marylandensis* emergence and appearance in the field of these suitable stages of *P. crataegella.* A more typical time interval would be 4 weeks. As has been previously noted, post-emergence behavior of these wasps is poorly known. Studies currently underway may shed some light on what *S. marylandensis* does during the weeks prior to oviposition. Despite its seemingly early emergence, *S. marylandensis* has become the dominant *P. crataegella* parasitoid in the area of study.

Sympiesis conica presented an emergence pattern quite different from that of *S. marylandensis.* Initial *S. conica* appearance on 18 April was more than 2 weeks after the first *S. marylandensis* emergence, and occurred while the latter was reaching peak emergence. Overwintering *S. conica* continued to emerge until 2 July, showing a rather diffuse pattern of emergence. When the emergence data from *P. crataegella* and the 2 *Sympiesis* species are analyzed using a median contingency table test, the hypothesis of identical median emergence dates is rejected at the 0.01 level. When just *P. crataegella* and *S. marylandensis* are considered using the median test, no significant

Table 2. Emergence dates for Finelli orchard material.*

Date	*P.c.*	*S.m.*	*S.c.*	*A.o.*	Other
4/19		2			
4/20		2			
4/21		1			
4/22	1	15			
4/23		8			
4/24		4			
4/25		6	1		
4/26		4	1		
4/27			2**		
4/28		2	1**		1**
4/29		2	3**		1**
4/30			3**		
5/1				1	
5/2				2	1**
5/3			1	2	
5/4				2	
5/5				2	
5/6				3	
5/7				3	1**
5/8				1	
5/9				1	
5/10					
5/11				1	

* Key: *P.c.—P. crataegella*; *S.m.—S. marylandensis*; *S.c.—S. conica*; *A.o.—A. ornigis.*
** Indicates hyperparasitism.

difference in the median emergence date is found ($P < 0.05$), confirming what Fig. 1 and Table 1 suggest: *P. crataegella* and *S. marylandensis* emerge concurrently, while *S. conica* appears later in the spring. Indeed, since by 2 July development of the second generation of *P. crataegella* larvae was underway, adults of the overwintering generation of *S. conica* overlapped with 2 generations of hosts in the field.

Several additional observations support the contention that *S. conica* emerges later than *S. marylandensis.* When later generations of parasitoids are considered during the growing season, *S. conica* adults are seen to emerge consistently later than those of *S. marylandensis.* Gathering accurate data on these later generations is difficult, due to the fact that individuals of a population are not well synchronized as they pass through developmental stages and generations may overlap. In the case of parasitoids found to be overwintering as larvae, the majority of those successfully reared turn out to be *S. conica.* Occasionally a parasitized mine contains a parasitoid pupa and the remains of a *P. crataegella* pupa. These rearings also yield *S. conica.* In the case of hyperparasitized *A. ornigis, S. marylandensis* was not found to function as an *A. ornigis* hyperparasitoid on apple, while *S. conica* was commonly recovered from *A. ornigis* cocoons (Table 2). This would suggest that oviposition by *S. conica* occurred after *A. ornigis* had reached its cocoon spinning stage. Thus it appears that the developmental schedule of *S. conica* lags behind that of *S. marylandensis* throughout the year.

The limited data on *A. ornigis* suggest that it is the final species of this complex to appear in the spring. However, this generalization certainly would not apply to all individuals. *S. conica,* with its extreme variability in emergence dates, actually overlapped with all 3 other species, and was the species with the final recorded emergence from the rearing chambers. Data from Table 2 indicate that *A. ornigis* emerges after *S. conica.* These data are consistent with those of Johnson et al. (1979), who found that in Ontario, Canada, the difference in median emergence dates between *P. blancardella* (a species similar to *P. crataegella*) and *A. ornigis* was approximately 3 weeks.

A. ornigis is heavily hyperparasitized (17 of 35, or 48%), hyperparasitism being determined when an *A. ornigis* cocoon yielded an adult of a species other than *A. ornigis.* It was necessary to dissect mines in order to assess the impact of hyperparasitism, and this time-consuming procedure was followed only for the additional series of rearings carried out using material from the Finelli orchard. (To the author's knowledge, this is the first record of *A. ornigis* serving as a host for *S. conica.*). Data collected from the rearing chambers cannot give an accurate picture of either the presence or degree of hyperparasitization of *A. ornigis,* especially since the predominant *A. ornigis* hyperparasitoid, *S. conica,* also attacks the primary host, *P. crataegella.*

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TISSUE GLYCOGEN OF *MYLABRIS PUSTULATA* THUNB. AND *PERIPLANETA AMERICANA* L. (INSECTA)

Dalbinder Singh Sidhu, Surinder Pal Kaur and Nirmal Kumar

Abstract.—The glycogen contents in the fat bodies, thoracic muscles, foregut, midgut, hindgut, ovaries and testes of *Mylabris pustulata* and *Periplaneta americana* have been studied. In *M. pustulata,* the major depot of glycogen contents (3.42 mg/g) has been noted in the fat bodies, while it is not so in *P. americana.* The midgut of both insects under investigation shows a higher level of glycogen than the rest of the tissues except fat bodies. In *M. pustulata,* the glycogen contents of ovaries are at a higher level than that of testes. In *P. americana,* the glycogen reserves are comparatively higher in ovaries and thoracic muscles than *M. pustulata.* The glycogen contents. It is known that insects contain digestive amylase in the midgut ferences ($P > 0.05$) while the rest of the tissues contain significantly different contents ($P < 0.05$).

Introduction

Glycogen, an important carbohydrate reserve in insects, is the first source of energy to be utilized under stress of starvation (Strauss 1911; Hill and Goldsworthy 1970). Most of the information with regard to the glycogen reserves in insects, available until recently, deals with its estimations from the whole body extracts; which of course does not provide any clue regarding the capacity of different tissues to retain and synthesize this compound. Moreover, work on individual tissues permits an insect biochemist to compare his results with the mammalian tissues where experimentation is not done on the whole body extracts. The distribution of glycogen in the tissues of insects has been studied in the past only by a few workers like Yeager and Munson (1941) in insect muscles, Wigglesworth (1949) in abdominal fat body and Nemec (1977) in the ovaries. The study in hand deals with the glycogen estimations from the different tissues of *Mylabris pustulata* and *Periplaneta americana,* and clearly, the aim is to elaborate this field so that in the long run some general and coherent trend in this respect can be deduced.

Table 1. Distribution of glycogen in different tissues of *Mylabris pustulata* and *Periplaneta americana.*

	mg glycogen ± SD/g wet tissue weight†	
Tissues	*M. pustulata*	*P. americana*
Foregut	1.51 ± 0.032**	1.56 ± 0.016**
Midgut	3.17 ± 0.110**	2.43 ± 0.123**
Hindgut	1.49 ± 0.036	1.16 ± 0
Ovaries	0.781 ± 0.004*	1.46 ± 0.024
Testes	0.660 ± 0	—
Fat bodies	3.42 ± 0.012	2.12 ± 0.008
Thoracic muscles	1.02 ± 0	1.67 ± 0.018

† Each value mentioned in the table is at least an average of five determinations. SD denotes standard deviation. *P* values have been calculated by applying Student's *t*-test of significance.

* $P < 0.05$.

** $P < 0.01$.

Materials and Methods

Mature adults of *Mylabris pustulata* were collected from kitchen gardens, and of *Periplaneta americana* from places such as kitchens and storerooms etc. from the Campus of Punjabi University, Patiala, India. Both the insects were dissected under physiological saline to obtain tissue samples from their respective foregut, midgut, hindgut, ovaries, testes, fat bodies and thoracic muscles. The samples taken were weighed and digested independently in 30% KOH for the extraction of glycogen. For extraction, the method of Heatly (1935) was employed while the estimation of glycogen was made colorimetrically according to Montgomery (1957).

Results and Discussion

The results of estimations of glycogen from different tissues of *M. pustulata* and *P. americana* are listed in Table 1.

In *M. pustulata,* the maximum glycogen contents have been recorded in the fat bodies, which indicates that this tissue is the major storage site for this energy reserve. This finding is in accordance with the observations of Kilby (1963), Gilmour (1965) and Wyatt (1967). However, in *P. americana,* the fat body glycogen, though quite high is little less than that of its depot in midgut.

The midgut of both the insects under study is quite rich in glycogen contents. It is known that insects contain digestive amylase in the midgut which hydrolyses dietary starch and glycogen and hence the absorption of digested food material takes place in this region. Treherne (1958) in *Periplaneta* and *Schistocerca* has observed that the absorption of glucose is largely confined to the midgut caeca. Thus the presence of a somewhat high concentration of glycogen in the midgut of both the insects suggests that a portion of the glucose after absorption gets converted into glycogen in this region of the alimentary canal. Wigglesworth (1949) in *Drosophila* and Mayer and Candy (1969) in *Locusta* have also observed that the midgut cells themselves are known to contain glycogen stores or it can be said that the glycogen anabolism takes place in the midgut cells. This is perhaps because the midgut converts surplus glucose into glycogen which is not readily utilized by the insect body.

In *M. pustulata,* the glycogen contents of ovaries are at a higher level than that of testes (Table 1). This is perhaps because of the necessity of this carbohydrate for vitellogenesis and for the formation of glycosaminoglycans present in the vitelline membrane and the chorion (Rockstein 1978). The glycogen which also serves as the principal carbohydrate in yolk, is usually synthesized in the ovary from glucose and trehalose derived from the fat body and the hemolymph. Similarly, the ovaries of *P. americana* also contain high concentration of glycogen contents. Moreover, it is known that the glycogen is also synthesized in the ovaries during the terminal phase of vitellogenesis (Rockstein 1978).

A comparison between the glycogen contents of foregut of *M. pustulata* and *P. americana* shows no significant difference ($P > 0.05$). Generally the foregut of insects is not involved in the absorption of glucose, but in *Periplaneta,* the crop has been found to have little importance in the absorption of glucose (Eisner 1955). According to above mentioned author, some lipase activity exists in the crop of *Periplaneta* as the result of transfer of secretions from the midgut into the foregut. So the presence of newly formed fatty acids facilitate a little absorption of glucose through the crop cuticle. Thus, the presence of more glycogen contents in the foregut of *P. americana* confirms that some absorption also takes place in the crop region of the foregut. As the foregut of *M. pustulata* shows no significant difference in this energy reserve from that of *P. americana,* it can be suggested that the foregut region of *Mylabris* too might be involved in the absorption of glucose like that of *Periplaneta.*

The glycogen contents of thoracic muscles of *P. americana* are significantly higher than that of *M. pustulata* ($P < 0.05$). It has been already reported that *P. americana* uses carbohydrate as the major source of energy for flight (Polacek and Kubista 1960) and the glycogen reserves of thoracic musculature comprise the major source of the utilized substrate (Downer and Matthews 1976). So the presence of more glycogen in the thoracic muscles of *P. americana* shows that it is more efficient in using this reserve than *M. pustulata.*

By comparing the glycogen contents of the two insects, it is evident that there exists significant variation with respect to midgut, hindgut, ovaries, fat bodies and thoracic muscles ($P < 0.05$) revealing a species specific distinctness in the metabolism of this compound in these tissues. At 1% level of significance, there is no difference in the glycogen reserves of foregut, midgut and hindgut. Although at 5% level of significance, foregut is the only tissue in the two insects where there exists no variation.

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INFLUENCE OF WEATHER ON PREDATOR/PREY RELATIONS: STINKBUGS AND TENT CATERPILLARS

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Abstract.—Cool spring temperatures suppressed the activity of predatory stinkbugs (*Podisus* spp.) but did not prevent the bugs' prey, tent caterpillars (*Malacosoma americanum* (F.)), from feeding and developing rapidly. Thus a cold snap in 1977 temporarily reduced the number of stinkbugs at caterpillar tents near Ithaca, New York, and enabled the prey to escape predation by growing to large sizes before warm weather returned.

Introduction

The physical environment can have an important influence on the effectiveness with which entomophagous insects reduce numbers of their prey. Studies in biological control reveal that climate often limits the effectiveness of both introduced and native natural enemies attacking insect pests: climatic conditions characterizing particular seasons and/or geographic regions often adversely affect the predators more than their prey (Messenger et al. 1976). Connell (1970) has suggested that not just the prevailing climate, but also *fluctuations* in weather may reduce the effectiveness of natural enemies because they are often more vulnerable to such fluctuations than are their prey. Examples include entomophagous insects that experience proportionately greater mortality than their prey during unusually cold winters (e.g., Lord and MacPhee 1953; Clausen 1958). In an intriguing extension of his hypothesis, Connell (1975) suggests that during the growing season, activity of natural enemies may be reduced temporarily during short periods of unfavorable weather. Prey may escape predation by growing to sizes invulnerable to predation during these relatively predator-free periods. Here I present an example illustrating the occurrence of this phenomenon among predatory insects and their prey.

Each spring in eastern North America, colonies of the eastern tent caterpillar (*Malacosoma americanum* (F.), Lasiocampidae) are attacked at the silken tents that they spin by predatory stinkbugs (Hemiptera: Pentatomidae) of the genus *Podisus* (Sullivan and Green 1950; Evans 1982). The following

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observations document the influence of the vagaries of spring weather on this predator/prey relationship.

Methods

In 1977–79 I examined the seasonal abundance of the stinkbugs in relation to the ontogenetic development of the tent caterpillars in a stand of scattered, small black cherry (*Prunus serotina* Ehrh.) and apple (*Malus sylvestris* Mill.) trees near Ithaca, New York. The predators were censused on various dates by counting the number of individuals observed per prey tent in 1977 and per tent-bearing tree in 1978 and 1979. At individual censuses, generally made in the afternoon, 50–250 tents were checked in 1977, 50–100 trees in 1978, and 50 trees in 1979. In all years, the entire surface of trees bearing tents was searched for stinkbugs.

The ontogenetic development of caterpillars was monitored each year by determining the instar and body length (mm) of representative individuals on different dates. Caterpillars were sampled by selecting randomly two caterpillars in 1977 and one in 1979 from the surface of 20–50 tents. A similar procedure was used to collect 150 caterpillars on 20 May 1978; on other occasions in 1978, the average length of prey was estimated by measuring representative individuals in the field.

Daily average air temperatures at 60 inches (152 cm) above ground for Ithaca, New York, were obtained from the Monthly Meteorological Summary for April and May 1977–79 prepared by the Division of Atmospheric Sciences, Cornell University. Voucher specimens of the stinkbugs have been deposited in the Cornell University Insect Collection (Lot No. 1086).

Results and Discussion

Each year stinkbugs first appeared at tents soon after the caterpillars hatched in April; the bugs peaked in numbers in May when the prey averaged 12–14 mm in length and were mostly in the fourth instar (Fig. 1). Three species of stinkbugs (*Podisus maculiventris* (Say), *P. placidus* Uhl., and *P. modestus* Uhl.) appeared at tents; they are treated together here (see Evans 1982 for detailed analyses of each species' exploitation of tent caterpillars). Stinkbug numbers at tents gradually declined after this peak in 1978 and 1979 as the caterpillars matured and abandoned tents in search of pupation sites. In 1977, this seasonal pattern was disrupted by inclement weather in early May. Stinkbug densities at tents during this time were clearly dependent on ambient temperature (Fig. 2). After peaking on 1 May, stinkbug numbers plummeted during the cold snap that followed (all three species' activity was suppressed). On seven of the next ten days, the average air temperature was less than 10°C; the mean temperature during this ten-day period was 9°C (the mean

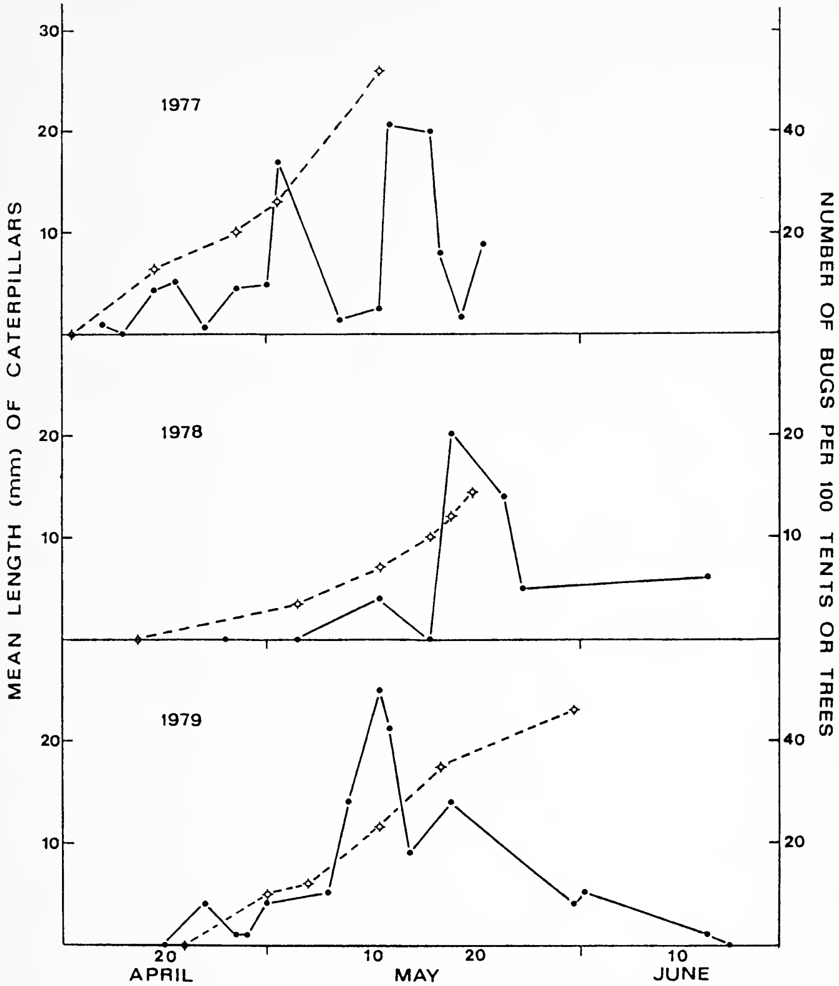

Fig. 1. The densities of stinkbugs at tents (solid lines) expressed as the number of bugs per 100 tents in 1977 and per 100 tent-bearing trees in 1978 and 1979, and the mean length (mm) of tent caterpillars (dashed lines) on various dates each spring.

temperature for 2–11 May was calculated as the mean of the ten daily average temperatures). In contrast, warmer weather prevailed during the same stage of the caterpillars' development in 1978 and 1979; the mean temperatures were 17°C and 14°C during the comparable ten-day periods (i.e., after caterpillars had grown on average to 13 mm in length and were fourth instars) in 1978 and 1979, respectively. Tent caterpillars were observed to feed actively during the cold snap in 1977; even the several inches of wet snow

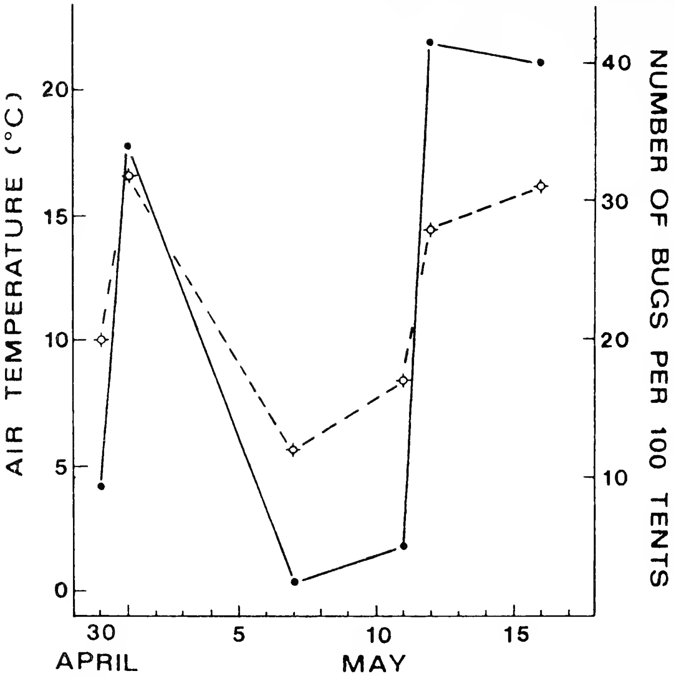

Fig. 2. The densities of stinkbugs at tents (solid line) and the average air temperature for various sampling dates, 30 April–16 May 1977 (temperatures were obtained from Monthly Meteorological Summaries prepared by the Division of Atmospheric Sciences, Cornell University).

that fell on 9 May failed to slow their activity for long. When stinkbugs reappeared at tents in large numbers with the return of warm weather on 12 May (Fig. 2), the caterpillars had achieved large sizes (Fig. 1).

The cold weather limited the effectiveness of the predators in two ways. First, by preventing predators from being active during a period of vigorous growth of the prey, the cold weather reduced the exposure of tent caterpillars to stinkbug attack. Secondly, it also enabled many caterpillars to escape stinkbug predation after warm weather returned. By the time bugs reappeared in large numbers, many prey were too large for the predators to subdue. In field observations of encounters between stinkbugs and healthy caterpillars >25 mm long, the predators (9–12 mm long) were repulsed by the vigorous side-to-side thrashings of the prey and soon abandoned the attack. Unlike earlier in the spring, the prey upon which the predators were found feeding after the cold snap were on average smaller than individuals in the caterpillar population at large: the median length of prey taken from stinkbugs on 11–17 May was 23 mm ($N = 23$) vs. a median of 27 mm ($N = 21$) in the caterpillar population at large on 11 May ($P = 0.06$, Wilcoxon two-sample test).

The quality as well as the relative size of prey attacked by stinkbugs also changed after the cold snap. Many stinkbugs were found after the cold snap at "old" tents from which most caterpillars had dispersed. Those few stragglers that remained to fall prey to the bugs generally were sluggish, inactive caterpillars. Probably many of these individuals were diseased and/or parasitized; Myers (1981), for example, reports that up to 90% of fifth-instar larvae of the western tent caterpillar (*Malacosoma californicum pluviale* (Dyer)) with delayed maturation are parasitized by tachinid flies. In a similar predator/prey interaction, *Podisus maculiventris* probably also acts selectively to remove parasitized and otherwise weakened larvae (with retarded development and little ability to defend themselves) from older tents of the fall webworm, *Hyphantria cunea* (Drury) (Morris 1963). Even the healthy tent caterpillars among the stragglers at old tents may have had reduced dispersal and reproductive capacity; such is the case for inactive larvae of *M. californicum pluviale,* which emerge from eggs containing few food reserves (Wellington 1977). Thus it appears that effective predation (i.e., killing of individuals not already destined for an early death) by stinkbugs was considerably reduced not only during but also after the cold snap in comparison to before.

In numerous case studies of biological control, natural enemies have proven more susceptible to pesticides than the insects that they attack (Messenger et al. 1976). The present example, in which fluctuation in weather adversely affects predatory insects more than their prey, also emphasizes the relative sensitivity of entomophagous insects to environmental perturbation. Further study is needed to test whether predation as a way of life for insects may, in comparison to herbivory, generally entail greater exposure and vulnerability to vicissitudes of the physical environment.

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SEASONAL OCCURRENCE OF FOUNDING QUEENS AND THE SEX RATIO OF *CAMPONOTUS PENNSYLVANICUS* (HYMENOPTERA: FORMICIDAE) IN NEW JERSEY

Harold G. Fowler and Radclyffe B. Roberts

Abstract.—Founding queens of *Camponotus pennsylvanicus* were collected in the field from early March through the middle of July from 1977 to 1981. No synchronization of population nuptial flights was detected. Sex ratios of colonies are male biased, contrary to previous reports.

The carpenter ant, *Camponotus pennsylvanicus* (DeGeer), is one of the most ubiquitous of all urban insects in the Northeast. As early as 1910, Wheeler reported on its synanthropic adaptations, and, if anything, this relationship has grown as urbanization has progressed. In spite of this fact, our knowledge of its biology has not notably improved since Pricer (1908) published his detailed studies. McCook (1883a, b), Blochmann (1885), and Pricer (1908) have described the initiation of an incipient colony by founding queens. Here, we describe the seasonal distribution of the nuptial flights, and the sex ratio of field colonies, both of which are important to understanding the reproductive strategy of this insect. We also discuss the implications of our observations on the organization of its population structure.

Methods

The data we report on here is largely field data that we have collected from 1977 to 1981, on the captures of alate or recently dealated queens of *C. pennsylvanicus* in central New Jersey. However, the data from 1979 is derived from student collections, as we were unable to collect during that year.

Sex ratio information was taken from colonies collected in their entirety in early spring, employing a modification of Vanderschaff's (1970) method. In all cases, colonies were collected before the mode of occurrences of nuptial flights, as inferred from our field data. Dry weights were determined for 30 males and females, and were used for subsequent interpretations.

Statistical tests employed here are of goodness of fit of distributions: the Kolmogrov-Smirnov test statistic, D; and the Log-Likehood Ratio test statistic, G (Zar 1974).

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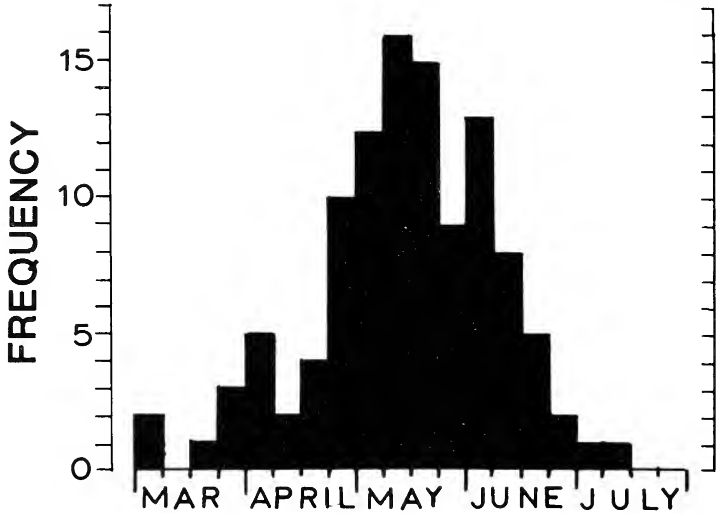

Fig. 1. The distribution of field collections of alate or recently dealate queens of *C. pennsylvanicus* from 1977 through 1981, in central New Jersey.

Results

A plot of the data of the occurrences of field captures of alate or recently dealate *C. pennsylvanicus* queens (Fig. 1) demonstrates that most nuptial flights occurred during spring. Surprisingly, founding queens were captured for more than four months (Fig. 1).

If we compare the data collection on an annual basis (Table 1), we find that we cannot reject the null hypothesis that there is significant variation in the numbers of queens captured (Kolmogrov-Smirnov $D = 0.12615$, $P > 0.05$), but we must conclude that there is a significant seasonal, or monthly,

Table 1. The monthly and yearly distributions of collections of alate or recently dealate queens of *C. pennsylvanicus* given in Fig. 1.

Month	Year					
	1977	1978	1979*	1980	1981	Sum
March	0	1	0	1	4	5
April	3	9	0	4	7	23
May	6	18	8	15	6	53
June	5	9	4	8	2	28
July	0	0	0	2	0	2
Sum	14	37	12	29	19	111

* All data from student collections.

Table 2. The sex ratios of reproductives from New Jersey field colonies of *C. pennsylvanicus*, and a comparison with data given in Pricer (1908).

Colony reference number		Alates collected		Proportion males
Pricer #1		350		0.4286
Pricer #2		370		0.4708
Pricer #3		323		0.3591
Pricer #4		206		0.4951
	Total	1,249	Mean ratio	0.4339
New Jersey colonies collected in spring 1980				
Queens present				
CP #32		526		0.6026
CP #39		410		0.4805
CP #40		1,009		0.5154
CP #42		1,120		0.6151
CP #45		260		0.4846
	Total	3,325	Mean ratio	0.5561
Queens not recovered				
CP #37		75		0.7600
CP #38		217		0.4746
CP #41		437		1.0000
	Total	729	Mean ratio	0.8189

effect on capture distributions (Kolmogrov-Smirnov $D = 0.181982$, $P < 0.0002$).

Field collected colonies of *C. pennsylvanicus* also were variable in sex ratio (Table 2). The mean ratio of males to females was 1.516, or 60.26% of all reproductives in the colonies were males. However, if we compare those colonies from which queens were not recovered with queenright colonies, we find that queenless colonies have a significantly higher frequency of males (0.81893 vs. 0.55188; $G = 189.579$, $P < 0.00001$). Also, our colonies collected in New Jersey had a significantly higher frequency of males than did Pricer's (1908) colonies (0.6026 vs. 0.4339; $G = 109.74$, $P < 0.00001$). Mean dry weight of female alates was 56.8 ± SD 12.3 mg, while that of the males was 9.3 ± SD 4.3 mg. Assuming equivalence in conversion costs, a female is thus 6.1 times more costly to produce than a male.

Discussion

Direct observations of synchronous mass mating swarms of *Camponotus* spp. have not been recorded. Males produce a mandibular gland pheromone which stimulates the females to flight (Holldobler and Maschwitz 1965). However, Veitinghoff-Riesch (1928) and Sanders (1972) have provided indirect evidence that synchronous swarming may occur in *C. herculeanus* (L.). Typically, alates depart from the colony individually, and ascend until they are no longer visible, presumably to mate in the air (Eidmann 1929; Sanders 1964).

The data that we have been able to collect does not suggest synchronous swarming of *C. pennsylvanicus* in New Jersey. Moreover, our data suggest that nuptial flights occur over a very long period of time, and generally involve a limited number of queens. Our data do not allow a consideration of the temporal range of the mating activities of males, but we assume that it must be similar. The distribution of our capture data does not differ significantly from carpenter ant complaints from the general public in New Jersey (Fowler and Roberts 1982), suggesting that the general public may respond to sightings of individual founding queens.

Trivers and Hare (1976) have extended the argument of sex ratio and incorporated it with the theory of kin-selection to argue that monogynous ants, such as *C. pennsylvanicus,* should have a sex ratio controlled by the workers. If so, the sex ratio should approximate 1 male to 3 females, on a per weight basis, given the asymmetries of genetic relatedness. A recalculation of Trivers and Hare's (1976) data for *C. pennsylvanicus,* based on a larger sample size for dry weight determinations, gives an inverse ratio of investment, of the weight ratio of females to males divided by the ratio of the number of males to females, of 7.92 for Pricer's (1908) data. For our data from New Jersey, this ratio is 4.07. If we examine the data from queenright and queenless colonies separately, we find an inverse ratio of investment of 5.8 for queenright colonies and 1.35 for queenless colonies. Only when a queen has died, or is lost, as was probably the case in our queenless colonies, does this ratio drop, as would be expected, under worker oviposition leading to increased production of males. As the ratio of investment was highly variable from colony to colony, it is likely that there is no optimum ratio of investment, as has been argued by Herbers (1979) and Cannings and Cruz Orive (1975).

If we consider an elementary model of sex ratio investment (Cannings and Cruz Orive 1975), in which the more abundant sex is shown to be the disperser, we may conclude that alate queens do not widely disperse, but rather males must if outbreeding is to occur. Isozyme studies of localized populations are needed to test this prediction.

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THERMAL REQUIREMENTS FOR POSTDIAPAUSE DEVELOPMENT AND SURVIVAL IN THE GIANT SILKWORM, *HYALOPHORA CECROPIA* (LEPIDOPTERA: SATURNIIDAE)

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Abstract.—We investigated the thermal requirements for development and survival in the giant silkworm, *Hyalophora cecropia* (L.) (Lepidoptera: Saturniidae) at 5 temperatures (L:D 16:8). The developmental times ranged from an average of 50 days at 15.6°C to 17 days at 26.7°C. Males developed slightly faster than females at all temperatures except 26.7°C. In females, the lower thermal threshold, *t*, and the thermal constant, *K*, were 10.4°C and 276 degree days (°d), respectively. In males, the respective *t* and *K* values were 9.2°C and 301 °d. The percentage mortality (pupal to adult) was very low (0 to 11%) at all temperatures. The sex ratio was approximately 1:1.

The annual life cycle of a univoltine insect species consists of a period of activity (reproduction and development), a period of dormancy (including diapause), and the intervening transitional periods (diapause induction and postdiapause development). To understand the phenology and population dynamics of univoltine insects, and to rear these species efficiently in the laboratory, it is important to understand the primary environmental factors regulating each phase.

The giant silkworm, *Hyalophora cecropia* (L.), is the largest and best-known of the North American saturniids. Much of the research on this univoltine insect has focused on its dormancy, including physiological and ecophysiological aspects of its diapause (e.g., Williams 1956, 1969; Mansingh and Smallman 1966; Sternburg and Waldbauer 1969, 1978; Waldbauer and Sternburg 1973, 1978; Willis et al. 1974; Waldbauer 1978).

Despite these important studies, a quantitative assessment of the factors controlling postdiapause development of the cecropia moth has not been made (see Waldbauer 1978). Because temperature is one of the most important abiotic factors influencing development in insects, we investigated the

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thermal requirements for postdiapause development and survival in *H. cecropia.*

Materials and Methods

We obtained ca. 70 viable eggs from a mated female caught in Ithaca, New York (Tompkins Co.). Following hatching, the larvae had access to a constant supply of cherry and black willow leaves. Initially, we placed 10 young larvae in each of 7 2-pint jars. As the larvae grew, we separated them so that there were 1 or 2 larvae per jar. In addition, we reared some of the large larvae in well-vented 12 × 12 × 6-inch plastic boxes. All of the containers were cleaned daily.

The eggs and young larvae were kept at room temperature and natural photoperiod. We maintained the older larvae at 24 ± 1°C, L:D 10:14. After the cocoons were spun, we held them under a 24 ± 1°C, L:D 10:14 regimen for 3½ to 4 weeks. Because no emergence occurred, we assumed that all individuals were in diapause.

Subsequently, we transferred the cocoons through a series of decreasing temperatures: 21, 18.3, 15.6, 10, and 4.4°C (all ±1°C, at L:D 10:14). We maintained the cocoons for 2 weeks under each condition, except at 4.4°C, where the cocoons were held for 4 months to allow for the completion of diapause.

To determine the effect of temperature on postdiapause development, we divided the cocoons into 6 groups of about 10 each. One group was transferred to each of the following 5 temperature conditions (15.6, 18.3, 21, 24, and 26.7°C) under long days (L:D 16:8) (Table 1). The sixth group was transferred to 24°C and maintained under short days (L:D 10:14); its served as a control to show that diapause had ended.

We recorded the number of days taken for the moths to emerge in each condition. The reciprocal of the mean developmental time (1/days) was plotted against temperature and the resulting curve was tested for linearity with the ANOVA test (Snedecor and Cochran 1967). The lower theoretical threshold temperature, t, was obtained by extrapolating the linear regression of 1/days vs. temperature through the x-axis. We then calculated the thermal constant, K, by the equation $K = y(d - t)$, where y is the mean developmental time in days, and d = temperature in °C (Andrewartha and Birch 1954).

Results

Table 1 shows the mean developmental times for each sex of *H. cecropia* (pupal to adult stages) at 5 constant temperatures. The number of days to emergence ranged from 15–20 days at 26.7°C to 38–62 days at 15.6°C. At all temperatures except 26.7°C, females took slightly longer to emerge than

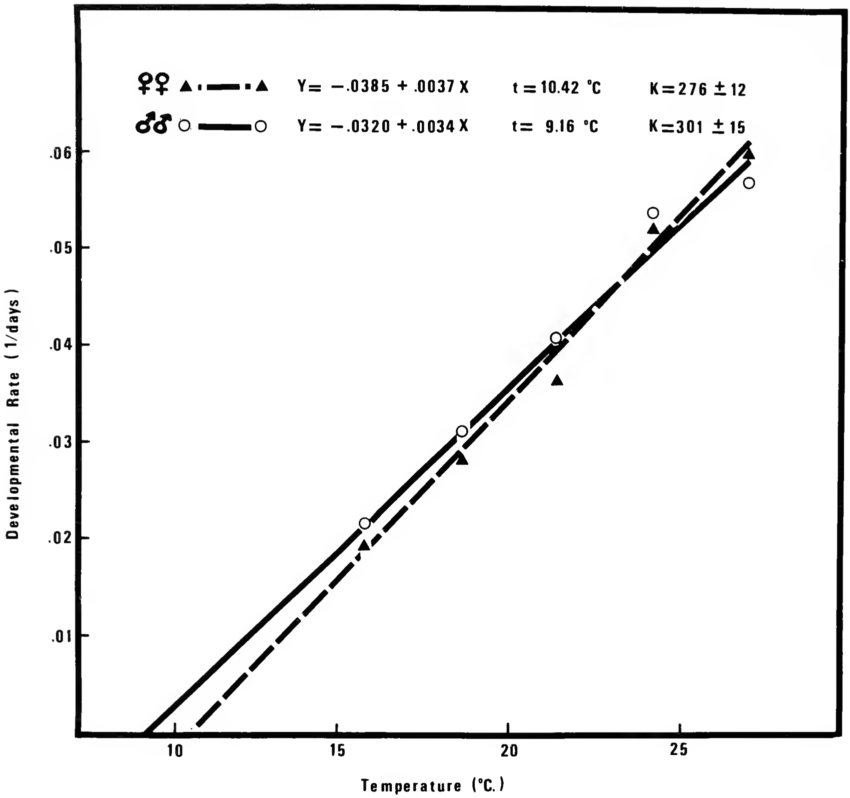

Fig. 1. Postdiapause developmental rates for the pupal to adult stages of *Hyalophora cecropia* at constant temperatures.

males, but the difference was only significant at 21°C (t-test, $P < 0.05$) (Table 1). The distribution of emergence was continuous for both females and males at each temperature except 15.6°C, where adults emerged more slowly and sporadically.

The lower theoretical threshold, *t*, is 10.4°C for females and 9.2°C for males (Fig. 1). The thermal constant, K ± SD, is 276 ± 12 and 301 ± 15 degree days (°d) above *t* for females and males, respectively. Development varied linearly with temperature between 15.6°C and 26.7°C ($P < 0.05$).

The overall sex ratio (all temperatures combined) was 57% females and 43% males. This ratio—calculated from a total of 56 including 4 unemerged animals that were dissected after death—did not differ significantly (chi-square test, $P < 0.05$) from a 1:1 ratio.

The percentage mortality of pupae and pharate adults was very low at all temperatures. However, at 26.7°C, approximately half of the emerged moths failed to expand their wings fully (Table 1).

Table 1. Postdiapause developmental rates, mortality, and sex ratio of *H. cecropia* at various constant temperatures. Females: $t = 10.4$°C; $K = 276$ °d. Males: $t = 9.2$°C; $K = 301$ °d.

Temp. (±1°C)	% mortality	Developmental time (days)			Sex ratio (%)	
		♀♀	♂♂	Combined	♀	♂
26.7	10 (10)*	17 ± 2.0** (5)	17.8 ± 2.1 (4)	17.3 ± 1.9 (9)	55	45
24.0	0 (8)	19.2 ± 1.3 (5)	18.7 ± 0.6 (3)	19.0 ± 1.1 (8)	62	38
21.1	0 (10)	27.6 ± 1.4 (7)	24.7 ± 1.2 (3)	26.7 ± 1.9 (10)	70	30
18.3	0 (10)	35.2 ± 2.3 (5)	33.8 ± 3.1 (5)	34.5 ± 2.7 (10)	50	50
15.6	11 (9)	52.3 ± 8.4 (3)	48.6 ± 7.2 (5)	50.0 ± 7.3 (8)	44	56

* (No.) = number tested.
** $\bar{x}$ ± SD.

Developmental rates of females and males under L:D 10:14 (24°C) were not significantly different from those under L:D 16:8 (24°C) (t-test, $P < 0.05$).

Discussion

Development and temperature.—Sternburg and Waldbauer (1969) observed that *H. cecropia* males emerge earlier than females under natural conditions. Our preliminary results (Fig. 1) suggest that the earlier emergence of males can be explained by differences in thermal requirements for the postdiapause development of the 2 sexes. That is, males begin development at a lower threshold temperature than females. In addition, males have a slightly faster rate of development than females at all but the highest temperature tested (Table 1).

The lower theoretical threshold temperature (t) for development and emergence was ca. 10°C. This is consistent with Williams' (1956) observation that some morphological development, but not emergence, occurred in *H. cecropia* at 6°C.

Emergence pattern and sex ratio.—Sternburg and Waldbauer (1969) and Waldbauer and Sternburg (1978) observed a distinct bimodal emergence pattern in field populations of *H. cecropia* in Illinois (i.e., emergence in the 2 broods was separated by ca. 1 month). They attributed the bimodality to variation in diapause termination, not to variation in rates of development after diapause had ended. In our experiments, emergence did not exhibit bimodality, but was unimodal at all temperatures. We suggest that the prolonged period of chilling experienced by our experimental animals allowed diapause to terminate in all individuals before transfer to warmer conditions and thus masked the expression of any variation in diapause termination that might have been present.

Our sex ratio data and photoperiodic tests are consistent with this hypothesis. Sternburg and Waldbauer (1969) found that 65% of their early-emerging brood and 43% of their late-emerging brood were females; whereas 57% of our adults were females (Table 1). This intermediate sex ratio suggests that if there were two broods in our population, both emerged simultaneously. Similary, developmental rates were not affected by photoperiod (L:D 16:8 and L:D 10:14), indicating that diapause had terminated in all individuals before removal from cold conditions. Thus, our results are consistent with Waldbauer and Sternburg's conclusion that bimodality in *H. cecropia* emergence is the result of variation in diapause termination, rather than post-diapause development.

The unimodal emergence pattern in our experiments may also have resulted from limited genetic variability. That is, natural *H. cecropia* populations from Ithaca, New York, may not have the genetic variability that produces bimodal termination. It is also possible that our experimental population, which was derived from limited stock, did not harbor the full range of variability. Thus, additional studies are needed to establish the relative roles of environmental and genetic factors in determining emergence patterns in *H. cecropia* populations in central New York.

Mortality.—The percentage mortality of immatures within coocons was low (~4%) and, apparently, unrelated to temperature over the range of temperatures we used (Table 1). However, at our highest temperature (26.7°C), almost half of the adults failed to expand their wings fully and died shortly after emergence. This mortality can be attributed to desiccation during emergence; *H. cecropia* emerges early in the day (Truman 1972) when daily temperatures are low and relative humidity is high. Therefore, we conclude that *H. cecropia* should be reared at temperatures around 24°C for relatively fast development and high rates of survival.

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RESOURCE ASSESSMENT BY ADULT AND LARVAL CODLING MOTHS

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Abstract.—Two-day-old adult and first-instar larval codling moths were assayed for ability to detect and avoid resource sites (=apples) already occupied by conspecifics (i.e., host discrimination). Under laboratory conditions, adults oviposited as readily in the presence of conspecific eggs and larvae as in their absence. Similarly, newly hatched first-instar larvae, when released in laboratory arenas, located and attempted to mount and bore into apples regardless of the presence or absence of older conspecific larvae. We contrast codling moth behavior and ecology with that of two other insect parasites of apple that are known to host-discriminate, the apple maggot fly and the European apple sawfly.

Introduction

Accumulating evidence suggests that individuals utilizing restricted (exhaustible) resources may suffer reduced fitness when living within populations below or above some optimal density range (Peters and Barbosa 1977; Prokopy 1981). Thus, selection may favor individuals that are capable of assessing population density and responding accordingly. Indeed, several different mechanisms have been demonstrated through which foraging animals assess resource quality, quantity, and "population load" of conspecifics, including biochemical, visual, and physical assessment systems (see Prokopy et al. 1982).

For the past several years we have been investigating resource assessment behavior of insects that parasitize (sensu Price 1977) apple fruit. Because individual apples are discrete, exhaustible resource units, we hypothesized that insects that exploit these hosts may avoid apples already occupied by a high density of conspecifics. To date, we have demonstrated that two parasites of apple, the European apple sawfly (*Hoplocampa testudinea*) (Roitberg and Prokopy in MS) and the apple maggot fly (*Rhagoletis pomonella*) (Prokopy 1972) are deterred, by an unknown mechanism and marking pher-

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omone respectively, from ovipositing in developing ovaries and growing fruit respectively, when such hosts are already parasitized by conspecifics. Van Lenteren (1976) defines this "refrainment response" as host discrimination, an ability that has been demonstrated in several entomophagous and phytophagous parasitic insects (Prokopy et al. 1982). In addition to host discrimination by the adults, larvae of *H. testudinea,* when searching for supplemental fruit, avoid hosts occupied by conspecific larvae (Roitberg and Prokopy in MS).

Previous research on resource assessment by a third major parasite of apple, the codling moth, *Cydia pomonella,* is inconclusive. For example, on the basis of distribution of codling moth (CM) eggs and larval-infested apples, Geier (1963) and Jackson (1979) concluded that codling moths probably do not host-discriminate. By contrast, Maclellan (cited in Wood 1965) suggested that freshly laid eggs may deter oviposition by foraging CM females. Van Lenteren et al. (1978) and Mackay and Singer (1982) demonstrated that, when used as the sole criterion, egg distribution data is at best weak circumstantial evidence on which to base conclusions about host discrimination ability.

CM females deposit eggs on or near apples. Following hatch, larvae locate, bore into, and utilize apples for food and shelter. Thus, two very different life forms must make choices of sites for exploitation. Because Ferro and Harwood (1973) demonstrated that individual apples support a finite number of larvae and that competition among larvae may lead to reduced size and fitness of adults, we were particularly interested in determining whether either adults or young larvae could detect presence of and avoid competition with conspecifics.

Materials and Methods

Wild female and male codling moths were collected using an ultraviolet lamp at Orchard Hill, Amherst, Mass. Moths were placed in plastic (11.5 cm × 8.0 cm) cylinders whose walls were covered with waxed paper. Each cylinder was provisioned with one small (ca. 3-cm-diam) apple, serving as an oviposition stimulus (Wearing and Hutchins 1973), and dilute sugar solution. The resulting eggs were held at 24°C, 40–60% R.H., 16L:8D until they matured to the black head stage (just prior to hatch). They then received one of two treatments: (1) transfer to petri dishes for larval behavior assays (see below), or (2) transfer to ca. 10-cm-diam McIntosh apples. In the latter case, resulting infested apples were placed in plastic trays that contained strips of corrugated cardboard which acted as resting and then pupation sites for mature larvae.

Assay of adult discrimination ability.—Following eclosion, female and male moths, reared from the 10-cm-diam apples described above, were placed in waxed-paper-lined cyclinders at a ratio of 1:2, respectively, to enhance probability of mating and to provide oviposition experience (Roitberg and Prokopy 1981). Females that oviposited while within the cylinders were selected for assays the following day. We performed three different experiments:

Experiment i: Two, 2-day-old females and three male moths were placed in a large (60 × 60 × 25 cm) Plexiglas-screen cage 5 hr prior to lights off. The floor of the cage was covered with roughened, No. 1 grade filter paper and the front and back walls of the cage were lined with waxed paper to provide an oviposition substrate. The other walls and ceiling remained as screen. Using Scotch™ double sticky tape, we affixed 25 evenly spaced 1-day-old CM eggs, collected as described previously, to one of the waxed-paper walls. To the other waxed-paper wall, we affixed similarly distributed, egg-free double sticky tape. Moths were left in the cages overnight and numbers of freshly-laid eggs were counted the following morning. The orientation of each cage was reversed with each replicate.

Experiment ii: This series of tests was similar to Experiment i except that no eggs were affixed to either waxed-paper wall. Instead, at the base of one waxed-paper wall, we placed two, small (ca. 8-cm-diam) McIntosh apples which were parasitized with two 10-day-old CM larvae. At the base of the other waxed-paper wall, we placed two unparasitized but similar McIntosh apples.

Experiment iii: Electrophysiological tests. We employed whole antennal preparations from 2-day-old CM females. The antennal base was placed on the indifferent electrode and the end of the flagellum on the recording electrode. Output was recorded on a Hewlett Packard FM tape recorder. We presented each of the following substrates 3 cm below each antennal preparation:

(1) One unparasitized 10-cm-diam apple.

(2) One 10-cm-old apple parasitized with two 10-day-old CM larvae.

(3) One glass flask, similar in size and shape to the apples and covered with moist tissue paper (to simulate moisture emanating from apples), to serve as a control.

(4) One glass microscope slide to which we fastened, with double sticky tape, 25, 16-hr-old CM eggs.

(5) One glass microscope slide to which we fastened, with double sticky tape, one 10-day-old CM larva (including some of its frass).

(6) One glass slide to which we fastened double sticky tape, to serve as a control.

Assays of larval discrimination ability.—Experiment i: Individual CM eggs, at the black head stage, were placed in plastic petri dishes (14.5 cm diam) along with and equidistant from (1) one small (8-cm-diam) unparasitized McIntosh apple, and (2) a similar apple parasitized by two 10-day-old CM

Table 1. Response of female codling moths to oviposition substrates with or without conspecifics.

Expt.	Treatment	N	$\bar{X}$ No. eggs laid/♀♀	P
i	Substrate harboring 25 conspecific eggs	9	10.8 ± 2.1 SE	N.S. X^2
	Substrate harboring no conspecific eggs		10.7 ± 2.4 SE	
ii	Substrate harboring 4 conspecific larvae/2 apples	13	10.3 ± 1.7 SE	N.S. X^2
	Substrate harboring no conspecific larvae/2 apples		11.5 ± 2.5 SE	

larvae. Each dish was oriented in a different direction. In addition, each dish was lined with moist filter paper from which two small circles had been cut. The apples were placed within the circles so that they did not touch the filter paper.

After hatch, larvae crawled on the surface of the filter paper and eventually contacted one of the apples. Due to experimental design, larvae displayed difficulty mounting apples from the filter paper. Therefore, we terminated each replicate when a larva attempted to crawl on an apple, recording search time, and search path of the larva and the parasitization state of the apple. Larvae were disqualified if (1) they failed to initiate search within 90 min, or (2) they crawled out of the petri dish.

Experiment ii: Individual eggs, at the black head stage, were placed on either (1) a small (10-cm-diam) unparasitized McIntosh apple, or (2) a similar apple parasitized by two 10-day-old CM larvae. Larvae were permitted to search on apples until they either (1) attempted to bore into the apple, (2) crawled up the stem, or (3) dropped from it. In the latter two cases, larvae were transferred to apples of the opposite type, and the test was repeated. In both Experiments i and ii, each apple and larva was used only once.

Results

Females oviposited as readily in the presence of conspecific eggs and larvae as in their absence (Table 1). In addition, electrophysiological recordings showed no difference in female antennal response to egg- and larval-treated glass slides compared with control slides. Also, whereas female antennae showed a strong and consistent positive response to whole apples versus none to glass flasks, there were no differences in response to parasitized versus unparasitized apples.

Results from the larval behavior experiments showed that newly hatched larvae do not host-discriminate (Table 2). Similar numbers located and attempted to mount parasitized versus unparasitized apples. In addition,

Table 2. Response of newly hatched codling moth larvae to parasitized and unparasitized apples.

Treatment	Host Condition Parasitized	 Unparasitized	P
Expt. ii—Larvae released on host			
Time to arrival at host	$\bar{X} = 8.5 \pm 2.5$ SE (N = 12)	$\bar{X} = 9.2 \pm 2.7$ SE (N = 16)	N.S. Mann-Whitney U
No. turns ≥45° while searching for the host	$\bar{X} = 8.5 \pm 2.1$ SE (N = 12)	$\bar{X} = 12.2 \pm 3.4$ SE (N = 16)	N.S. Mann-Whitney U
Arrivals at host type	12/28	16/28	N.S. X^2
Expt. ii—Larvae released on host			
Time until contact with stem base	$\bar{X} = 13.0 \pm 4.6$ SE (N = 14)	$\bar{X} = 9.3 \pm 5.1$ SE (N = 15)	N.S. Mann-Whitney U
Time until boring initiated	$\bar{X} = 15.5 \pm 4.3$ SE (N = 14)	$\bar{X} = 31.6 \pm 9.8$ SE (N = 15)	N.S. Mann-Whitney U
Acceptance of host fruit	14/16	15/16	N.S. X^2

there were no statistically significant differences in search speed or turning rate of larvae that located either parasitized or unparasitized hosts (Table 2). Similarly, when directly placed on apples, newly hatched larvae readily accepted (i.e., bored into) apples regardless of parasitization state.

Discussion

Resource assessment by most animals is a complex process, shaped in part by ecological, physiological, and phylogenetic constraints. Thus, different animals facing similar foraging problems may, over evolutionary or contemporary time, employ widely different solutions (cf. Wright's "adaptive landscape," Wright 1931). The present study strongly suggests that the codling moth, in contrast to at least two other major parasites of apple (*R. pomonella* and *H. testudinea*), does not partition resources through avoidance of occupied resource sites.

Roitberg (1981) analyzed ecological correlates of phytophagous insects that have been demonstrated to avoid ovipositing at resource sites harboring high density of conspecifics. Correlates common to most of these species included: (1) association with host plants that persist over several parasite generations, (2) comparatively narrow host range, (3) limited mobility of parents and offspring, and (4) restricted sites of parasitization within individual host plants. In addition, Singer and Mandracchia (1982) noted that most, though not all, host-discriminators lay single eggs. While codling moth fits the stereotype of a "typical" host-discriminator, two important differences should be noted. First, adults choose only the proximate area of a host for subsequent exploitation. It is the larvae that make the final choice as to which apple will be exploited for food and shelter. Second, larvae are relatively mobile and are not restricted to individual hosts. By contrast, *R. pomonella* larvae are unable to emigrate to new hosts should their current host prove unsuitable (pers. obs.).

Our results provide strong evidence that the codling moth does not discriminate against occupied resources. Still, several alternate hypotheses are possible. First, adult host-discrimination behavior may have been adversely affected by experimental conditions, i.e., cage enclosure. We reject this hypothesis on the basis of evidence from moths enclosed in small (ca. 300-cc) containers, where eggs were often distributed in small clusters. In contrast, moths distributed eggs singly in the large assay cages, paralleling the distribution of eggs in nature (Geier 1963). Second, we may have employed such high concentrations of conspecific eggs or larvae that the host assessment system was overstimulated, leading moths to oviposit at random. We are unable to refute or substantiate this hypothesis for codling moth or any other phytophagous host-discriminator. Third, with regard to CM larvae, the physical structure of the arena may have disrupted normal host assessment behavior. Our observation of larval behavior argues against this hypothesis, in that assay larvae moved freely within the assay arenas and appeared to readily detect the presence of both apples present.

Two features of codling moth behavior, while lacking any overt host-discrimination, may provide for reduced competition of offspring. First, adults tend to oviposit in areas of high fruit density (Jackson 1979), thereby providing greater levels of resource availability. Second, each oviposition is preceded and followed by a period of flight (Geier 1963). This action reduces the chance of sib-sib larval competition. Similar behavior has been demonstrated for other insects, including *H. testudinea* (Roitberg and Prokopy 1980) and *R. pomonella* (Roitberg et al. 1982).

Finally, we reemphasize the potential danger of unidimensional, deterministic approaches to studies of insect resource assessment behavior and expectation of universal host-discrimination ability (cf. Gould and Lewontin 1979). Codling moth adult oviposition and larval host-location behavior is probably influenced by several factors, all of which may determine future fitness of individuals. These could include: energetic costs to foraging by adults and larvae, foraging-associated risks to predation, structure of resource patches and abiotic factors. As an example, newly hatched larvae may risk threat to life if resources are not quickly located (Jackson and Harwood 1980). Therefore, host discrimination may be of lesser importance to these animals compared to a species such as *R. pomonella.* The cost of developing and maintaining a host-discrimination information processing system may outweigh the benefits (Jackson 1979). In conclusion, while we may analyze animal behavior from particular theoretical perspectives, we should maintain our awareness of the complexity and stochastic nature of behavioral and ecological events.

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THE LONE STAR TICK, *AMBLYOMMA AMERICANUM* (LINNAEUS): NEW DISTRIBUTION RECORD FOR NORTH AMERICA (ACARINA: IXODIDAE)

John P. McKeon, Thomas F. Bast and Edward M. Bosler

Abstract.—A new distribution record for *Amblyomma americanum* (L.) within northeastern New York State is established. Previous reports indicate this species was limited to extreme southeastern sections of the state. The finding of three adult ticks in Saratoga County increases the recorded distribution of this species.

The Lone Star tick, *Amblyomma americanum* (L.), is known to be well established throughout the southern section of the United States (Bishopp and Trembley 1945; Burgdorfer 1969). Previous occurrences of *A. americanum* from New York have been limited, reported only from the southeastern sections of the state, most notably Suffolk County (Good 1972), Nassau County (Benach pers. comm. 1982) and New York City (Rehn 1953; Benach pers. comm. 1982). One engorged tick was removed from a human in Catskill, Greene County, N.Y. in 1954 but it was reported that this person had recently visited the Long Island area previous to the discovery (Jamnback 1969). No other reports from upstate New York have occurred during the previous 50 years (Anastos et al. 1978).

On 8 June 1979, one adult male *A. americanum* was found preparing to attach to the upper leg of a human male adult. The tick was encountered during a walk through an old-field type habitat in the Town of Wilton, Saratoga County, N.Y. On 12 June 1980, one adult female tick was removed from a human male who had been walking in a field in the Town of Greenfield, Saratoga County. Subsequent field collections failed to recover any additional ticks. An engorged female tick was removed from a hospital emergency room female patient on 28 August 1981. The tick was likely encountered near the patients home in the Town of Moreau, Saratoga County. The general locations of these three reports are found in Fig. 1.

These collections indicate that an apparent indigenous, overwintering population of *A. americanum* now has a limited distribution in Saratoga County. The medical significance of this new record may be important due to the Lone Star tick's capability as a vector of Rocky Mountain spotted fever

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Fig. 1. Known distribution of *Amblyomma americanum* (L.) in Saratoga County, New York.

(Harwood and James 1979) which is known to be endemic in *Dermacentor variabilis* (Say) populations near these areas in Saratoga County (McKeon et al. in preparation for publication).

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MORTALITY FACTORS, POLLEN UTILIZATION, AND SEX RATIO IN *MEGACHILE PUGNATA* SAY (HYMENOPTERA: MEGACHILIDAE), A CANDIDATE FOR COMMERCIAL SUNFLOWER POLLINATION

V. J. Tepedino and D. R. Frohlich

Abstract.—Data on the nesting biology of *Megachile pugnata* was obtained from 359 trap-nests at two sites in northern Utah. Bees made an average of 3.8 cells per nest and provisioned cells exclusively with pollen from the Compositae. Approximately 12% of all offspring were killed by either the clerid predator *Trichodes ornatus* or the chalcid parasite *Melittobia* sp. An additional 30–38% of offspring failed to complete development to the adult stage. Most of this immature mortality occurred during the overwintering and incubation stages. The sex ratio of the populations varied between 1.4 to 1.8 (♂/♀). Nests with with 3 or fewer cells had a lower percentage of male offspring than all other nests combined. It may be possible to increase the percentage of female bees by decreasing the depth of the nesting hole.

Introduction

Megachile (*Sayapis*) *pungata* Say is a gregariously nesting leafcutting bee distributed throughout most of the United States and southern Canada (Hurd 1979). The species commonly nests in pre-existing holes in wood and readily accepts sumac trap-nests (Medler 1964) or artificial wooden domiciles as nesting sites. The potential importance of *M. pugnata* as a pollinator in commercial sunflower fields has recently been recognized (Parker 1981) and is currently under study (Parker and Frohlich unpubl.).

Relatively little information is available on the biology of this potentially manageable species. Medler (1964) reported on the nest architecture and nest associates found in 20 sumac trap nests in Wisconsin. Parker (1981) and Hurd (1979) noted that *M. pugnata* visits a variety of flower species, but Hurd (1979) suggested that composite species are preferred. These records are based on flower visitations only; actual pollen usage has not been examined.

In this paper we report on mortality factors, pollen usage and sex ratio from 359 nests obtained from artificial domiciles at two sites in northern

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Utah. Of especial interest is the relationship between mortality factors, sex ratio and number of cells per nest. Information on these parameters enable us to make suggestions regarding the size of nesting materials that might be offered to populations in commercial sunflower fields so as to minimize mortality and increase the percentage of females.

Methods

Nests of *M. pugnata* were obtained from trap-nest blocks placed at two sites in Cache Co. in northern Utah. The Faust site (42 km south of Logan, Cache Co., Utah, 1,800 m elevation) is on a hillside with a SW exposure. It is covered by large stands of mature aspen (*Populus tremuloides*) which are surrounded by open, grassland meadows. The Blacksmith Fork site (27 km SE of Logan, 1,500 m elevation) is on a canyon floor surrounded by maple–box elder with an understory of *Hydrophyllum, Cirsium* and *Balsamorrhiza.* Trap-blocks were made of pine wood, and contained 50 drilled holes into which paper soda straws were inserted (7 mm diameter, 15 cm deep). Blocks were attached to dead trees with holes oriented horizontally.

Blocks were collected during the first week of July and maintained at room temperature in the laboratory until 1 September when nests were dissected. During dissection we recorded the contents of each cell, causes of mortality, and prepared pollen slides (Beattie 1971) from uneaten provisions or from pollen adhering to the cell walls. Live larvae were put into gelatin capsules and maintained at 4°C from 30 September until 9 June when they were incubated at 29°C. Adults were weighed upon emergence and released in a commercial sunflower field (Parker and Frohlich unpubl.).

Results

We recovered 359 completed and plugged *M. pugnata* nests from the two sites (165 Blacksmith Fork, 194 Faust). The sites differed significantly in the distribution of nests by cells per nest (χ^2 contingency tables, $\chi^2 = 12.59$, df = 6, $P = 0.05$): Blacksmith Fork nests averaged fewer cells per nest (3.5, SD 1.5) than did Faust nests (4.1, SD 1.6) (Fig. 1a). Overall, average cells per nest (3.8, SD 1.6) was similar to Medler's (1964) findings for holes of the same depth.

In contrast to Medler's (1964) report that *M. pugnata* is univoltine in Wisconsin, Utah populations had a partial second generation that emerged during the last half of August. Parker and Frohlich (unpubl.) also found a partial second generation in Utah populations. The sites differed in the percent of total offspring that emerged rather than entering diapause: Faust had significantly fewer emergent bees (3.3%) than did Blacksmith Fork (7.3%) ($\chi^2 = 8.90$, $P < 0.005$). There was rarely more than one emergent individual per nest.

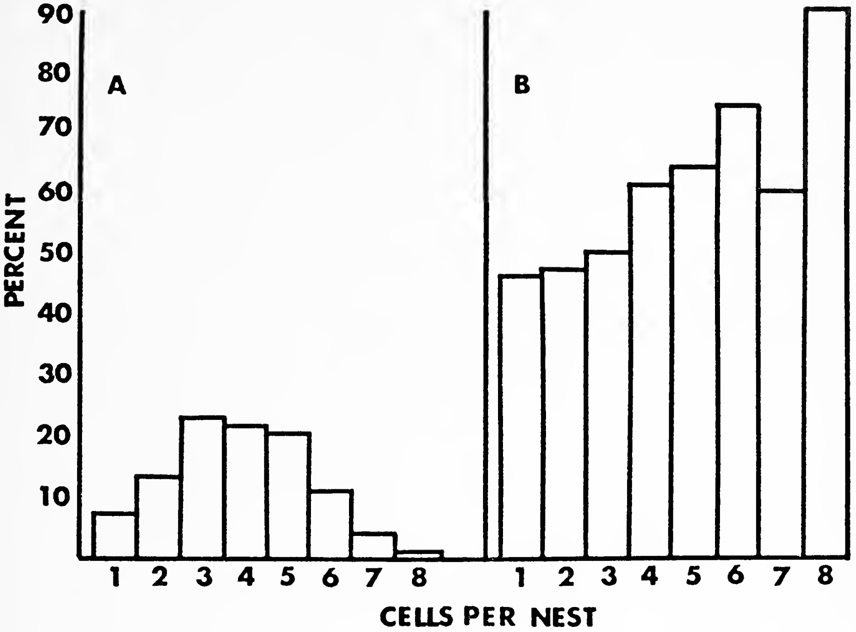

Fig. 1. a. Percent frequency distribution of nests by number of cells per nest. b. Percent of live adults that were males by number of cells per nest. Both sites combined for each figure.

Mortality factors.—Mortality factors included developmental arrest in all stages and various predators and parasites (Table 1). Mortality was significantly higher at Blacksmith Fork than at Faust ($\chi^2 = 8.8$, $P < 0.005$) and this was primarily due to the larval and sib caused categories. The latter category requires clarification. Bees that developed directly to the adult stage without an intervening period of diapause, destroyed any siblings between themselves and the nest entrance when they emerged. Apparently, egress could be achieved only at the expense of nest-mates. The higher percentage of emergent bees at Blacksmith Fork caused a significantly higher incidence of sib caused mortality at that site than at Faust ($\chi^2 = 36.9$, $P < 0.001$).

Most immature mortality occurred during larval and pupal stages: a smaller proportion of cells contained provisions but no egg, or unhatched eggs (Table 1). Most of the larval and pupal mortality was sustained during the overwintering and incubation treatments (Faust, larval 55.1%, pupal 88.3%, Blacksmith Fork, larval 64.0%, pupal 77.8%) and may have been due to maintenance at inappropriate temperatures (see also Medler 1964). The incubation treatment appeared to be especially detrimental to females; significantly more females than males died as pupae or adults during incubation (Faust, $\chi^2 = 12.2$, $P < 0.001$; Blacksmith Fork, $\chi^2 = 6.5$, $P < 0.02$).

Table 1. Percent mortality by stages in the life cycle due to developmental arrest or to parasites and predators (PP). Sib caused mortality was due to emergence of a partial second generation. Based upon 827 cells (Faust) and 579 cells (Blacksmith Fork).

	Provision	Dead egg	Larvae	Pupae	Adult	PP	Sib caused	Σ mortality
Faust	4.1	4.4	8.6	9.3	1.8	12.7	0.7	41.6
Blacksmith Fork	1.9	5.2	14.9	6.2	3.3	11.7	6.4	49.6

Predators and parasites destroyed approximately 12% of the cells at each site. Most of this mortality was caused by clerid beetles (*Trichodes ornatus,* 47.6% Faust, 71.2% Blacksmith Fork) and the chalcid parasite *Melittobia* sp. (39.1% Faust, 18.2% Blacksmith Fork). Small percentages of cells were destroyed by the chalcid *Monodontomerus* and the cuckoo bee, *Coelioxys alternata* Say. *Melittobia* and *Coelioxys* were also recorded by Medler (1964).

We compared the incidence of mortality among nests with different numbers of cells to determine if mortality was associated with nest size. Nests from both sites were combined and then grouped by number of cells. Numbers of dead and live individuals were then tabulated for each nest size category. No association between nest size and mortality was found ($\chi^2 = 6.53$, df = 5, $P > 0.25$).

Sex ratio.—Megachile pugnata is a markedly dimorphic bee: using weights as an estimate of body size gave a ♀/♂ size ratio of 1.82 ($\bar{x}$ ♂ = 62.7 mg, SD 9.8, N = 65, range = 41.0–84.7; $\bar{x}$ ♀ = 114.3 mg, SD 20.3, N = 74, range = 69.5–165.7). The expected sex ratio for the population was thus, 1.82 ♂ : 1 ♀ (Torchio and Tepedino 1980). The sex ratio of live offspring at Faust (1.76) did not differ from the expected value ($\chi^2 = 0.08$, $P > 0.75$) but the sex ratio at Blacksmith Fork (1.37) was significantly biased towards females ($\chi^2 = 5.55$, $P < 0.025$). These results were unchanged when dead but sexable individuals were included in the tests.

We examined the occurrence of male and female individuals in nests by grouping nests with the same number of cells for both sites and then tabulating the number of males and females at each cell position. All nest sizes (2 to 6 cells/nest; too few 7 and 8 cells available for statistical testing) had significantly more females in inner cells and more males in outer cells (χ^2 tests, all $P < 0.005$ or less). Thus, *M. pugnata* is similar to the alfalfa leafcutting bee, *M. rotundata* (Fabr.) (Stephen and Osgood 1965) and other megachilid bees (Krombein 1967) in the placement of males and females in the nest.

There was a significant association between the sex ratio and cells per nest (Fig. 1b). Nests with 1–3 cells had lower percentages of males (48.7%) than did nests with ≥4 cells (65.5%) ($\chi^2 = 17.1$, $P < 0.001$). Thus, as cells are added to three-celled nests, there is a much greater probability that they will be males than females.

Pollen utilization.—We examined pollen samples from 1,203 cells at both sites. Few cells contained anything other than composite pollen, although the presence of more than one species of composite was not uncommon. In all, only 0.6% of all pollen grains at Faust and 2.5% at Blacksmith Fork were of non-composite species. It seems clear that the preferred pollen of this species, at least in northern Utah, is of the Compositae.

Discussion

Megachile pugnata possesses several characteristics in common with the semi-domesticated pollinator of alfalfa, *M. rotundata,* which make it an excellent prospect for the pollination of commercial sunflowers. The species is widespread in occurrence, accepts man-made nesting materials and populations are readily obtainable from appropriate habitats (Parker and Frohlich unpubl.). The species can also be manipulated through temperature treatments to ensure synchronization of emergence with sunflower anthesis. In addition, Utah populations appear to exclusively collect the pollen of composites.

Additional work is required to determine the most appropriate temperature at which overwintering bees should be held and subsequently incubated so as to reduce mortality. This is particularly important because the data suggest that females, which are more valuable as pollinators than males, are more susceptible to the temperature treatments employed here. Some of this mortality may be unavoidable, however, because it is necessary to hold bees at cold temperatures beyond their "normal" emergence times (June) to synchronize their emergence with sunflower bloom in mid-July.

The depth and diameter of nesting holes influences the number of cells made per nest and the sex ratio of the alfalfa leafcutting bee, *M. rotundata* (Stephen and Osgood 1965; Gerber and Klostermeyer 1972). A similar effect is likely for *M. pugnata.* Although we have no data on the influence of different diameter holes, it is likely that a decrease in the depth of holes from the 15 cm used here, to 7.5 cm, would result in an increase in the percentage of female offspring. As Stephen and Osgood (1965) found for *M. rotundata, M. pugnata* uses 15 cm holes inefficiently: only 3 to 4 cells were made in most nests and much unutilized space remained. In addition, nests with 4 or more cells had significantly more males than nests with fewer cells (Fig. 1b). Thus, when space was more completely utilized, it was allocated to the less valuable (from the viewpoint of pollination) males. It is possible that a reduction in depth of nesting holes would increase the proportion of nests with fewer cells and thereby increase the percentage of female offspring. Whether or not such a procedure would reduce the total number of offspring produced because of increased time spent in plugging shallower nests with fewer cells, and in searching for new nesting holes (Stephen and Osgood 1965), needs to be studied.

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DISJUNCT SYNCHRONIC POPULATIONS OF 17-YEAR PERIODICAL CICADAS: RELICTS OR EVIDENCE OF POLYPHYLY?

Chris Simon[1] and Monte Lloyd

Abstract.—The theory and biogeography of brood formation in periodical cicadas is reviewed in light of the extraordinary number of different "broods" represented on Long Island and its immediate vicinity. Detailed emergence records, with dates and exact localities, are given in an appendix. We present data which suggest that the evolution of Brood I on Long Island may have been independent of the evolution of Brood I in Virginia. Possible evolutionary scenarios are discussed in light of allozymic and morphometric findings.

Periodical cicadas (Homoptera: Cicadidae: *Magicicada*) are confined to the eastern deciduous forest of the United States; they are not found in the largely coniferous forests of Canada and the northern United States (Marlatt 1907; Dybas and Lloyd 1974). During the most recent (Wisconsin) glacial advance, ending about 12,000 years ago, most of the periodical cicadas' present range was covered by spruce forests (Delcourt and Delcourt 1981 and references therein). It is doubtful whether the recent ancestors of *Magicicada* spp. could have lived in such forests. The species of trees now characteristic of the eastern deciduous forest were confined to small refugia along river courses in the southern United States. A dry oak/hickory/southern pine forest covered the southern states outside of the refugia except for peninsular Florida (sand dune scrub) and the Mississippi basin (cypress/gum).

Today, we find the three morphologically distinct species of periodical cicadas split up into 12 major dyssynchronous 17-year broods (*M. septendecim, M. cassini, M. septendecula*) and three 13-year broods (*M. tredecim, M. tredecassini, M. tredecula*), each with its characteristic range. These broods, or year classes, were mapped by Marlatt (1907). (Updated maps can be found in Lloyd and Dybas 1966; Dybas and Lloyd 1974; and Simon 1979a.) It is difficult to believe that the broods, as we know them today, could have existed prior to the Wisconsin glaciation. Periodical cicadas undoubtedly moved south with the deciduous forest as the ice advanced and must have

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migrated back north as the various tree species recolonized (Davis 1976). It is likely that the past 12,000 years have seen the active proliferation of new broods from one or a few ancestral broods. The most interesting feature of periodical cicada evolution is that whatever happened must have involved all three species because all can now be found coexisting in almost every brood.

Recently, it has become possible to bring new information to bear on the questions surrounding periodical cicada evolution, namely electrophoretic data on allozymes (Simon 1979a, b) and morphometric data on wing venation (Simon 1982). Thus the alternative evolutionary schemes, which flow rather easily from biogeography can now graduate from being idle speculation to being testable hypotheses.

We propose to treat this subject in full detail in a series of forthcoming papers, but our present purpose is more limited and sharply focused. Here, we will be immediately concerned with only five of the 17-year broods: XIV, X, IX, V, and I. All five of these broods co-occur on Long Island, New York. They must either have recently immigrated (since Long Island is a terminal moraine) or very recently have evolved in situ. It is rare to have so many different broods reported from so small an area. Most of our knowledge comes from the observations of one man, William T. Davis, who lived on Staten Island, New York for many years and kept a close watch for periodical cicadas emerging on Staten Island (Simon 1979c) and on Long Island (see Appendix I). According to these records, Long Island appears to be either (1) a microcosm of rampant evolution of cicada broods or (2) an area into which many broods have recently immigrated, with still more recent extinctions in large mainland areas, leaving behind relict populations of several broods.

In this paper, we bring together the available evidence from published records and unpublished correspondence concerning exact localities and emergence dates for the six periodical cicada broods known for Long Island. Each of these is compared biogeographically with the nearest known representative of the same brood on the mainland (i.e., those populations with adults emerging in the same year). As we discuss in detail below, all the Long Island "broods" except XIV, and possibly X, are disjunct, suggesting either a relict status or a polyphyletic origin, as described earlier (hence the quotation marks around broods). Further, we have collected adult specimens of Broods I and XIV from Long Island and from a representative sample of their geographic ranges and analyzed them phylogenetically using comparative wing-morphometric and allozymic data to test the theories of brood formation.

Although Long Island is an excellent place to study periodical cicadas, we should acknowledge the possibility that there may, after all, be nothing more unique about Long Island than the fact that William T. Davis was watching it. Perhaps equally close observations on other areas would turn up many more cases of disjunct, relatively small, unrecorded populations which correspond to the emergence years of existing broods.

Theory of Brood Formation

A series of papers (Marlatt 1907; Alexander and Moore 1962; Lloyd and Dybas 1966; Lloyd and White 1976; White and Lloyd 1975, 1979; Simon 1979a, b, 1982; Simon et al. 1981; Lloyd et al. in prep.) has given us a theory of brood formation that postulates two kinds of accelerations in the cicadas' life cycle: (1) those of one year, supposedly brought about by a single historical episode of extraordinary weather, which affects an entire population within part of the range, and (2) those of four years, supposedly brought on by nymphal crowding which affects only part of a population and generates two broods four years out of phase which coexist in the same woodland.

Seventeen-year cicada broods.—If we take the centrally-located Brood XIV as the putative ancestral brood, then the formal scheme shown in Fig. 1 can be visualized. With both 1-year and 4-year accelerations occurring, it is possible to derive a given brood in two different ways (or more, if the scheme is extended). For example, Fig. 1 shows that Brood IX could be derived from X by a 1-year acceleration, or from XIII by a 4-year acceleration. The most immediate check we have on the validity of such hypotheses is biogeography. Thus the conversion X → IX (shown by a solid line in Fig. 1) was a likely event because Broods IX and X have broadly contiguous ranges in the Appalachians. Brood XIII, by contrast, is confined to northern Illinois and eastern Iowa, a less plausible derivation (therefore shown as a dashed line). In some cases, the biogeography is equivocal, e.g., VI → V and IX → V both involve broods with closely associated ranges, so each is represented by a solid line.

Broods III and IV pose a problem: they have nearly contiguous ranges through east central Kansas, Missouri and Iowa so we can reasonably derive III from IV, but none of the supposed ancectral broods—V (Ohio), VIII (Pennsylvania), VII (New York)—have ranges anywhere near those of III and IV. In this case, we would postulate that Brood IV came from a separate glacial refugium and III was subsequently derived from it. A less plausible alternative is that Brood V once existed in the Mid-West (where it was derived from VI, which is recorded from Wisconsin) but has since become extinct.

Thirteen-year cicada broods.—Lloyd and Dybas (1966) proposed that 4-year accelerations, by occurring repeatedly, might have been selected for and the process thereby become genetically assimilated (Waddington 1953, 1956). This scheme has the great advantage that it provides a mechanism whereby the 13-year life cycle can be derived from the 17-year one without

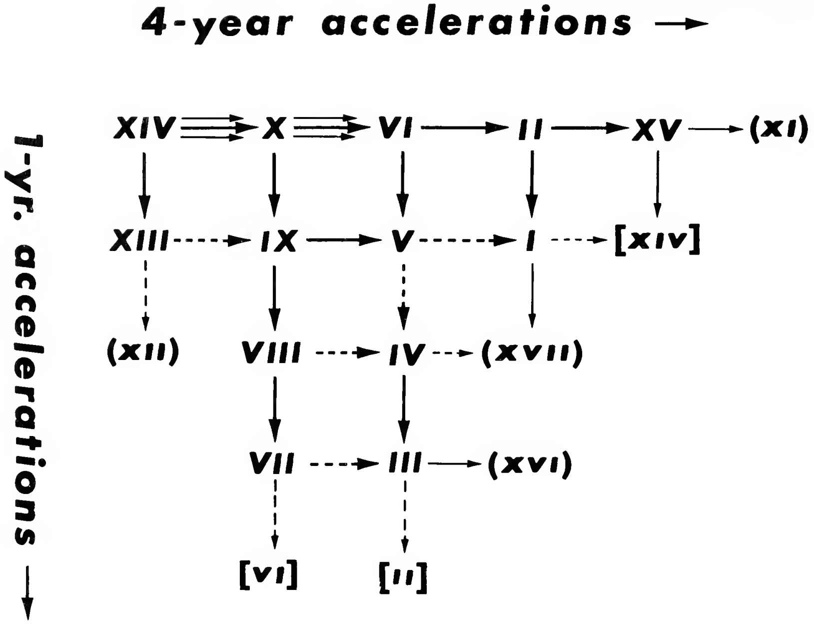


Fig. 1. Formal scheme for deriving all 17-year periodical cicada broods from the postulated ancestor, Brood XIV, by a combination of 4-year and 1-year accelerations, modified from Lloyd and Dybas (1966). Solid single arrows indicate that the two broods have contiguous or closely associated geographic ranges; dashed arrows, that they do not. Triple arrows indicate that the broods' ranges are closely associated in three different parts of the country, suggesting the possibility of polyphyletic origins. Broods in parentheses are of doubtful existence, consisting of very few records; no arrows lead from them. Broods in square brackets could be derived as shown, but there is no need to postulate such a derivation, since a simpler way exists to derive them, starting with Brood XIV.

losing the periodicity in the process (by the generation of intermediates) or the complete elimination of one life cycle by the other. The problem is that the biogeography does not seem to fit. The progression XIV → X → VI → II → XV → XI does make geological sense, but it ends up with the very small Brood XI in New England (Brood XI was well known to the Pilgrims but is now extinct; Lloyd and White 1976) while 13-year cicadas occupy a very broad range in the southern and Mississippi Valley states.

Biogeography might have us postulate that the 13-year cicadas existed in northern deciduous forest refugia during Wisconsin times. They may indeed have evolved from a progression of 4-year accelerations, like we now postulate for XIV → X → VI → II → XV → XI, but this may have happened during a previous interglacial period. This would not be a surprising conclusion, since there have been 16 interglacial epochs in the past two million years (Wright 1976), but we might still need to postulate a separate full-glacial refuge for the 13-year cicadas. The alternative prediction would have 13-year cicadas evolving in the present interglacial, in situ in part or the whole of their present range by many 4-year accelerations from one or more 17-year parental broods. Allozymic data (Simon 1979a) suggest that the three or four 13-year broods which are not extinct evolved from a single 17-year ancestor. We may never know the history of the other 13-year broods which were last recorded in the early 1900's and late 1800's and were poorly collected.

The pattern of distribution of 13-year Brood XIX in relation to 17-year Broods III and IV suggests that 13-year cicadas may be advancing into the range of 17-year cicadas. Lloyd, Kritsky and Simon (in review) propose that hybridization between 13- and 17-year cicadas in zones of contact has led to the exclusion of the 17-year parental brood via nymphal competition from a second generation 13-year hybrid brood. They present the following genetic hypothesis: Parental generation—DD = 17-year and dd = 13-year; F1 generation—Dd = all 17-year; F2 generation—DD, Dd = 17-year and dd = 13-year, which could never breed with their 13-year grandparent's descendants, and could only breed with their 17-year sib's descendants every 221 years, but by that time the 17-year brood will have been eliminated from the area by nymphal competition.

Evidence for four-year accelerations.—The fact that the largest broods of 17-year cicadas overlap widely and are separated by four years suggested to Lloyd and Dybas (1966) that they could have been derived from each other by a 4-year shortening of the life cycle. They suggested that this shortening could occur through the temporary deletion of a postulated supernumerary 6th nymphal instar. White and Lloyd (1975) excavated 13- and 17-year cicada nymphs of the same age and found that rather than possessing an extra instar, the 17-year nymphs differed from the 13-year ones in that the 17-year nymphs grew much more slowly during the first four years of life. Lloyd and White (1976) postulated that this 4-year inhibition in growth might be broken by the stimulus of early nymphal crowding, leading part of the population to emerge four years ahead of schedule. Simon's (1979a) phylogenetic analysis of allozymic data for two 17-year broods and three 13-year broods is compatible with this scheme.

Three years after Lloyd and Dybas (1966) published their hypothesis, a 4-year acceleration was observed in the suburbs of Chicago, where literally hundreds of thousands of periodical cicadas emerged four years ahead of schedule. Only one brood of periodical cicadas (Brood XIII) had ever been recorded from that area, so these cicadas could have had no other origin. The remainder of the brood emerged, on schedule, in 1973, in enormous abundance (many millions) with negligibly few appearing during the intervening years. The two species present in Chicago, *Magicicada septendecim* and *M. cassini,* both participated in this event, although the many thousands that emerged in 1969 were not enough to satiate predators, and apparently left negligibly few descendants (Lloyd and Dybas in prep.). If they had successfully reproduced, a disjunct population of Brood IX would have been created, living sympatrically with Brood XIII in Chicago.

Lloyd and White (1976) found Broods X and XIV living sympatrically in northern Kentucky and documented quantitatively the proportion of cicadas in each brood by measuring 4-year-old eggnest scars, and those of the current year (1974) after Brood XIV had emerged. They made the important theoretical point that once accelerated individuals establish a "beachhead" that is large enough to satiate predators, then conversion to the accelerated brood (Brood X in this case) can be a gradual process extending over many generations. There is a geographical gradient from mostly Brood XIV in Tennessee to mostly Brood X in Indiana, suggesting that the conversion is taking place at a faster pace farther north.

An interesting case exists in New Jersey where Brood XV, a very small brood, is located in counties noted for their abundance of Brood II. A few thousand individuals of Brood XV emerged in Union, Essex, and Bergen counties in 1975. This brood was recorded in these localities in the latter half of the 19th century (Weiss 1916), but no notice had been taken of them since that time. The cicadas that did emerge disappeared after only a week. It is unlikely that they left enough progeny to survive 17 years, emerge, and reproduce. Brood XV is probably not (and probably never has been) a self-reproducing brood, but rather has been regenerated each 17 years from particularly dense populations of Brood II. Observations of Brood II in 1979 proved that they appeared in abundance in *exactly* the same suburban yards where Brood XV had appeared in 1975 (C. Simon unpubl. field notes). In other words, Brood II may be in a very early stage of the process of converting to Brood XV, where there is as yet no "beachhead" of XV established.

A similar situation may exist with Brood VI. It is a very wide-ranging but strongly patchy brood found throughout the eastern United States (Marlatt 1907). Its modern range is poorly documented because of its patchiness. Brood VI is largely sympatric with Brood X, the next most wide-ranging of all the periodical cicada broods. If Brood VI was merely repeated 4-year accelerations of dense populations of X, then the scatter of VI-populations would be understandable. However, there are some counties in Georgia and North Carolina where populations of VI are reported, but none of X (Marlatt 1907). The conversion X → VI may therefore be in a stage intermediate between XIV → X and II → XV, which is the progression one would expect if the ancestral brood were XIV (Figs. 1, 2).

Evidence for one-year accelerations.—Several examples can be found of broods that abut each other and are separated by one year (I–II, III–IV, VIII–IX, IX–X, XXII–XXIII). Broods separated by one year never overlap. Broods XXII and XXIII are known to occur less than one mile apart near

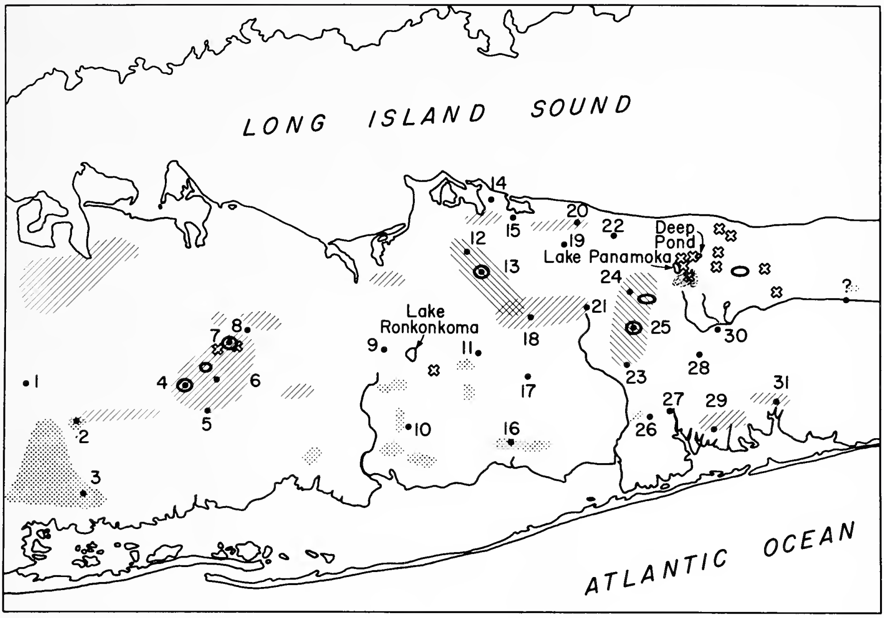


Fig. 2. Central Long Island, encompassing all periodical cicada records except possible Brood II, 1911 localities from Brooklyn (only a few individuals). Locality information is taken from W. T. Davis's field notes and publications, from newspapers, and from personal observations. These sources are detailed in Appendix I. The numbered dots are towns reporting Brood XIV (dates are given in Appendix I): 1 = Hicksville, 2 = Farmingdale, 3 = Massapequa, 4 = Wyandanch, 5 = Deer Park, 6 = Half-Hollow Hills, 7 = Dix Hills, 8 = S. Commack, 9 = Ronkonkoma, 10 = Bohemia, 11 = Farmingville, 12 = East Setauket, 13 = Port Jefferson, 14 = Belle Terre, 15 = Mount Sinai, 16 = Patchogue, 17 = Medford, 18 = Coram, 19 = Miller Place, 20 = Sound Beach, 21 = Middle Island, 22 = Rocky Point, 23 = Yaphank, 24 = Ridge, 25 = Brookhaven National Laboratories, 26 = Shirley, 27 = Mastic, 28 = Manorville, 29 = Center Moriches, 30 = Calverton, 31 = Eastport, ? = Riverhead. Crosshatching = Brood XIV from Davis's personal records. Inverse cross-hatching (upper left to lower right) = personal observations of C. Simon in 1974. Broods other than XIV are indicated as follows: light, regular stipple = Brood X; small, heavy circles or ellipses and hollow "x's" = Brood V; irregular stipple (near Lake Panamoka) = Brood IX.

Utica, Mississippi, as do Broods I and II in the George Washington National Forest near Luray, Virginia (C. Simon unpubl. field notes). Broods IX and X come close to overlapping, being reported from many of the same counties in West Virginia (Marlatt 1907), but there are no known cases of their occurring sympatrically in the same woods. (We predict that none will be found, for reasons given below.)

The usual geographic pattern is for the accelerated periodical cicada brood to replace its fellow farther to the north. Alexander and Moore (1962) suggested that, ". . . prolonged or repeated periods of extreme cold caused summation of diapauses . . . and thus caused those populations closer to the glacial boundary to emerge earlier." We now understand from more recent palynological studies (Delcourt and Delcourt 1981) that the deciduous forest refugia were nowhere near the glacial boundary, but the principle remains the same: a single historical episode of unusually cold weather could affect nymphal development.

The physiological machinery by which periodical cicadas seem to "count" 17 (or 13) years is still a mystery, but it could well be cued to some hormonal change taking place in their host trees. If unusual weather on some historical occasion could cause, say, unseasonal defoliation with a second leafing out later in the summer, the concomitant hormonal change in the tree might cause the cicada to "count" an extra winter and emerge one year ahead of schedule (Lloyd and White 1976). The important point is that one would expect all of the cicadas to be affected by such a change, not just a part of the population. For this reason, broods which are separated by one year would not be expected to overlap except by secondary movements which are known to occur slowly, if at all (Karban 1981; Lloyd, White, and Stanton 1982).

Theoretically, there are three reasons why broods one year out of phase should never coexist sympatrically in the same woods: (1) The climatic aberration by which they supposedly arose would be expected to affect the entire population, as just stated. This reasoning does not apply to 4-year accelerations if these arise through effects of crowding, which could well affect only part of a patchily-distributed population. (2) The numerical response of predators (Murdoch and Oaten 1975) should fall heavily on any brood lagging one year behind another, probably eliminating the lagging brood. Escape from predator build-up is theorized to be the whole advantage of coupling periodicity with the long life cycle. It enables periodical cicadas to satiate predators on every emergence, and presumably accounts for their great abundance compared with non-periodical cicada species (Lloyd and Dybas 1966). Parasitoids such as the tiny wasp *Lathromeris cicadae,* for example, prey heavily on periodical cicada eggs during an emergence year (Marlatt 1907), but must have alternative hosts in other years. After four years, the numerical response would surely have dissipated itself, so a brood lagging by four years should not be eliminated by this cause. (3) Newly-hatched nymphs of the leading brood will settle underground and have the advantage of being already established by the time young nymphs of the lagging brood appear. Given that the cicadas are very abundant, the leading brood may preempt all the suitable feeding sites, leaving nothing for the lagging brood. This and predator satiation are the two basic assumptions used by the model of Hoppenstaedt and Keller (1976) to explain the origin of periodicity. Their model works well, but depends sensitively on the suitable choice of parameter values (May 1979).

White and Lloyd (1979) report a case in northern Kentucky where substantial numbers of cicadas emerged in 1975, the year *after* a dense emergence of Brood XIV in 1974. Presumably, this occurred because of malnutrition associated with extreme crowding—known from previous evidence (White and Lloyd 1975) to be a real possibility. Based on considerations (2) and (3) above, they predict that a new "Brood XV" will not become established sympatrically with Brood XIV.

There is evidence to suggest that considerations (2) and (3) above would not prevent the coexistence of broods four or more years apart. The same area in Kentucky has Brood X and XIV living sympatrically. Excavations of the nymphs (White and Lloyd 1979) show that they are living at different depths: Brood X below 15 cm, for the most part, and Brood XIV above. This is reasonable since the larger nymphs probably require larger roots and the greatest concentration of small roots is near the surface (Rogers 1940). This means, that 4-year-old nymphs may well have moved down to larger roots and would then not preempt feeding spaces from another brood lagging by as much as four years.

Based on these considerations, there is a priori reason to think that the carrying capacity of the roots of woody plants for cicada nymphs should be greater if the nymphs belong to two broods four or more years apart than if all cicadas belong to the same brood. This hypothesis was supported by the study of Simon, Karban and Lloyd (1981). This argument suggests that selection should favor 4-year jumps in the life cycle over 1-year jumps provided that the accelerating individuals are numerous enough to satiate predators.

Long Island Broods

Fig. 2 summarizes the existing information for Long Island. The patterns of stippling, cross-hatching, or discrete symbols identify the broods. Arabic numbers are keyed to place names for Brood XIV only. Locality records, dates, and sources of information are given in Appendix I. Notice that there is evidence for the presence of Brood II on Long Island (which is anticipated from its distribution on the mainland) but it occupied only the extreme western edge of the island across a narrow straight from Staten Island.

Fig. 3 attempts to place the broods of Long Island into the biogeographical context of those on the mainland. Ten broods are shown: five that occur on Long Island (XIV, X, IX, V, I) and five others (XI, VIII, VI, II, XV) that occur, or formerly occurred, nearby. Two of the broods found on Long Island (XIV, X) are also found in New Jersey, but the other three (IX, V, I) have their nearest mainland representatives 350 km or more away, in western Virginia, West Virginia, and Ohio. These, certainly, must be considered disjunct distributions.

The relevance of the other broods shown in Fig. 3 (XI, VIII, VI, II, XV)

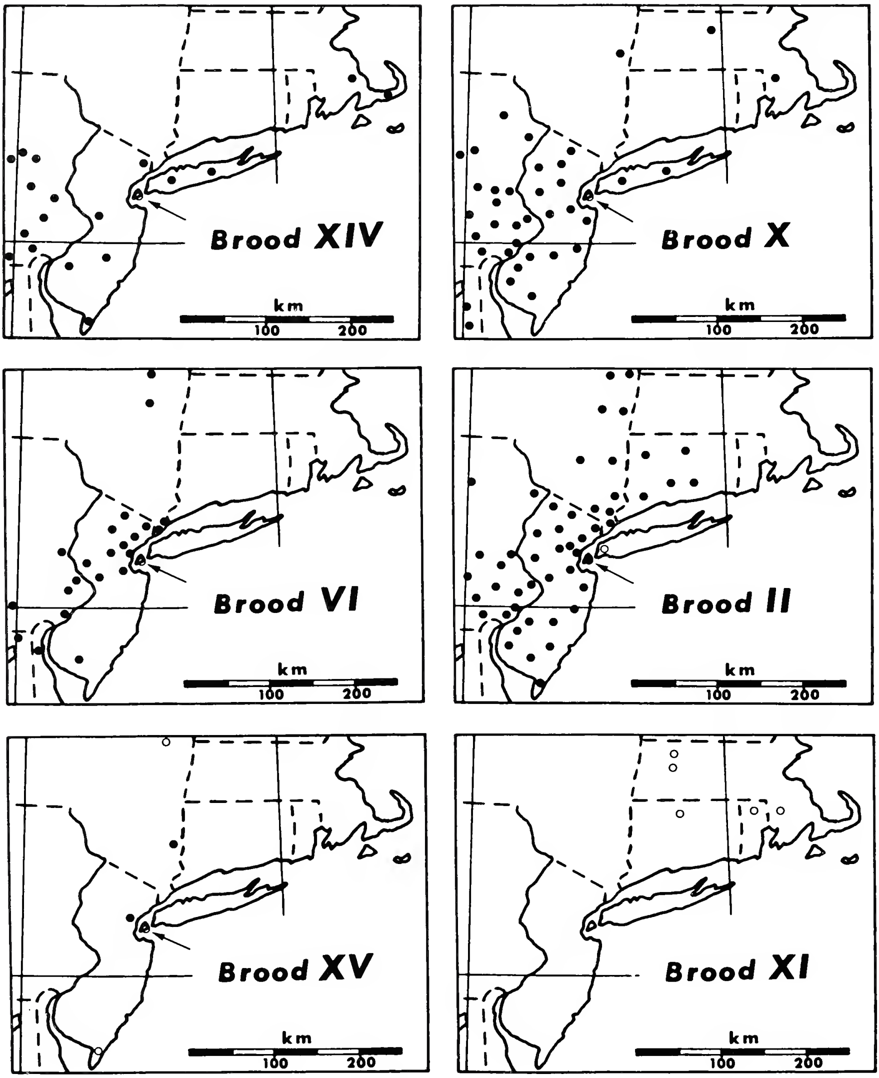
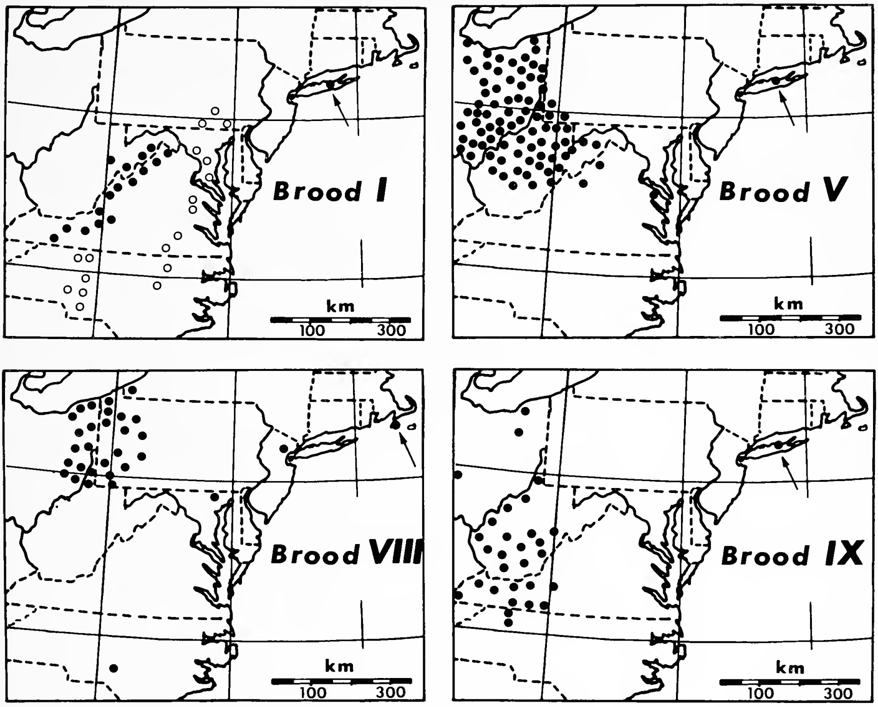


Fig. 3. Biogeography of periodical cicada broods in relation to Long Island, based on county records from Marlatt (1907). Some of these populations have subsequently become extinct; recently documented cases of local extinction are plotted as open circles rather than as solid dots. Left (above): local distributions near Long Island of the six broods on the "main sequence" of 4-year accelerations postulated by Fig. 1. All of these broods occur (or did occur) in the vicinity of Long Island (often with two or three occurring in the same county). The predominant brood on Staten Island (arrow) is II, but there are well-documented records of periodical cicadas having emerged at one time or another in synchrony with Broods XIV, X, VI, and XV (Simon 1979c). Right (facing page): complete distributions for four other broods—three of these occur on Long Island (I, V, IX) and one on Martha's Vineyard (VIII), indicated



by the arrows. These broods, according to Fig. 1, can all be derived from the "main sequence" broods by one or two 1-year accelerations, and in every case the main center of distribution of the brood is over 500 km from corresponding mainland populations.

can be judged in relation to Fig. 1. For example, Broods VI and II occur so nearby on the mainland that they may once have existed on Long Island, given rise to VI → V and II → I respectively, then later become locally extinct. On the other hand, Broods IX and X occur on Long Island (see Appendix I) so the progression may have been X → IX → V → I. The question is of unusual interest, since the two kinds of acceleration (1-year versus 4-year) are postulated to derive from very different causes.

The presence of Brood VIII on Martha's Vineyard (Fig. 3) is interesting. In this case, IX → VIII is the only reasonable derivation we can offer, since there is no evidence that a Brood XII ever existed. The records of IX on Long Island suggest that it may also have occurred on Martha's Vineyard at one time. Notice that the two broods on the end of the 4-year acceleration sequence, XV, and XI, are (or were) located not far from Long Island. Indeed, it can be said that the 17-year broods in southern New England and Long Island (with the exception of Brood XIV) are the most derived from the point of view of Fig. 1. Furthermore, if we allow the possibility of Brood

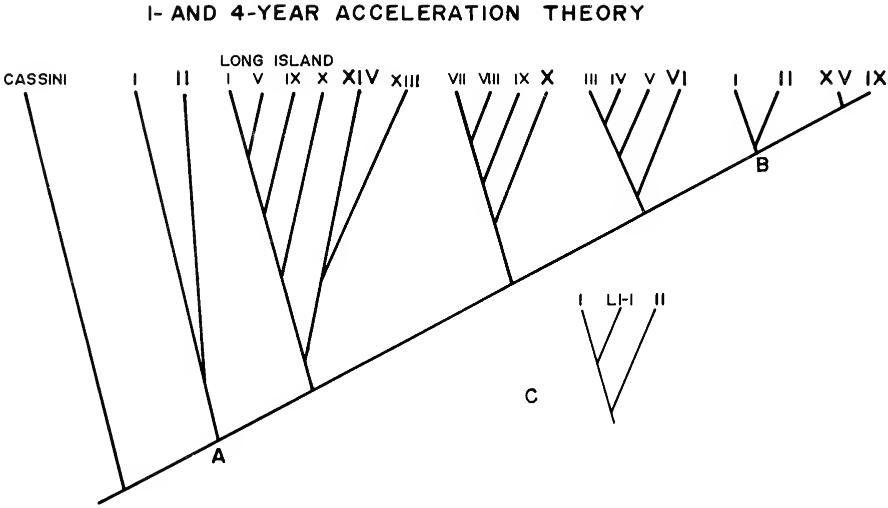


Fig. 4. A phylogenetic tree depicting the major events of Fig. 1. Large roman numerals represent broods derived via 4-year accelerations. Broods shown in parentheses in Fig. 1 are omitted from this figure. Small roman numerals represent broods formed via 1-year accelerations with the exception of the Long Island broods (see text for hypotheses of origin). "A" is the position of Broods I and II according to a separate Pleistocene refuge theory, while "B" shows the position of Broods I and II according to Fig. 1. "C" depicts Brood I plus the Long Island populations of Brood I (LI-I) as a monophyletic group.

XIV being polyphyletic, it is theoretically possible to derive the northeasternmost XIV populations from Brood XV by a 1-year acceleration as shown also in Fig. 1.

Fig. 4 summarizes, phylogenetically, the hypotheses of brood formation discussed above. Large roman numerals identify "major" broods which are largest and supposedly derived via 4-year accelerations. Smaller roman numerals identify broods derived via 1-year accelerations from larger broods. Broods I and II are shown in two positions on the tree: position "A" would result if I and II refuged separately during the Pleistocene (as suggested by Simon 1979a); position "B" would result if I and II were derived via accelerations from Brood VI (as suggested by Lloyd and Dybas, 1966). The Long Island broods are shown as derived from Brood XIV on Long Island.

Relationships of Brood XIV

Simon (1979a, b) demonstrated that both *M. septendecim* (Brood XIV) and *M. tredecim* (Brood XXIII) are allozymically homogeneous among populations sampled from a broad geographic range, but at the same time, different from each other and from conspecifics (*M. septendecim* Brood XIII, and *M. tredecim* Broods XIX and XXII). Data for thirteen populations of

Table 1. Allele Frequencies and Sample Sizes for Brood XIV, *Septendecim*.

		Allele frequency at each locality													
Locus	Allele	MA-A	MA-B	NY-B	NY-C	NY-D	NY-E	PA-A	MD-A	NC-A	NC-B	NC-C	KY-A	KY-B	χ^2
PGM	105	.055	0	.005	0	0	.005	.004	.011	.006	0	.008	0	0	
	100	.778	.750	.715	.756	.741	.772	.751	.780	.736	.803	.738	.767	.715	7.5 ns
	98	0	0	0	.005	0	0	0	0	0	0	0	0	0	
	95	.217	.250	.280	.239	.258	.222	.239	.209	.258	.197	.254	.233	.284	7.9 ns
	90	0	0	0	0	0	0	.005	0	0	0	0	0	0	
Sample size:		90	90	100	90	89	90	90	91	89	89	63	45	79	
αGPD-I															
	100	.244	.261	.320	.310	.258	.280	.256	.297	.275	.264	.274	.272	.231	
	95	.750	.739	.680	.690	.742	.720	.744	.703	.725	.736	.726	.728	.769	6.6 ns
	90	.006	0	0	0	0	0	0	0	0	0	0	0	0	
Sample size:		90	90	100	90	89	75	90	91	89	89	62	91	80	
βEST	100	.283	.247	.175	.260	.152	.206	.156	.185	.258	.292	.262	.280	.253	
	95	.717	.753	.825	.740	.848	.794	.844	.815	.752	.709	.738	.714	.741	30.5***
	90	0	0	0	0	0	0	0	0	0	0	0	.005	.006	
Sample size:		90	89	100	90	89	90	90	89	89	89	63	91	80	
MI	105	—	—	—	—	—	—	.078	.061	.044	.054	.033	—	—	
	100	—	—	—	—	—	—	.900	.939	.944	.932	.943	—	—	3.3 ns
MI	95	—	—	—	—	—	—	.017	0	.011	.014	.024	—	—	
	90	—	—	—	—	—	—	.005	0	0	0	0	—	—	

Table 1. Continued.

Locus	Allele	Allele frequency at each locality													χ^2
		MA-A	MA-B	NY-B	NY-C	NY-D	NY-E	PA-A	MD-A	NC-A	NC-B	NC-C	KY-A	KY-B	
Sample size:		—	—	—	—	—	—	90	90	45	74	61	—	—	
PHI	−95	—	.018	—	—	—	—	0	.006	.006	.011	0	0	0	
	−100	—	.982	—	—	—	—	1.000	.994	.994	.989	.991	1.000	1.000	7.3 ns
	−105	—	0	—	—	—	—	0	0	0	0	.008	0	0	
Sample size:		—	56	—	—	—	—	90	90	89	45	61	91	80	
NDH$_t$	110	0	0	0	.005	0	0	0	0	0	.005	0	0	0	
	105	0	0	.009	0	0	.005	0	.005	.055	0	0	.006	0	
	100	.978	.994	.982	.977	.967	.990	.989	.990	.967	.989	1.000	.977	.994	13.4 ns
	95	.022	.006	.009	.017	.033	.005	.011	.005	.028	.006	0	.017	.006	
Sample size:		90	90	100	90	89	90	90	90	89	89	61	91	80	

Allele frequencies, sample sizes, and heterogeneity χ^2 values for Brood XIV.*

* χ^2 calculations are explained in text and have n − 1 degrees of freedom. ns means not significant and *** means significant at the .001 level. Localities are identified to state by the standard two letter postal code. Within states localities are as follows: MA-A, Finney Lane, Centerville; MA-B, Churchill Drive, E. Falmouth; NY-B, Janet Drive, Terryville; NY-C, Tyler Avenue, Miller Place; NY-D, Deer Park; NY-E, Applecrest Drive, Mastic; PA-A, Peters Apple Orchard on PA 94; PA-B, on I-76, 1.6 mi N. Jct. PA-23; MD-A, University of Maryland Fruit Experiment Station, Hancock; NC-A, Wacovia National Bank, Ashville; NC-B, Spruce Pine High School, Spruce Pine; NC-C, on Blue Ridge Pkwy 1.5 mi N. Jct. US 70; KY-A, on KY 70, 1 mi E. Jct. Mammoth Cave; KY-B, on US 127, 4 mi S. Swallowfield.

Brood XIV are given in Table 1 (polymorphic loci only). Twelve of the enzyme loci studied were monomorphic. Of the seven polymorphic loci, only one (β-esterase) showed any among-population heterogeneity. Workman and Niswander's (1970) formula for the heterogeneity chi-square for allele frequencies was used as a test. As a check, heterogeneity G-statistics were also calculated (Sokal and Rohlf 1969) and gave identical results. Chi-square values for each polymorphic locus are given in Table 1.

Although β-esterase varied among populations, this variation ranged from only 0.709 to 0.848 (frequency of the most common allele). Note that four of the 13 populations sampled were located on Long Island (Terryville, Miller Place, Deer Park, and Mastic; see Fig. 2 for locations). Comparing these four to the other localities, we see a larger range within a 25 mile radius on Long Island (0.740–0.848) than is found between North Carolina and Massachusetts (0.709–0.753). Furthermore, the Long Island samples were all taken from very similar pine-oak woodlands; a habitat which differs very little from that of the Massachusetts samples and which differs a great deal from the diverse montane forests of the North Carolina samples. In other words, there appears to be no consistent trend in allele frequency at the β-esterase locus with distance, latitude, or habitat type; the small amount of variation that is present appears to be random. The Long Island populations do not differ as a group from the other eight populations sampled.

Analysis of periodical cicada morphology seems to show the same picture. Examination of 48 wing-vein characters shows that populations within broods differ very little in comparison to the differentiation which has occurred among broods (Simon 1982). Discriminant analysis based on these 48 characters could not distinguish populations, but broods were clearly distinct. When the results of the discriminant function analysis were graphed, the 95 percent confidence ellipses for all Brood XIV population means overlapped almost completely. Thus we see a striking degree of morphological and allozymic homogeneity within Brood XIV and no evidence to suggest polyphyly.

Long Island Brood I

As shown in Fig. 3, Brood I occupies a large section of the Shenandoah Valley of Virginia and near-by valleys in West Virginia. In 1978, we were interested to find a population of Brood I at Ridge, New York (on Long Island) which had been described in W. T. Davis' 1927 correspondence. Several other Long Island Brood I sites were described in Davis' publications and personal notes (see Appendix I) but we were unable to confirm these. We mapped the Ridge population (Fig. 5) and also documented the presence of Brood XIV whose eggnests occurred in the exact same trees (Simon et al. 1981). We surveyed the Brood I emergence area by driving and listening

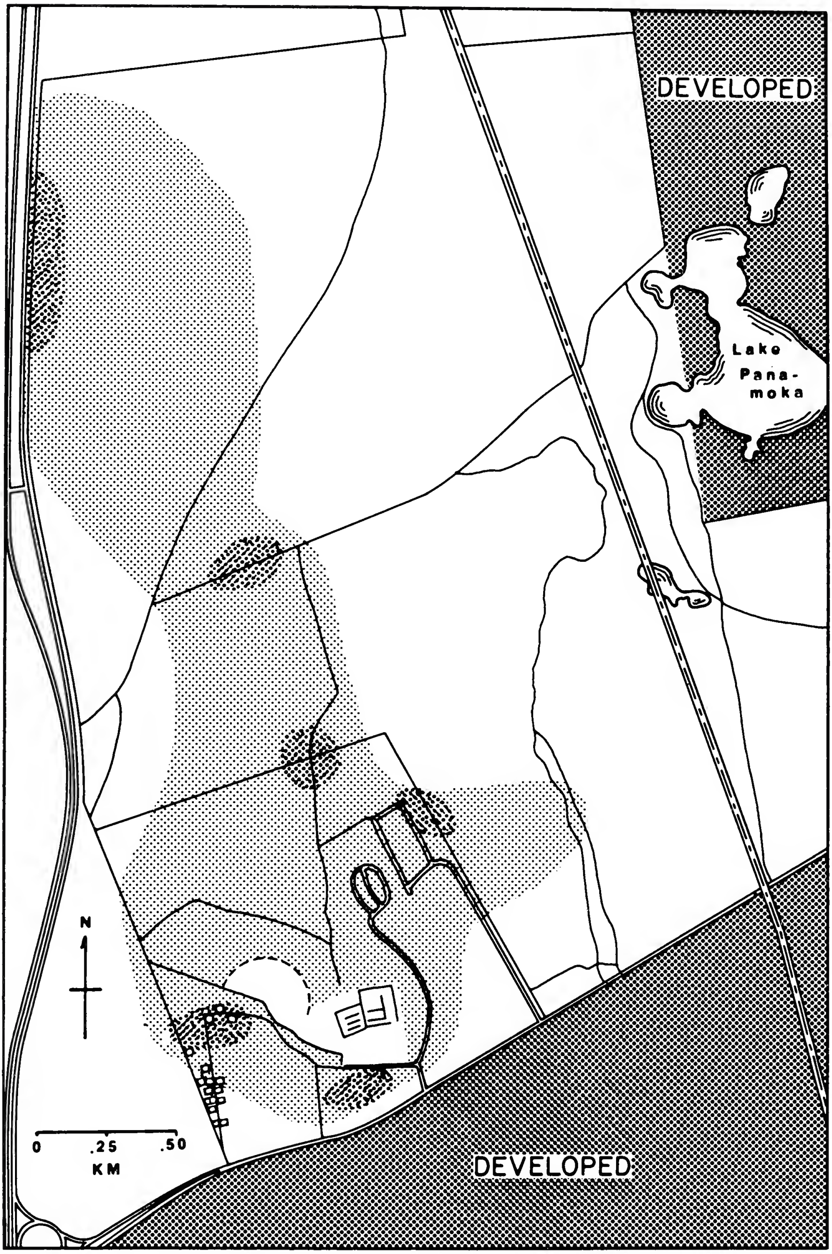


Fig. 5. Map showing the location of the study area near Ridge, Long Island. The William Floyd Parkway runs along the western edge of the map, Middle Country Road (New York Route 25) angles east-northeastward near the southern edge, and a power line runs roughly north-south just to the west of Lake Panamoka. Single lines are sandy fire lanes; double lines, paved. Areas marked "developed" are in housing; the remainder is sandy oak scrub. The oak

along the sand fire-lanes. Heavy chorusing centers of Brood I are shown in Fig. 5 by ellipses of heavier stippling among the light stipple. Broods I and XIV are the only two Long Island broods whose populations have been documented to occur in exactly the same trees. Our study site at Ridge is the only case where reproductive success of Long Island Brood I in successive generations has been verified. Notice from Fig. 2 that Brood XIV occupies a very large portion of Long Island.

The fact that Brood XIV is much more abundant in the area than is Brood I would suggest that I is derived from XIV. However, deriving I directly from XIV would be contrary to the theory (Fig. 1) which makes no provision for 4-year *decelerations.*

Given the evidence that Brood XIV on Long Island is not independently derived, the theory requires that we derive I from XIV by one of three pathways: XIV → X → VI → II → I, or XIV → X → VI → V → I, or XIV → X → IX → V → I (see Fig. 1). The third hypothesis is appealing in that there are now populations of Brood V, five or six kilometers northeast of our study site across Lake Panamoka (Fig. 2) and populations of Brood IX are known to have emerged very near there in 1918 (Appendix I; Fig. 2). Furthermore, there are a substantial number of Brood X populations on Long Island, one of which is directly south of our study site (Fig. 2). Brood VI has never been reported on Long Island and Brood II is only known from the westernmost corner of the island. In other words, the third hypothesis for the origin of Brood I is strengthened not only by the presence of the intermediary links but also by the complete absence of any other broods.

Allozymic and morphometric data.—The collection of adults from the Long Island Brood I population (LI-I) allowed us, for the first time, to examine a disjunct population, in this case separated by 275 km from the nearest recorded population of this brood and 475 km from the nearest extant population (Fig. 3). If this disjunct population was morphologically and/or allozymically distinct, we hypothesized that a phylogeny based on these data would place LI-I as the sister group of XIV rather than as the sister group of I.

A comparison of wing morphometric data (characters same as those illus-

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scrub is almost a pure stand of *Quercus ilicifolia,* which burns at erratic intervals and is seldom more than 1.5 m tall. Interspersed are occasional pitch pines (*Pinus rigida*) and white oaks (*Quercus alba*), 3–4 m high. Blueberries (*Vaccinium* sp.) and huckleberries (*Gaylussacia* sp.) are also found, as well as sweet fern (*Comptonia peregrina*), bracken fern (*Pteridium aquilinum*), and winged sumac (*Rhus copallina*). Judging from eggnest scars, Brood XIV emerged throughout the oak scrub area in 1974. Light stippling indicates the area where Brood I also appeared in 1978. The heavier dots within the light stippling represent the loudest chorusing centers of Brood I. Small squares in the lower left are quadrats sampled by Simon et al. (1981).

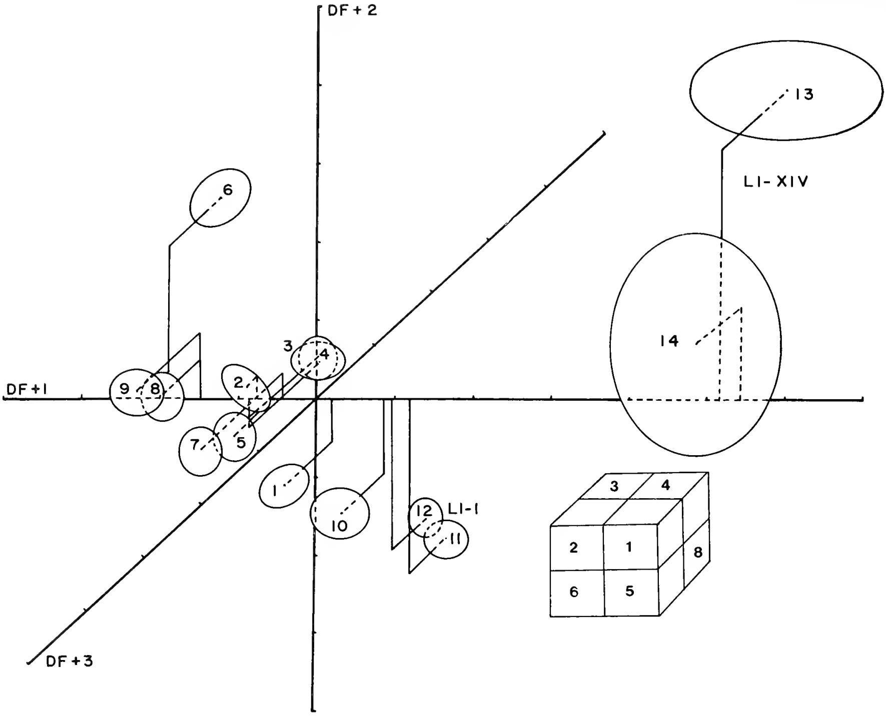

Fig. 6. Three-dimensional plot of brood mean scores of wing measurements on three discriminant function axes with 95 percent confidence ellipses about the means. Sample sizes are given in the text. If we number the octants as shown in the inset cube, then Broods I (ellipses 1–5) and II (ellipses 6–10) fall within octants 2, 3, 5, 6, and 7; LI-XIV (ellipses 13 and 14) falls within octants 1 and 4; and LI-I (ellipses 11 and 12) falls within octant 8. LI-XIV ellipses are larger due to smaller sample size per population.

trated in Simon 1982) for Broods I, II, XIV, and LI-I via discriminant function analysis is shown in Fig. 6. Sample size per population/number of populations were: 20/5, 20/5, 10/2, 20/2, respectively. Note that Broods I and II are not recognizable as two distinct groups; their populations intermingle even when plotted in three dimensions. Populations of LI-XIV and LI-I, on the other hand, are quite different from populations of Broods I and II and from each other (Fig. 6).

A phylogenetic tree was constructed using the wing morphometric data. Forty-eight wing vein characters were measured for four 17-year broods (sample size/number of populations): I (100/5), II (100/5), XIV (80/8), XIII (100/2), and LI-I (40/2); and one 13-year brood: XXIII (80/8). Five populations of *M. tredecassini* (90 individuals/5 populations) were measured to serve as an outgroup to root the tree. Many of these measurement characters were not significantly different ($P > 0.05$) among the broods examined. To

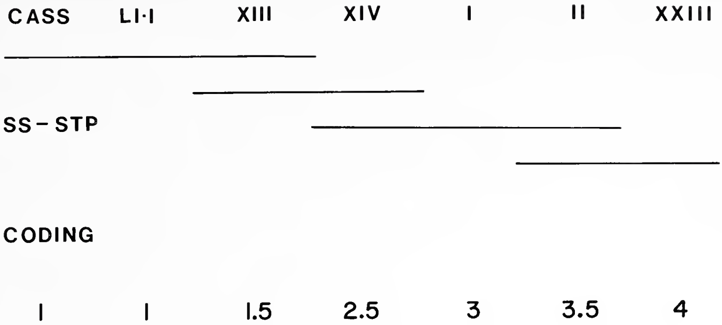

Fig. 7. An example of the coding procedure used for each of the 48 wing morphometric characters. The upper half of the figure depicts the bar diagram resulting from a sum of squares simultaneous test procedure (SS-STP) for a single character. Bars unite statistically homogeneous groups. The lower half shows the coding of the bars for that character. The coded information was used to create a phylogenetic tree using the Wagner procedure.

remove differences among populations which were not statistically significant, all broods which did not differ for a particular character were pooled. This pooling was accomplished by performing a posteriori grouping tests (sums of squares simultaneous test procedure, Sokal and Rohlf 1969) for each character and then coding the resulting bar diagrams (Simon 1983).

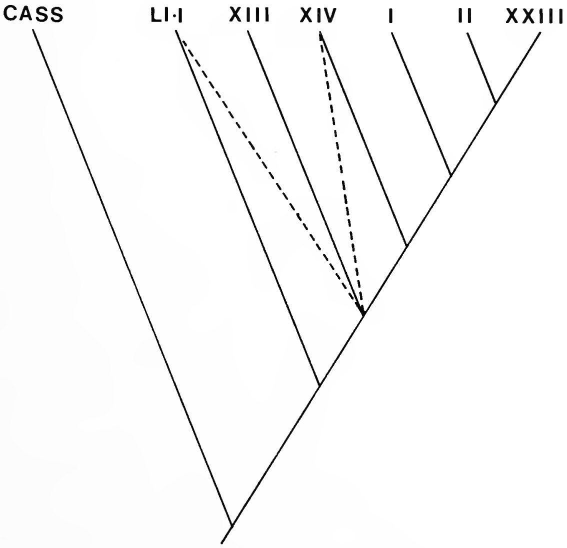

Fig. 8. Wagner phylogenetic tree based on wing vein characters. The shortest tree is represented by solid lines. Dashed lines indicate a phylogenetic hypothesis which is only 18 percent longer.

Table 2. Weighted average allele frequencies and sample sizes used in allozymic analyses. Very rare alleles are omitted from the table so that not all loci sum to 1.00. Heterogeneity chi-square (χ^2) values indicate that essentially no differentiation has occurred. Enzyme abbreviations are given in the text.

			PGM			α-GPD			β-EST			MPI			PHI		NDHt		
Brood	Sample size	N	95	100	105	90	95	100	90	95	100	95	100	105	100	105	95	100	105
XIV	1,095	13	0.241	0.754	0.004	0.001	0.726	0.273	0.001	0.771	0.228	0.013	0.930	0.055	0.995	0.004	0.014	0.984	0.003
I	288	3	0.221	0.782	0.007	0.000	0.752	0.248	0.000	0.844	0.156	0.003	0.966	0.031	1.00	0.000	0.009	0.983	0.008
II	384	6	0.254	0.740	0.006	0.000	0.717	0.283	0.000	0.821	0.179	0.010	0.961	0.029	1.00	0.000	0.010	0.981	0.010
LI-I	96	1	0.203	0.792	0.005	0.000	0.708	0.292	0.000	0.812	0.188	0.021	0.969	0.010	0.964	0.036	0.000	0.985	0.010
χ^2_{3df}			3.4*	4.6*			2.6*	2.5*		19.7**	19.1**		19.9†	18.1†	45.6††			0.4*	6.6*

* Not significantly heterogeneous.

** Significantly heterogeneous at the 0.001 level but I, II, and LI-I are not significantly heterogeneous and LI-I and XIV are not significantly heterogeneous.

† Significantly heterogeneous at the 0.001 level but I, II, and LI-I are not significantly heterogeneous and XIV and II are not significantly heterogeneous.

†† Significantly heterogeneous at the 0.001 level but I, II, and XIV are not significantly heterogeneous.

An example of the coding procedure is given in Fig. 7. This procedure retains more information than previously proposed coding procedures (Mickevich and Johnson 1976). The coded data was used to construct a phylogenetic tree using the Wagner-78 program written by J. S. Farris (see Farris 1970). The resulting tree is shown in Fig. 8.

The phylogenetic tree based on wing morphometric data places the LI-I populations in the most ancestral part of the tree. Because it is so unlikely that the small population of Brood I on Long Island could be a remnant of the ancestor of Brood XIV, which covers much of the eastern United States, alternative phylogenetic hypotheses were examined. Alternative trees which placed LI-I as the sister group of I and II or XIV were examined but proved to be less compatible with the data (i.e., produced much longer trees). It was, however, possible to create a tree in which Broods XIV, XIII, and LI-I all originated at approximately the same time. This tree (shown by dotted lines in Fig. 8) was only 18 percent longer than the shortest tree. No significance tests exist for comparison of phylogenetic trees.

The morphometric phylogenetic hypothesis generated above could be explained by the following evolutionary scenario. Brood XIV was the ancestral brood and at one time covered most of the eastern United States. Very early in its history it gave rise to Broods XIII and LI-I. Broods I and II were later derivatives followed by the conversion of southern populations into 13-year Brood XXIII. This scenario is compatible with Lloyd and Dybas' (1966) scheme shown in Fig. 1.

Allozymic analyses of Broods I, II, LI-I, and XIV were less informative. Table 2 presents the results. Heterogeneity chi-square values indicate that essentially no differentiation has occurred. The enzymes α-glycerolphosphate dehydrogenase (α-GPD), phosphoglucomutase (PGM), and nothing dehydrogenase (NDHt) are homogeneous in allele frequency across all broods. Esterase (β-esterase) shows significant differentiation but Broods I, II, and LI-I taken as a group are not significantly heterogeneous and LI-I and XIV taken as a group are not significantly heterogeneous. Mannosephosphate isomerase (PHI) is significantly heterogeneous across all broods but I, II, and LI-I and XIV and II are not significantly heterogeneous. Phosphoglucose isomerase (PGI) is significantly heterogeneous across all broods but I, II and XIV are not significantly different as a group. In other words there is little allozymic information on which to base a phylogenetic tree.

Clearly, additional data are needed. Populations of LI-V will be collected in 1982 in addition to Brood V from Ohio, West Virginia and Virginia. These cicadas will be analyzed both allozymically and morphometrically. We can say, however, that LI-I is morphologically different from Broods I, II and XIV and that a phylogenetic analysis suggests that LI-I evolved independently of Brood I in Virginia.

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Appendix I

This appendix summarizes Long Island periodical cicada locality records. This compilation is useful as many of the records are not conveniently accessible being contained in newspapers, private notes, and old, not widely circulated journals. Localities are organized by brood in chronological order.

Brood I.—**1910:** ". . . in the Half Way Hollows near Wyandanch, Long Island" at the Holmes farm, "they had been very numerous . . . . The species occurred in great numbers in the same territory [same trees] in 1906 . . . .

In the Long Island locality [in 1910] they were certainly numerous enough to lay a great many eggs, and may possibly establish a new brood" (Davis 1910). "It was ascertained, however, that the cicadas had occurred in great numbers in still another locality in 1910, in a place further to the north [of the Holmes farm] and nearer to the Dix Hills" (Davis 1911). **1927:** In a letter to W. T. Davis from Albert A. Arnold dated July 11, 1927, Arnold reports *Magicicada* at two localities: 1) Along Middle Island Road (from Coram) near Camp Upton (now Brookhaven National Laboratory) "covering all the scrub oaks"; 2) On the road leading from Coram to Riverhead on the flat portion of land just east of "the road which formerly led into Camp Upton property and extending for quite some distance on both sides of this road." A reference in W. T. Davis' personal notes explains that *Magicicada* collected from Camp Upton on June 15, 1927 were "found in abundance." **1944:** In a letter to W. T. Davis dated June 22, 1944, Roy Latham listed the following periodical cicada localities: 1) Dix Hills in between Commack Road and Deer Park Avenue south of 25; 2) on 25 several miles east of Ridge, on the north side of the road, "a small colony"; 3) on 25 near the junction of 25A (east of Ridge) and for a mile farther. "Just east of there" he reports "a large colony on both sides of the road—greatest abundance on the north"; 4) Along old country road, north of Riverhead and on 25. Scattered individuals were seen "up to two miles east of Riverhead."

Brood II.—**1911:** "The 17-year cicada occurs on Long Island, New York, in numbers at the most unexpected times .... Brood 2 [1911] was in its usual abundance on Staten Island and in the valley of the Hudson, but on Long Island very few of the cicadas were found .... But one or two individuals were reported from the western end of the island during 1911" (Davis 1915). **1945:** We have found no reference to Brood II in 1945 other than this strange article from *Newsday,* May 30, 1974—"Everyone remembers Brood II, which covered Long Island in 1945 and left newspaper editors, pesticide manufacturers and other disaster-lovers counting the years until it was due again in 1962. Only, Brood II did not keep its appointment." **1962:** On June 14, 1962, *The New York Times* published a small article entitled, "Scientists Mystified as 17-year Locust Shuns Two Counties." In this article they commented on the extreme abundance of cicadas in the Hudson Valley, metropolitan New Jersey and Staten Island and added, "but in Westchester and Nassau counties, the schedule notwithstanding, the shrill cry of the locust has not been heard."

Brood V.—**1914:** Davis (1915) wrote, "Returning to Wading River on July 24 [1914], we noticed from the car window, about a mile to the west of the railroad station, many oaks and other trees on the north side of the track in which the cicadas had laid their eggs, causing the death of the smaller branches . . . we found that the seventeen-year cicada had been very common about Deep Pond and on the easterly side of Long Pond [now Lake Panamoka]

. . . . Under the date of June 9, 1914, Dr. Frank Overton . . . wrote me that the seventeen-year cicadas were spread over several square miles northwest of Calverton, about two miles from the Deep Pond locality mentioned above. He said that he had taken particular notice of them for three miles along the Riverhead, Coram road about one or two miles north of the station. They reached all the way to the elevated lots and even scattering ones were found nearly into Riverhead." Davis (1924) presumably reasoning from 1914 records predicted that, Brood V would appear "in 1931 in the Half Way Hollow Hills, also in the hills north of Holbrook and at Wading River." **1965:** On June 6, 1965 *The New York Times* noted that, ". . . 17-year locusts were reported this week in the Lake Panamoka area of Wading River and a vast peach orchard off North Road in Calverton." *Newsday* also carried the story: ". . . the insects have appeared this year on Long Island in Calverton and around Lake Panamoka near the Riverhead-Brookhaven town line." Brewster (1965) reported that ". . . May 23rd the 17-year locust (periodical cicada) emerged in wooded areas at Lake Panamoka and several days later at Calverton." A population of cicadas was noted at the Transient Camp Area of Wildwood State Park, Wading River and also across from the picnic and parking areas (J. R. Wildt pers. comm.). They were also seen along River Road in Calverton, in Lewin's Peach Orchard adjoining Wildwood State Park (R. H. Brewster pers. comm.), and on 25A approximately one mile southeast of the junction of Sound Avenue (John Waskewicz pers. comm.) in that same year (1965). In 1982 they were again seen in Wildwood State Park (Camping area E and adjoining Lewin's Orchard). They were very abundant east of the junction of 25A and 25. Oviposition was relatively heavy along the roadside but no flagging was observed.

Brood IX.—**1918:** Davis (1920) found periodical cicadas "in the woods along the road between Manorville and Wading River." He collected some "about one mile north of the Middle Country Road." These were the only ones observed in 1918 and none were there in 1919.

Brood X.—**1902:** Davis (1920) quoted the eighteenth report of the N.Y. State entomologist (1902, p. 113) as follows, "The insects were observed . . . at Wantagh, Nassau Co., also between Massapequa and Amityville, between Sayville and Oakdale, east of Patchogue to Brookhaven and also to the north of Medford and Holtsville, and a small brood [sic] northeast of Riverhead, all in Suffolk Co." Davis (1907) reported that although a friend had seen hundreds of exuviae of the 17-year locust in Prospect Park, Brooklyn, he had only obtained three adults and he "attributed their scarcity to the English Sparrow." **1919:** *The New York Times* of June 17th 1919 (p. 25: 3) talked with farmers in the vicinity of Farmingdale, Bethpage, and Massapequa who reported thousands of cicadas doing damage to fruit trees and other hardwoods. Old residents claimed that 17 years before they were not nearly so numerous. Davis (1919) recorded "17-year cicadas singing at Mastic, L.I. during the first week of June." In another publication (Davis 1920) he noted them as occurring on South Country Road just east of Carman's River, and in the woods just east of Patchogue; also from Wantagh to Farmingdale and as far north as Central Park on Long Island; finally, north and east of Massapequa rail road station. **1936:** *The New York Times* (June 12, 1936, p. 4:7) reported that the cicadas were found "first in Carmen Ave., Farmingdale . . . since then the swarms have been reported at Massapequa, and all through Suffolk scrub oak along the Motor Parkway from Medford westward to Farmingdale." They were also seen along the Sunrise Highway in Massapequa Park. **1970:** *Newsday* (June 5, 1970, p. 12) lists two exact localities Skylark Drive (Holtsville) and Springdale Drive (Ronkonkoma). They explained that "officials of the State Conservation Department and County Agricultural Extension Service said . . . that they have received hundreds of complaints this month about the insects. Most of the calls have come from an area including Ronkonkoma, Holtsville, Islip, and Sayville, where the influx is concentrated." The same newspaper (June 23, 1970) reported 17-year cicadas in Bohemia on eighth Street near the South Side Sportsman's preserve. They must have been abundant because, "50 Bohemia residents . . . signed petitions appealing for help to fight the alarming problem of swarming cicada locusts [sic]."

Brood XIV.—**1906:** From personal observation and from other sources, Davis (1923) discovered that the 1906 Brood XIV covered "in a general way territory along the north shore from Oyster Bay to Wading River, extending south to Farmingdale and eastward through the central portion of the island to Manorville. There were also colonies at Moriches and Eastport." Davis (1907) additionally noted that cicadas were collected in Yaphank in 1906 from the same locality in which they were exceedingly abundant in 1855. **1923:** Davis (1924) reported that "during the summer [of 1923] I received . . . considerable information regarding the distribution of [Brood XIV] . . . . The area already given for the appearance of the brood in 1906 was almost exactly duplicated." In the same paper, Davis mentions finding two species (*M. septendecim* and *M. septendecula* from the descriptions) at the Holmes farm near Wyandanch. "The large form extended southward to the railroad and beyond." This locality is important because Davis reported finding Brood I in the same apple trees in 1910 and 1944. *The Brooklyn Eagle* (June 5 and 6, 1923) noted that cicadas were heard in Yaphank and Camp Upton on the previous Saturday. Among Davis' personal notes and letters, we found the following exact locality descriptions: 1) May 30, 1923 F. M. Schott saw many cicada openings in the ground and later heard them in Pinelawn and Wyandanch; 2) Arthur H. Helme saw cicadas "in great numbers 1 mile east of Port Jefferson between Port Jefferson and Crystal Brook at the place known as Old Place (letter of June 6). On June 14 (in litt.) they were still emerging at Belle Terre and there was a colony at Middle Island. Helme also noted great numbers of these insects from a point southeast of Port Jefferson Station all along the route from there to Rocky Point, along the wooded stretches south of the new state road, and at some spots extending north of the railroad; 3) Edward Bell (letter of June 18, 1923) said that the cicadas were continuous along the Motor Parkway from Farmingdale to the road running from Smithtown to Islip; 4) J. Nichols (letter of June 20, 1923) reported seeing the cicadas in the woods boarding the Mastic railroad station; 5) Roy Lantham (letter of August 24, 1923) searched the island from Orient to Calverton and never found them east of Calverton; 6) Finally, E. S. Miller (letter of September 12, 1923) summarized, "they seemed to work in a strip across the island from Rocky Point to South Setauket in width and thence across the island through Ridge, Middle Island and Coram, thence across to the south side—Moriches to Brookhaven (worst from Ridge to Coram). **1957:** *The New York Times* (May 28, 1957) notes "the heaviest infestation is reported in the Huntington-Deerpark area. None has been reported in Nassau County." **1974:** *Newsday* (May 30, 1974) listed two street addresses (52 Livingston St., Deer Park; 171 Eastwood Ave., Deer Park) and said that county agents received approximately 350 calls from "an area ranging from Hicksville in the west to Mastic and Port Jefferson in the east, with a concentration from the Medford and Dix Hills–Deer Park area." *Newsday* (May 31, 1974) reported cicadas at 19 Deer Lane, East Setauket. The following list of localities was compiled in 1974 (1 = personal observation, 2 = record of county agent, 3 = record of exterminators): Babylon (3), Belle Terre (1), Bohemia (2, 3), Brentwood (3), Brookhaven Labs (1, 2), Calverton (3), Center Moriches (2), Coram (1, 2), South Commack (1, 3), Deer Park (1, 2), Dix Hills (1, 2), East Setauket (1, 2, 3), Farmingville (2), Hicksville (2, 3), Manorville (2), Massapequa (3), Mastic (1, 2), Medford (3), Middle Island (3), Miller Place (1), Patchogue (2, 3), Port Jefferson Station (1, 2), Ridge (1, 3), Riverhead (2), Rocky Point (3), Ronkonkoma (2), Shirley (3), Sound Beach (2), and Terryville (1, 2).

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BOOK REVIEWS

The Pentatomoidea (Hemiptera) of Northeastern North America with Emphasis on the Fauna of Illinois. J. E. McPherson. Southern Illinois University Press. 1982. 240 pp. $30.00.

The field of hemipterology, like many others in entomology, suffers not so much from a lack of research, as from a lack of assimilation. The present book provides a compendium of biological information on our native stinkbugs and their allies. In all the book treats 120 pentatomoid species, approximately one-third of the Nearctic fauna. The geographical coverage is the northeastern quadrant of North America; those states and provinces to the north and east of Missouri.

The book is very much in the tradition of Blatchley's "Heteroptera of Eastern North America" and Hart's "Pentatomoidea of Illinois." In the years since the publication of these earlier works virtually every tribe and large genus in the superfamily has seen some revision. McPherson's book updates the nomenclature and provides keys with illustrations for the identification of species.

The books greatest value, however, is in the presentation of detailed ecological data, gleaned from an extensive but scattered literature on the subject. This information, including food plants (or prey), behavior, seasonality, distribution and parasites, is presented with ample documentation in an objective and scholarly manner. Host plants are not simply cited, but observations on abundance, whether or not the insect was actually seen feeding, and if immature stages were present, are also included. This attention to detail precludes the readers often time-consuming task of tracking down the original source. Nevertheless, a useful and voluminous bibliography has been appended.

There are some problems with the key to the genera of Pentatomini, but these problems will remain until generic distinctions have been clarified by future taxonomic work. The keys do work better than those presently available. In this reviewer's opinion at least some of the space (22 pages) devoted to Illinois county records could have been put to better use with figures. There is a complete lack of habitus drawings, and the few body outlines provided (e.g., *Rhytidilomia senilis*) only vaguely resemble the insects intended.

This book is obviously the result of painstaking research, and these minor problems do not detract from the main value of the book; an informative and up-to-date reference on the biology of the pentatomoid Hemiptera.

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The American Cockroach. William J. Bell and K. G. Adiyodi, eds. Chapman and Hall, London-New York, and Methuen, New York. 1981. 529 pp. $65.00.

The Laboratory Cockroach. W. J. Bell. Chapman and Hall-Methuen. 1982. 161 pp. $13.95.

There exist 47 species of cockroaches (*Periplaneta*) and four occur in the United States, but to non-experts it will come as a surprise that none of these are endemic to America. The name of the cosmopolitan American cockroach, *P. americana,* is misleading, as this insect is of African origin. The importance of cockroaches cannot be overemphasized to entomologists. This large volume, edited by Bell and Adiyodi, provides an integrated account of the biology of *P. americana.* Eighteen authors contributed 16 chapters that are up-to-date and written with authority. The authors describe the distribution, life cycle and biologic importance, osmoregulation, excretion, fat body composition and metabolism, nervous system, neurosecretion and hormones, sense organs, rhythms, muscular activity, reproduction, pheromones, behavior, embryonic and post-embryonic development, and regeneration. The chapters give an excellent indepth review and they contain a wealth of information about nearly all aspects of interest to those working with cockroaches. Each chapter is concise and the information presented in a critical manner. The more than 1,250 references are combined at the end of the volume. A short subject index is provided. The volume is well planned and edited. It will prove quite valuable to entomology students and teachers. "The Laboratory Cockroach" nicely supplements the authoritative book, providing lab exercises on the anatomy, nutrition, circulation, metabolism, reproduction, embryogenesis, regeneration, metamorphosis and behavior. I missed the inclusion of exercises dealing with cellular and molecular aspects. The manual can be recommended highly for entomology courses.

Karl Maramorosch, *Rutgers—The State University*

Plant Protection: An Integrated Interdisciplinary Approach. Webster H. Sill, Jr. Iowa State University Press. 1982. 297 pp. $23.95.

This unique book brings together aspects of entomology, plant pathology, nematology and weed science, as they pertain to plant protection. The extensive plant protection experience of the author, who has worked for many years as consultant in the tropics of India, the Philippines, and Taiwan, provided the background for this very readable and useful text. The book is aimed at practicing plant protection workers, at entomologists and plant pathologists, as well as students at colleges and universities. In the first chapters political, social, and economic factors of plant protection, quarantine, storage and marketing are discussed. Monitoring and forecasting of outbreaks and the use of computers are stressed. The chapter on chemical control of insects also deals with pesticides, pheromones, juvenile hormones and insect sterilants. A separate chapter is devoted to pesticide compatibility and toxicology and another chapter to biological control of arthropods, diseases, nematodes, weeds and animal pests. Other chapters cover in detail biological control by antagonism and synergism, breeding for resistance to arthropods, and vertebrate pests. Two separate chapters are devoted to integrated and combined controls, using weed and pest, as well as nematode and pest controls. The volume concludes with a list of cited, and of other, useful references, and with a subject index. As a whole, this volume is a well written contribution that brings together for the first time all aspects of plant protection. In my opinion this book should be of wide interest to entomologists engaged in biological, chemical, and integrated control and I recommend it with enthusiasm to all who work in the field of crop protection.

Karl Maramorosch, *Rutgers—The State University*

The Ecology of Pests—Some Australian Case Histories. R. L. Kitching and R. E. Jones, eds. Published by CSIRO, Melbourne. 1981.

"The Ecology of Pests," edited by Kitching and Jones, is a soft-cover book that comprises review articles on pests found within Australia. The editors have not attempted to include all of the major pests in Australia but instead have selected pertinent examples of contemporary pest ecology. The pests included are organisms of rather diverse life history patterns. Most of the case histories focus on insects (aphids, codling moth, light-brown apple moth, mosquitoes, Australian bushfly, cabbage butterfly and the *Sirex* woodwasp) but there are chapters on the skeleton weed, kangaroos and the "crown of thorns" starfish. Though these pests are discussed from the Australian perspective most are introduced species and will be of interest to ecologists familiar with these species elsewhere in the world. There are interesting historical discussions on the introduction of the organism to Australia (if it is an alien species) and how it came to be regarded as a pest. The chapters illustrate the type of information needed to evaluate the pest status of an organism and to develop control measures that are more specific and, in the long run, more effective than chemical pesticides alone.

The contributors are affiliated with the CSIRO or universities within Australia. The authors present a general overview of the current status of the pest species and have had considerable research experience with the pest that they discuss. Most have used the life-system analysis approach and some present formal models of the ecological processes that affect the population dynamics of the pest. Using modern concepts, the contributors demonstrate how data collected in the field and the laboratory can be integrated to interpret and analyze field populations.

This book will be of interest to ecologists, entomologists and agriculturists. Most of the data presented result from field studies but results from laboratory experiments are also given. Natural enemies of the pests receive adequate attention and their potential role as biological control agents is discussed. The text is carefully edited and well supplemented with figures and tables. The subject index is good and chapter references are provided. Thus, this book will be useful to students and serve as additional reading material for courses on experimental ecology, field ecology and integrated pest management.

Timothy J. Kurtti, *Waksman Institute of Microbiology, Rutgers University*

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INDEX TO SCIENTIFIC NAMES OF ANIMALS AND PLANTS
VOLUME XC

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3. Non-parasitic insect species in close proximity to active bee nests. p. 184.
4. The pests of major crops and their control measures. pp. 198–200.
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A REVISION OF THE GENUS *LINCUS* STÅL (HEMIPTERA: PENTATOMIDAE: DISCOCEPHALINAE: OCHLERINI)

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Abstract.—The genus *Lincus* is redefined and *Minilincus* Ruckes, 1958, placed in synonymy. The 30 known species of *Lincus* are described or redescribed and a key provided to assist in their recognition. New species are: *anulatus, breddini, convexus, croupius, fatigus, incisus, laminatus, leviventris, manchus, modicus, operosus, repizcus, singularis, sinuosus, substyliger, tumidifrons, vallis, vandoesburgi* and *varius.*

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The genus *Lincus* was last defined by Stål (1872) in a key to related genera. At that time the genus was monotypic, based on *Pentatoma rufospilota* Westwood, and characterized largely by an elongated lobe at each anterolateral angle of the pronotum. The form of these lobes no longer distinguishes *Lincus* because among species subsequently and correctly added to the genus the pronotal lobes vary much in shape and degree of development. A revision of *Lincus* is desirable not only to redefine the genus but also to lessen the difficulty of identifying the contained species, most of which have been unrecognized previously.

The genus is meagerly represented in collections, and rare is the series taken at the same time, unless at a light, that contains both sexes. Consequently, knowledge of geographical distribution and variation is sketchy, and the correct association of sexes becomes a greater problem than usual, especially so because most species are poorly endowed with useful taxonomic characters other than the genitalia. As specimens of the genus accumulate in collections, so too should information on distribution and variation as well as evidence to corroborate or refute my conclusions with regard to the association of sexes.

Lincus Stål

Lincus Stål, 1867, p. 524.
Minilincus Ruckes, 1958, pp. 14–15. **New Synonymy.**

Type species. Lincus: Pentatoma rufospilotus Westwood, 1837. *Minilincus: Minilincus parvulus* Ruckes, 1958.

Labium originating behind imaginary plane bisecting head at anterior limit of eyes when viewed ventrally and perpendicularly to longitudinal axis of thorax and abdomen; second rostral segment extending a little past mesocoxae; apex of rostrum reaching penultimate or ultimate abdominal segment. Antennae 5-segmented, basal segment reaching or surpassing apex of head. Juga as long as or longer than tylus, sometimes contiguous apically. Length of head before ocelli 0.6–0.8 of width across eyes. Anterolateral angles of pronotum usually developed into prominent lobe, this sometimes expanded apically. Scutellum longer than wide at base, 0.4–0.5 as wide at distal end of frena as at base. Costal angle of coria extending past apex of scutellum. Metasternum flat or weakly tectiform mesially. Pygophore deeply and broadly emarginate mesially; a hemispherical impression present mesially between bottom of pygophoral emargination and inferior ridge (Fig. 2).

Comments. Ruckes (1958) separated *Minilincus* from *Lincus* on the basis of smaller size, lighter color and reduced pronotal lobes. These differences are of specific value only and *Minilincus* is therefore considered to be a junior synonym of *Lincus.*

Those few species of *Lincus* of which sufficient specimens were available for dissection share several characteristics that may be common to the genus. These characteristics are excluded from the generic description because of the meagerness of the evidence.

The proctiger is essentially tubular, usually duck-bill shaped, with a ventral opening (Figs. 39, 47, 99); it often protrudes well beyond the posterior pygophoral margin (Figs. 48, 112). The parameres are relatively small, not visible within the genital cup, and doubtfully functional (Figs. 5, 38, 102). The aedeagus is typically discocephaline, heavily pigmented and sclerotized excepting the conjunctiva, which is restricted to a sheath around the projecting portion of the ejaculatory duct; the ejaculatory duct emerges subapically and ventrally (Figs. 4, 42, 103).

The spermathecal bulb is spherical with 3 equidistant appendages that curve basad and, viewed terminally, clockwise (Figs. 43, 44).

Among ochlerines, the only genera with a flat or weakly tectiform metasternum are *Lincus* and an unnamed genus. The latter genus differs from *Lincus* in that the costal angles of the coria project little if at all caudad of the scutellar apex, and the scutellar width at the end of the frena is about 0.6 the basal width rather than 0.5 or less as in *Lincus.*

The subfamily and tribe to which *Lincus* belongs have been characterized recently (Rolston and McDonald, 1979; Rolston, 1981).

SPECIES GROUPS OF CONVENIENCE

As an aid to identification, the 30 known species of *Lincus* may be arranged in species groups of convenience.

The "hatchet-lobed" group of 9 species has the anterolateral pronotal angles enlarged into lobes that are expanded subapically (into a form which I fancy resembles a hatchet blade) or that are broad throughout their length (Figs. 1, 12). *L. convexus, croupius, fatigus, incisus, operosus, securiger, sinuosus, spathuliger* and *vandoesburgi* belong in this group. Most of these species have relatively large eyes, the width of each eye being equal to or greater than one-half of the interocular width.

The "swollen head" group is readily recognized by the tumescent vertex of the head. Included here are *L. parvulus, singularis* and *tumidifrons.* This is an artificial assembly if ever there was one.

In the "little-eyes" group the width of each eye is less than one-half of the interocular width. This group consists of 7 species: *L. armiger, discessus, leviventris, manchus, modicus, repizcus* and *varius.*

In the "big-eyed" group of 10 species, by contrast, the width of each eye is equal to or greater than one-half of the interocular width. The included species are *L. breddini, dentiger, lamelliger, laminatus, lobuliger, rufospilotus, styliger, substyliger* and *vallis.*

Finally, there is *L. anulatus,* which stands by itself as the only relatively gaudy member of a drab genus. The femoral and tibial bands distinguish this species, which refuses to fall neatly into any of the above species groups.

Too much should not be inferred from the above groupings with respect to phylogeny. The ancestral form of *Lincus* presumably resembled *L. discessus* and other species of the "little-eyed" group without notably developed pronotal lobes, but the lines of evolvement from this form are unclear. Enlargement of the anterolateral pronotal denticles into lobes and widening of the eyes did not go hand in hand. In both the "little-eyed" and "big-eyed" groups there is considerable variation in the degree of lobe development, and although most species in the "hatched-lobed" group have enlarged eyes, others do not. The most parsimonious hypothesis regarding intrageneric lineage is that either pronotal lobe enlargement or eye widening evolved more than once, as did the tumescent vertex.

KEY TO *Lincus* SPECIES

1.	Pronotal lobes expanded subapically, if expansion slight then each lobe wider than anterior–posterior diameter of an eye (Figs. 1, 12)	2
–	Pronotal lobes parallel sided or tapering toward apex, if slightly expanded subapically then much narrower than anterior–posterior diameter of an eye (Figs. 30, 34)	10
2(1).	Pronotal margins caudad of lobes expanded on each side into obtuse projection (Figs. 1, 8)	3
–	Pronotal margins sinuous or straight (Figs. 10, 12)	4
3(2).	Second antennal segments about half as long as first, incision between lobe and anterolateral margin of pronotum extending mesad little beyond lateral limit of eye (Fig. 1)	*vandoesburgi,* new species
–	Second antennal segments subequal to first in length; incision extending mesad to middle of eye (Fig. 8)	*incisus,* new species
4(2).	Second antennal segments about half as long as first	*spathuliger* Breddin
–	Length of second antennal segments subequal to or greater than first	5
5(4).	Pronotal lobes strongly deflexed	6
–	Pronotal lobes horizontal or reflexed	7

6(5). Pronotal lobes strongly expanded subapically (Fig. 10); juga contiguous before tylus ..... *fatigus,* new species
– Pronotal lobes weakly expanded subapically, broad throughout their length (Fig. 12); juga little longer than tylus ..... *croupius,* new species
7(5). Small species, about 10 mm or less in length 8
– Larger species, more than 11.5 mm in length 9
8(7). Anterolateral pronotal margins strongly sinuous (Fig. 16); margins of mesial pygophoral emargination produced anteromesad on each side at dorsal limit of emargination (Fig. 17) ..... *sinuosus,* new species
– Anterolateral pronotal margins moderately sinuous (Fig. 19); margins of mesial pygophoral emargination uniformly narrow, without projections (Fig. 20) ..... *operosus,* new species
9(7). Incision caudad of pronotal lobes reaching mesad to middle of eye; lobes projecting laterad of eye by 0.2 width of eye or less; lateral margins of juga converging toward apex (Fig. 22) ..... *convexus,* new species
– Incision caudad of pronotal lobes reaching mesad from lateral limit of eye by about 0.2 width of eye; lobes projecting laterad of eye by about 0.5 width of eye; lateral margins of juga subparallel between anteocular concavity and apex (Fig. 25) ..... *securiger* Breddin
10(1). Vertex of head strongly convex, appearing swollen 11
– Vertex of head normally convex 13
11(10). Small species, about 9 mm in length; distance across ocelli greater than interocular width; second antennal segment at least as long as first ..... *parvulus* (Ruckes)
– Larger species, about 11–14 mm in length; distance across ocelli and interocular width subequal; second antennal segment shorter than first 12
12(11). Lateral angle of basal plates produced, projecting over base of 8th paratergites (Fig. 35); pronotal lobes projecting laterad of eyes about 0.3 width of eye ..... *singularis,* new species
– Lateral angle of basal plates not produced (Fig. 37); pronotal lobes seldom projecting as far laterad of eyes as 0.3 width of eye ..... *tumidifrons,* new species
13(10). Femora with broad preapical fuscous ring ..... *anulatus,* new species
– Femora not annulated 14
14(13). Width of eye less than half of interocular width 15
– Width of eye at least half of interocular width 21
15(14). Pale narrow yellow low ridge on ventral surface of head running from base of head to antennifer at mesial margin of eye 16
– Venter of head caudad of eye smooth excepting punctures 20
16(15). Lateral margins of abdominal venter with large yellowish brown macule on each segment 17
– Abdominal venter uniformly colored 19
17(16). Lateral margins of head converging from preocular concavity toward apex ..... *repizcus,* new species
– Lateral margins of head parallel between preoccular concavity and apex 18
18(17). Pygophoral emargination U-shaped ..... *discessus* (Distant)
– Pygophoral emargination V-shaped ..... *varius,* new species
19(16). Disk of abdominal venter multitudinously and very shallowly cratered laterally; mesial margin of 9th paratergites not reflexed ..... *modicus,* new species
– Abdominal venter nearly smooth, impressions faint; mesial margin of 9th paratergites narrowly but strongly reflexed (Fig. 65) ..... *leviventris,* new species
20(15). Ocelli large, greatest diameter of each about 0.30–0.35 of distance between ocelli ..... *manchus,* new species

– Ocelli smaller, greatest diameter of each about 0.22 of distance between ocelli .... *armiger* Breddin

21(14). Incision caudad of pronotal lobes reaching mesad as far as middle of eye (Fig. 71) .... *breddini*, new species

– Incision caudad of pronotal lobes shallower 22

22(21). Length of pronotal lobes from base of incision to apex of lobe subequal to width of lobes at base (Fig. 75) .... *lamelliger* Breddin

– Pronotal lobes triangular or if not triangular longer than wide at base (Figs. 90, 95) 23

23(22). Males 24

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24(23). Apex of proctiger transversely convex, narrowly rounded from dorsal view (Fig. 99) 25

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25(24). Mesial emargination of pygophore U-shaped from caudal view (Figs. 80, 85) 26

– Mesial emargination of pygophore lyre-shaped or V-shaped from caudal view (Figs. 91, 97) 28

26(25). Posterior margin of pygophore in profile strongly convex (Fig. 81) .... *lobuliger* Breddin

– Posterior margin of pygophore in profile sinuously linear (Fig. 86) 27

27(26). Elevated rim along lateral margins of pygophoral emargination disappearing beneath bottom of emargination (Fig. 85); 2nd and 3rd antennal segments subequal in length, 5th almost uniformly colored .... *rufospilotus* (Westwood)

– Elevated rim along lateral margins of pygophoral emargination disappearing on level with bottom of emargination (Fig. 88); 3rd antennal segment about 1.5 times length of 2nd, basal 4th of 5th segment paler than remainder of segment .... *vallis*, new species

28(25). Pygophoral emargination lyre-shaped from caudal view, narrowed where rim along emargination first becomes prominent about a 3rd of distance from dorsal margin of pygophore to bottom of emargination (Fig. 91) .... *dentiger* Breddin

– Pygophoral emargination V-shaped from caudal view 29

29(28). A single broad lamina present in genital cup on each side of posterior wall (Fig. 99) .... *styliger* Breddin

– Two smaller laminae present in genital cup on each side of posterior wall (Fig. 101) .... *laminatus*, new species

30(24). Apical expansion of proctiger about a 4th wider than proctiger at base of expansion (Fig. 107); rim of pygophoral emargination continuing into genital cup as lamina on each side .... *substyliger*, new species

– Apical expansion of proctiger about three-fourths wider than proctiger at base of expansion (Fig. 112); rim of pygophoral emargination continuing into genital cup as low ridge on each side .... *subuliger* Breddin

31(23). Lateral margins of head subparallel between anteocular concavity and apex (Fig. 79) 33

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32(31). Pronotal lobes triangular, projecting laterad of eyes by about 0.2 width of eye .... *dentiger* Breddin

– Pronotal lobes elongated, projecting laterad of eyes by about half the width of an eye .... *styliger* Breddin

33(31). Rugose interstices between punctures on abdominal venter brownish yellow, punctures and area around punctures much darker .... *lobuliger* Breddin

–	Abdominal venter uniformly dark or nearly so	34
34(33).	Smaller species, about 5.7 mm wide at humeri	*subuliger* Breddin
–	Larger species, about 6.5 mm wide at humeri	*rufospilotus* (Westwood)

Lincus vandoesburgi, new species
(Figs. 1–7)

Description. Appearing dark brown above and below due to thick fuscous to dark castaneous punctation on yellowish background. Yellowish brown macule present on humeri, along base of scutellum near angles and in middle, on disk of each corium and on each connexival segment. Abdominal venter dark castaneous mesially. Thoracic sterna and much of pleura black. Appendages predominately yellowish brown.

Antennal segment 2 short; length of segments 0.8–1.0, 0.4–0.5, 1.0–1.2, 1.6–2.0, 2.5–2.6 mm. Head 2.3–2.6 mm wide across eyes, 2.1–2.3 mm long. Width of eyes about half of interocular width, slightly greater than anterior–posterior diameter of eyes. Distance across ocelli slightly greater than interocular width, 1.2–1.3 and 1.1–1.2 mm respectively. Juga and tylus equally long, lateral jugal margins before anteocular concavity converging slightly toward apex of head (Fig. 1).

Pronotal lobes extending laterad of eye by 0.6–0.8 width of eye, much expanded apically and curved dorsad. Anterolateral pronotal margins produced into obtuse projection laterad of lobe on each side, leaving curved incision between this margin and lobe. Disk rugosely punctate. Width at humeri 6.0–6.7 mm, mesial length 2.6–2.8 mm.

Scutellum 3.6–4.1 mm wide at base, 4.5–5.0 mm long, with black triangular fovea containing a few punctures at basal angles. Disk rugosely punctate basally.

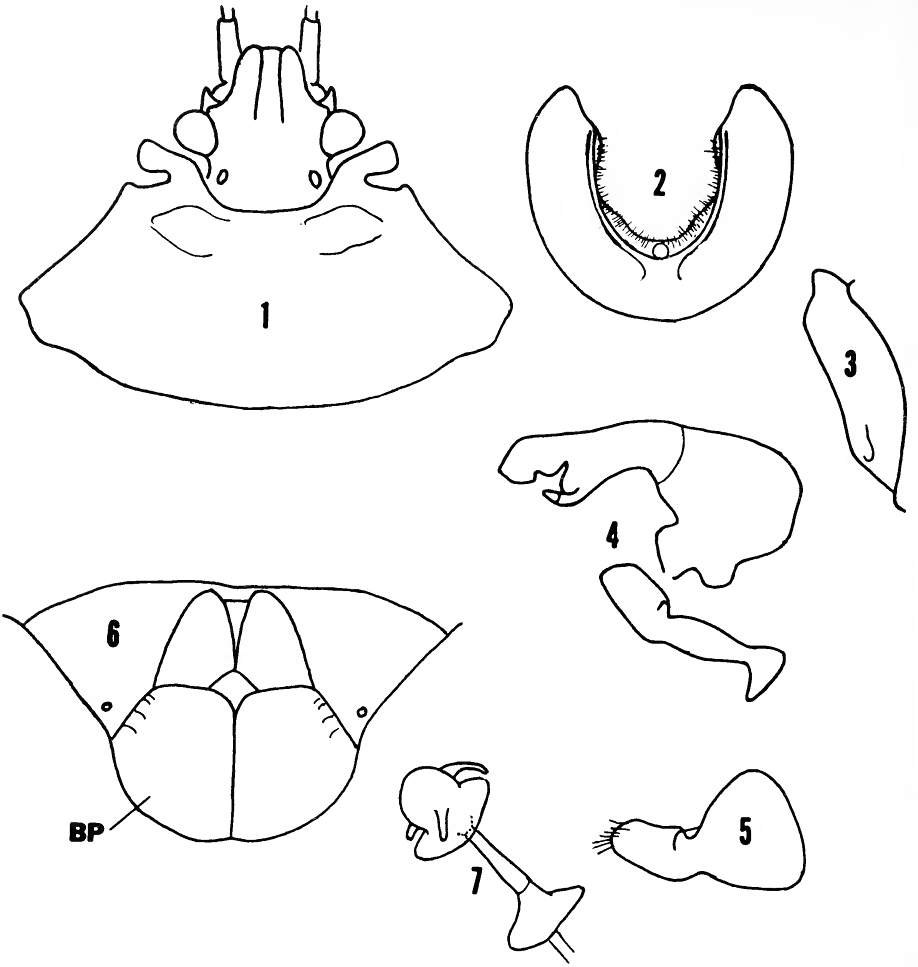
Basal plates truncate apically, sometimes lightly impressed along lateral margins (Fig. 7). Distal portion of spermatheca as in Figure 6; three projections on bulb curving basad and clockwise from terminal view of bulb.

Large mesial emargination of pygophore slightly concave at dorsal limits on each side; in dissected pygophore emargination entad of external rim sinuous (Fig. 2); pygophore in lateral view as in Figure 3. Proctiger protruding, visible from above. Parameres short relative to phallus (Fig. 4), transversely expanded basally (Fig. 5).

Length 12–13.3 mm.

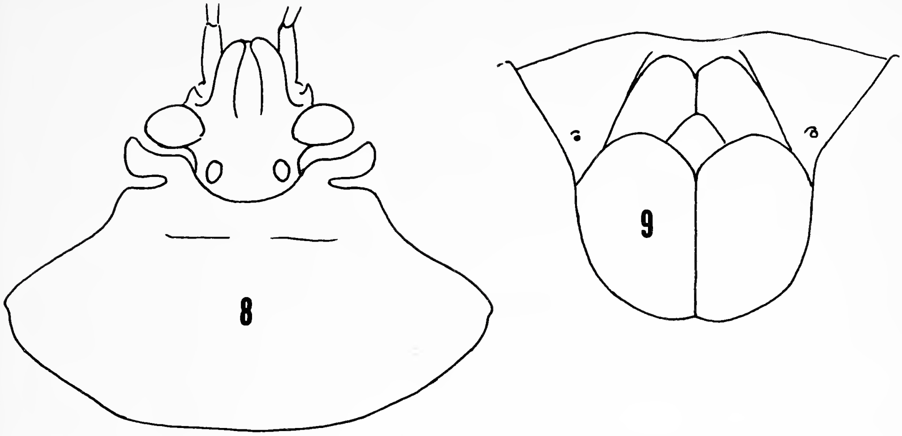
Distribution. Surinam.

Holotype. ♀, labeled "Museum Leiden, Dr. D. C. Geijskes, Paramaribo, Cultuuruin, 28 VIII 1938" Deposited in the Rijksmuseum van Natuurlijke Historie.



Figs. 1–7. *Lincus vandoesburgi.* 1. Head and pronotum. 2. Pygophore, caudal view, proctiger removed. 3. Same, lateral view. 4. Relationship of aedeagus and parameres within pygophore, right lateral view, basal plate omitted. 5. Right paramere, dorsal view. 6. Genital plates, caudoventral view; basal plate (BP). 7. Distal parts of sphermatheca.

Paratypes. 5♀♀, 7♂♂. Same data as holotype (2♀♀, 3♂♂ RNH; 1♀ LHR); same data as holotype except date "24 VIII 1938" (♂ RNH), "29 VII 1938" (♀ RNH) and "14 IV 1938" without word Cultuuruin (♂ LHR); (a) "Surin. 1158-19 P. H. v. Doesburg, Jr." (b) "611" on red label (♂ RNH); (a) "on roots Liberian coffee" (b) "Jaglust plantation" (c) "Paramaribo, Surinam. D. G. VII-28-33" (d) "Lincus spathuliger Bredd. det. H. G. Barber" (♀ AL);



Figs. 8, 9. *Lincus incisus.* 8. Head and pronotum. 9. Genital plates, caudoventral view.

same data without determiner's name (♂ USNM); (a) Victoria, oliepalm, 15-6-77, V. Slobbe (b) L. P. 815 (c) Surinam (♂ USNM).

Comments. The shape of the pronotum and the short 2nd antennal segment are together diagnostic. *L. spathuliger,* which is known only from the female holotype, appears to differ only in lacking the obtuse projection on the anterolateral pronotal margins just laterad of the lobes. Since the provenance of *L. vandoesburgi* is Surinam and that of *L. spathuliger* is Peru, it is possible that these two taxa are subspecies.

This species is named in honor of Dr. P. H. van Doesburg, Jr. of the Rijksmuseum van Natuurlijke Historie.

Lincus incisus, new species
(Figs. 8, 9)

Description. Fuscous to black with rugose interstices between punctures; discal spot on each corium, last 2 antennal segments, rostrum and tarsi yellowish brown.

Antennal segments 0.9, 1.2, 1.3, 1.4, 1.9 mm in length; basal segment extending well beyond apex of head. Rostral segments 2–4 about 2.4, 2.0, 1.8 mm in length. Eyes wider than anterior–posterior diameter, 0.8–0.85 mm wide and 0.6 mm in diameter from dorsal view. Interocular width and distance across ocelli equal, 1.15 mm; greatest diameter of ocelli 0.3 mm. Juga nearly contiguous apically, their lateral margins before anteocular concavity tapering slightly toward apex (Fig. 8). Width of head across eyes 2.8 mm, length 2.2 mm. Vertex nearly flat.

Pronotal lobes expanded apically, projecting horizontally laterad of eyes by about 0.3 width of eye; incision caudad of lobes extending mesad from lateral limit of eye by about 0.4 width of corresponding eye. Width of pronotum at humeri 6.5 mm, mesial length 3.0 mm. Disk rugosely punctate, interstitial rugae yellowish brown. Anterolateral margins produced into obtuse angle caudad of apex of lobes.

Scutellum 4.0 mm wide at base, 5.1 mm long. Triangular black fovea present in each basal angle. Disk rugose.

Posterior margins of basal plates evenly convex (Fig. 9).

Length about 12.8 mm.

Distribution. Surinam. Known only from holotype.

Holotype. ♀, labeled "Museum Leiden, Suriname, Mapane area, Blakka Watra, 26. V. 1960, Ph. van Doesburg, jr." Deposited in the Rijksmuseum van Natuurlijke Historie. The 5th segment of the right antenna is glued on the label.

Lincus spathuliger Breddin

Lincus spathuliger Breddin, 1908, pp. 31–33, figs. 15, 16; Gaedike, 1971, p. 99 (lectotype designated).

Diagnosis. Pronotal lobe on each side extending laterad of eye by distance nearly equal to width of eye, expanding toward apex, leaving deep narrow incision between posterior margin of lobe and anterolateral margin of pronotum; latter margin sinuous, quite convex caudad of lobe. Second antennal segment about one-half length of first. Juga and tylus subequal in length; lateral jugal margins subparallel between concavity above antennifers and apex of head. Posterior margin of basal plates obtusely angled where base of 9th paratergites meet 8th paratergites.

Length including membranes about 11 mm.

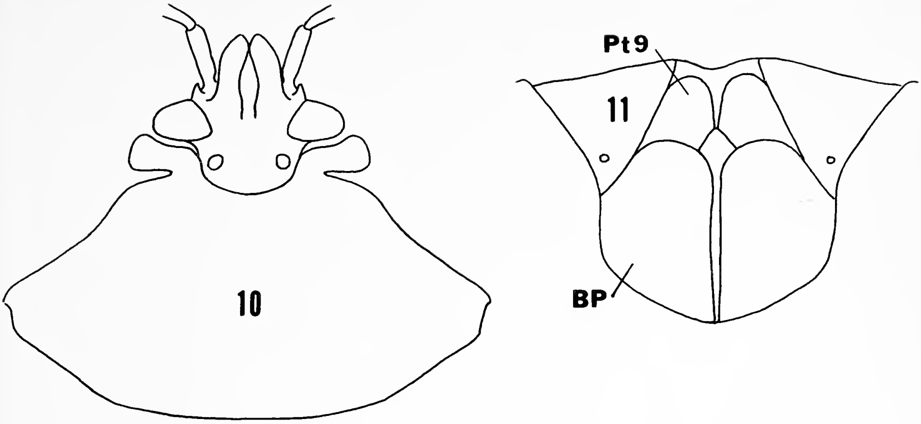
Distribution. Known only from lectotype collected at Marcapata, Peru.

Comments. Of those species with apically expanded pronotal lobes, only this species and *vandoesburgi* have short second antennal segments, about half as long as the first. *L. spathuliger* is distinguished from *L. vandoesburgi* by the absence of a subapical projection on the anterolateral pronotal margins.

The lectotype was examined.

Lincus fatigus, new species
(Figs. 10, 11)

Description. Mostly fuscous; discal spot on each corium, mesial spot at base of scutellum, last 2 antennal segments, some interstitial rugae on scu-



Figs. 10, 11. *Lincus fatigus.* 10. Head and pronotum. 11. Genital plates, caudoventral view; basal plate (BP); 9th paratergite (Pt9).

tellum, tarsi and scattered flecks on venter yellowish brown; some interstitial rugae on anterior disk of pronotum and humeri reddish.

Antennal segments 1.0, 1.3, 1.4, 1.5, 1.9 mm long; first segment projecting well beyond apex of head. Head 2.9 mm wide across eyes, 2.4 mm long. Eyes wider than anterior–posterior length, each eye 0.9 mm wide, 0.6 mm long. Distance between lateral limits of ocelli greater than interocular distance, 1.3 mm across ocelli, 1.1 mm between eyes. Juga contiguous before tylus (Fig. 10).

Pronotal lobe extending laterad of eye on each side about 0.4 width of eye, much expanded apically and bent ventrad; narrow incision between posterior margin of pronotal lobe and convex expansion of anterolateral pronotal margin reaching nearly to middle of eye. Pronotal disk rugosely punctate. Width at humeri 7.3 mm, mesial length 3.4 mm.

Scutellum 4.6 mm wide at base, 5.3 mm long. Deep fovea present in basal angles. Basal part of disk comparable to pronotum in rugoseness.

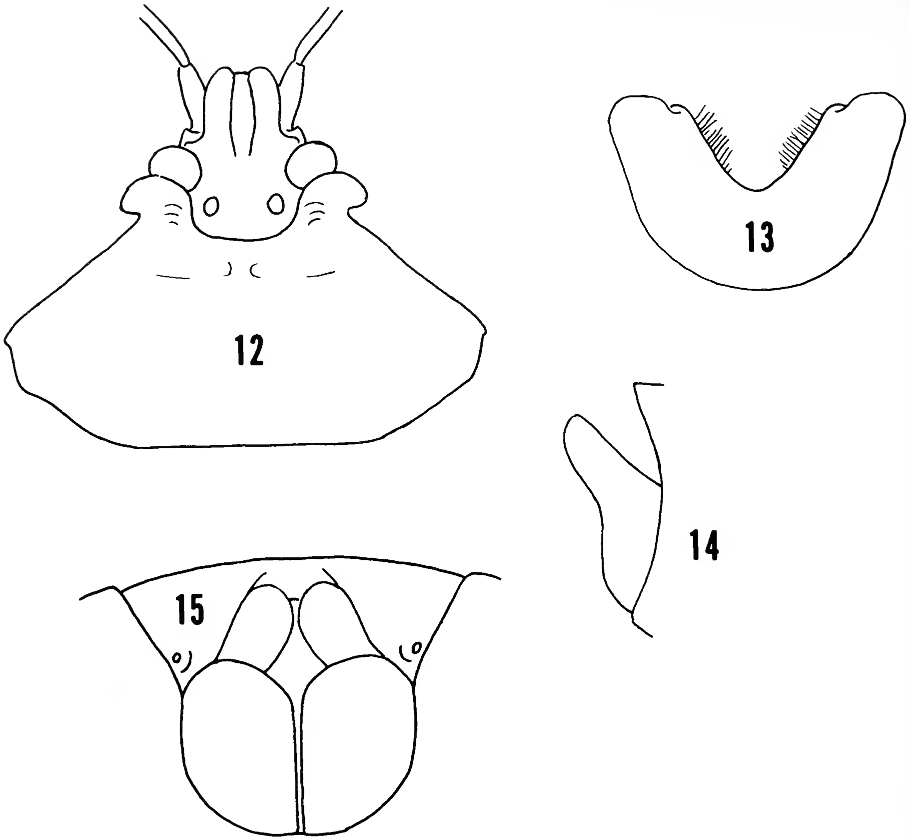
Basal plates broadly rounded at posterior margin, rather smoothly surfaced with a few large punctures laterally. Paratergite 9 transversely convex (Fig. 11).

Length about 13.5 mm.

Distribution. Surinam. Known only from type.

Holotype. ♀, labeled "S. Suriname, Sipalivini, 14 June 1963, P. H. v. Doesburg Jr." and on red label "609". Deposited in the Rijksmuseum van Natuurlijke Historie. The last 3 rostral segments, most of middle legs and part of antennal segment 5 on left are missing.

No paratypes.



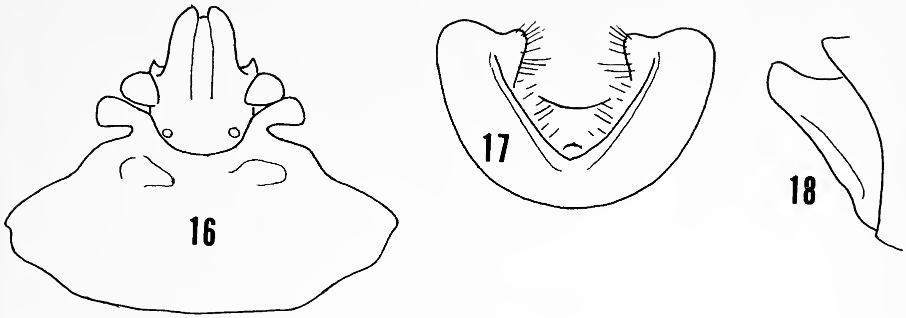
Figs. 12–15. *Lincus croupius.* 12. Head and pronotum. 13. Pygophore, caudal view, proctiger omitted. 14. Same, lateral view. 15. Genital plates, caudoventral view; basal plates and 9th paratergites partially opened.

Lincus croupius, new species
(Figs. 12–15)

Description. Mostly fuscous; last 2 segments of antennae, discal spot on each corium, rostrum and tarsi yellowish brown.

Antennal segments 0.8, 1.1–1.2, 1.0–1.1, 1.3, 1.7 mm in length, first projecting slightly beyond apex of head. Head 2.3 mm wide across eyes, 2.0–2.1 mm long. Eyes wider than anterior–posterior diameter, each 0.6–0.7 mm wide, 0.45–0.5 mm in diameter. Distance across ocelli greater than interocular width, 1.1–1.15 mm across ocelli, 1.0–1.05 mm between eyes. Juga slightly longer than tylus. Rostral segments 2–4 about 2.6–2.7, 2.1, 1.9–2.0 mm in length.

Pronotal lobes broad throughout, little expanded apically, deflexed toward



Figs. 16–18. *Lincus sinuosus.* 16. Head and pronotum. 17. Pygophore, caudal view, proctiger omitted. 18. Same, profile.

apex, concave basally, extending laterad of eye on each side about 0.5 width of eye (Fig. 12); emargination caudad of lobe not reaching mesad as far as lateral limit of eye. Anterolateral margins caudad of lobes nearly straight. Pronotal disk rugose. Width of pronotum across humeri 5.8–6.2 mm, mesial length 2.6–2.8 mm.

Scutellum 3.8 mm wide at base, 4.3–4.6 mm long. Basal angles shallowly foveate. Disk rugose basally, smoother than pronotum.

Genital plates as in Figure 15.

Outline of pygophoral emargination interrupted near dorsal margin dorsad of setose patch (Fig. 13). Posterior margin of pygophore sinuous in profile (Fig. 14).

Length about 10 mm.

Distribution. Brazil (Amapa), French Guiana.

Holotype. ♂, labeled (a) "Rio Pelioca, Terr. Amapa, Brasil, 4-VIII-1957, J. Lane Leg." (b) "Coleção J. Lane." Deposited in the Museum de Zoologia, São Paulo.

Paratype. ♀, labeled "Museum Paris, Guyane Franç, Camopi, F. Geay, 1900" (b) "693" (AMNH).

Comment. This species resembles *L. fatigus* in having deflexed pronotal lobes. The lobes are much broader basally and the juga much shorter, relative to the tylus, in *L. croupius* than in *L. fatigus.*

Lincus sinuosus, new species
(Figs. 16–18)

Description. Dark brown with yellowish brown vermiform short lines above and below, most of these marking elevated rugae; basal half of head fuscous; humeri, 3 basal spots on scutellum, spot on disk of each corium and in middle of each connexival segment yellowish-brown.

Antennal segments 0.7, 0.7, 1.1, 1.1 mm long (5th missing); first segment reaching apex of head. Head 2.05 mm wide across eyes, 1.9 mm long. Eyes wider than anterior–posterior diameter, each about 0.5 mm wide, 0.4 mm in diameter. Interocular width 1.1 mm, greater than distance of 1.0 mm between lateral margins of ocelli. Juga longer than tylus, convergent apically, their lateral margins above antennifers subparallel. Rostral segments 2–4 about 2.4, 1.9, 1.7 mm long.

Pronotal lobes expanded apically, their anterolateral margins narrowly reflexed, each lobe projecting laterad of eye by about 0.7–0.8 width of eye (Fig. 16); emargination between pronotal lobe and anterolateral margin of pronotum on each side extending mesad of lateral limit of eye for 0.3–0.4 width of eye. Anterolateral margins of pronotum caudad of lobes strongly sinuous. Disk rugose, impressed adjacent to concavity in anterolateral margins. Width across humeri 5.1 mm, mesial length 2.2 mm.

Scutellum 3.0 mm wide at base, 3.8 mm long. Disk less strongly rugose than pronotum. Triangular fovea in basal angles black, containing a few small punctures.

Mesial emargination of pygophore U-shaped, its margins produced anteromesad on each side near dorsal limit of emargination (Fig. 17). Dorsal margin on each side of emargination slightly sinuous from caudal view. Profile of pygophore as in Figure 18.

Length about 9.9 mm.

Distribution. Peru. Known only from holotype.

Holotype. ♂, labeled "Piches & Perene Vs, 2000–3000 ft. Peru, Soc. Geog. de Lima". Deposited in U.S. National Museum. Type no. 76687. This specimen lacks both front legs, the left middle leg, right antenna and last segment of the left antenna.

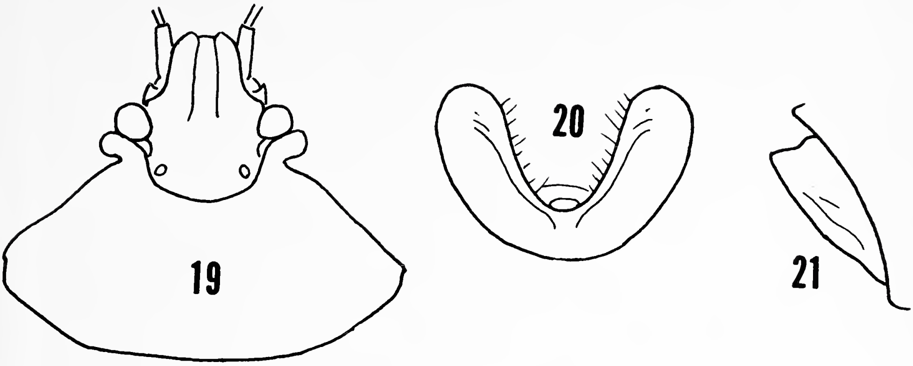
No paratypes.

Comments. Within the group of species with apically expanded pronotal lobes, this species, the preceding species (*croupius*) and the following species (*operosus*) are the smallest. Each differs markedly from the others in the form of the anterolateral pronotal angles.

Lincus operosus, new species
(Figs. 19–21)

Description. Light brown above and below (perhaps somewhat callow) with red eyes, dark punctures dorsally and on the thoracic venter; mesial spot at base of scutellum and on each connexival segment, mottling and interrupted submarginal lateral band on abdominal venter, all yellowish brown.

Antennal segments 0.6, 0.5, 0.7, 1.1, 1.5 mm long; first segment slightly



Figs. 19–21. *Lincus operosus.* 19. Head and pronotum. 20. Pygophore, caudal view, proctiger omitted. 21. Same, profile.

surpassing apex of head. Head width across eyes and length equal, 2.0 mm. Eyes wider than anterior–posterior diameter, about 0.48 mm wide, 0.4 mm in diameter. Interocular width of 1.15 mm greater than distance of 1.05 mm between lateral margins of ocelli. Juga slightly longer than tylus, apically convergent, their lateral margins subparallel above antennifers. Vertex strongly convex but not tumescent. Rostral segments 2–4 about 2.1, 1.6, 1.6 mm long.

Pronotal lobes apically expanded and reflexed, each projecting laterad of eye by about 0.3 width of eye (Fig. 19); emargination between pronotal lobe and anterolateral pronotal margin on each side extending mesad of lateral limit of eye by about 0.1 width of eye. Anterolateral pronotal margins caudad of lobes moderately sinuous, narrowly and strongly reflexed. Disk rugosely punctate; punctures deep but not unusually large. Width of pronotum across humeri 4.6 mm, mesial length 1.9 mm.

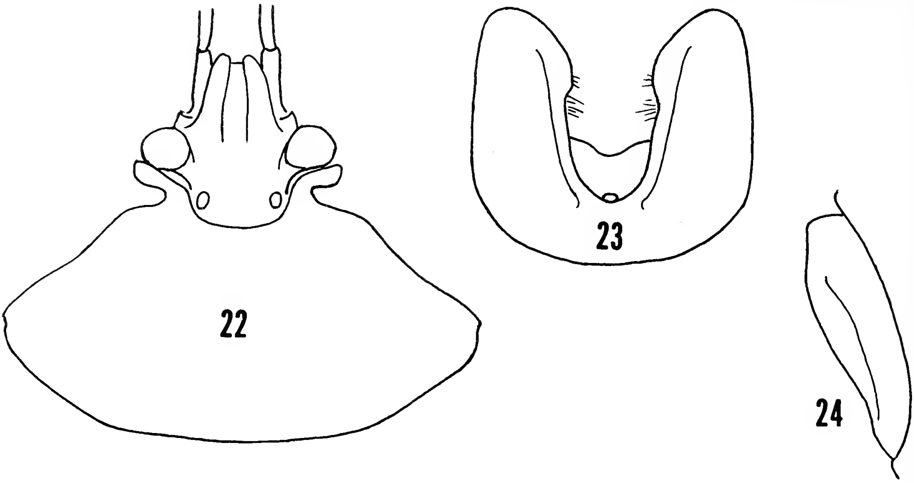
Scutellum 2.9 mm wide basally, 3.3 mm long. Disk rugosely punctate basally; rugosity and puncture size diminishing toward apex. Fovea in basal angles triangular, darker than adjacent disk, containing a few fine punctures.

Mesial emargination of pygophore U-shaped, its margins without productions, sparcely setose (Fig. 20). Dorsal margin on each side of pygophore convex. Hemispherical impression at bottom of mesial pygophoral emargination clearly visible, prominent. Posterior surface of pygophore nearly linear in profile (Fig. 21).

Length about 9.4 mm.

Distribution. Venezuela. Known only from type.

Holotype. ♂, labeled (a) "Venezuela. On orchid" (b) "Insp. House. D.C. 7.14.39". Deposited in U.S. National Museum. Type no. 76689.



Figs. 22–24. *Lincus convexus.* 22. Head and pronotum. 23. Pygophore, caudal view, proctiger omitted. 24. Same, lateral view.

No paratypes.

Comments. This specimen was intercepted at a plant quarantine station in a shipment of orchids which may or may not have been the host.

Lincus convexus, new species
(Figs. 22–24)

Description. Dark castaneous to black with many interstitial rugae between punctures and a small macule on each humerus, at basal angles and middle of scutellar base, on disk of each corium and on connexival segments yellowish brown. Dorsum unusually convex, dorsal and ventral surfaces similarly arched transversely from lateral margins.

Juga longer than tylus, their lateral margins before anteocular concavity decidely converging toward apex of head (Fig. 22). Vertex normally convex. Antennal segments 0.8, 0.9, 1.3, 1.6 mm long (5th missing); basal segment reaching apex of head. Rostral segments 2–4 about 2.5, 2.1, 2.1 mm in length. Eyes from dorsal view 0.65–0.7 mm wide, their anterior–posterior diameter 0.55 mm. Interocular width 1.4 mm; distance across ocelli 1.3 mm. Width of head across eyes 2.7 mm, length 2.3 mm.

Pronotal lobes expanded toward apex, horizontal, extending laterad of eyes by about 0.1 width of eye. Incision caudad of pronotal lobes extending mesad to middle of eye. Width of pronotum at humeri 6.3 mm, mesial length 2.9 mm. Disk rugose.

Scutellum 4.0 mm wide at base, 5.0 mm long. Fovea in basal angles triangular, black, containing 1 or 2 deep punctures.

Mesial emargination of pygophore U-shaped; low setose projection within genital cup partially visible where rim of emargination begins dorsally (Fig. 23). Mesial depression at base of inferior ridge small. Proctiger narrowly rounded apically. Posterior margin of pygophore in profile sigmoid (Fig. 24).

Distribution. Peru. Known only from holotype.

Holotype. ♂, labeled (a) "Monson Valley, Tingo Maria, XI-2-1954" (b) "E. I. Schlinger & E. S. Ross, collectors". Deposited in the American Museum of Natural History. Fifth antennal segment on right, 4th and 5th on left, right tarsi on fore and middle legs and tibiae on left fore leg missing.

Lincus securiger Breddin
(Figs. 25–29)

Lincus securiger Breddin, 1904, p. 154; Breddin, 1908, pp. 29–31, figs. 9–11; Gaedike, 1971, p. 99 (lectotype designated).

Diagnosis. Pronotal lobe on each side extending horizontally laterad of eye by about 0.5 width of eye, expanding toward apex; narrow incision between lobe and anterolateral pronotal margin extending mesad of lateral limit of eye by about 0.3 width of eye (Fig. 25). Juga exceeding tylus, their lateral margins tapering sinuously toward apex. Distance between lateral limits of ocelli subequal to interocular width. Width of each eye about 0.2 greater than anterior–posterior diameter, 0.6–0.7 of interocular width. First and 2nd antennal segments subequal in length, 1st surpassing slightly apex of head. Basal plates obtusely angled where base of 9th paratergites and 8th paratergites meet (Fig. 26). Dorsomesial pygophoral margin on each side of setose border of mesial emargination with small convexity from caudal view (Fig. 27), this convexity part of tumescence within genital cup on each side of mesial emargination (Fig. 29). Rim of mesial emargination convex in profile (Fig. 28).

Length 12.6–12.8 mm.

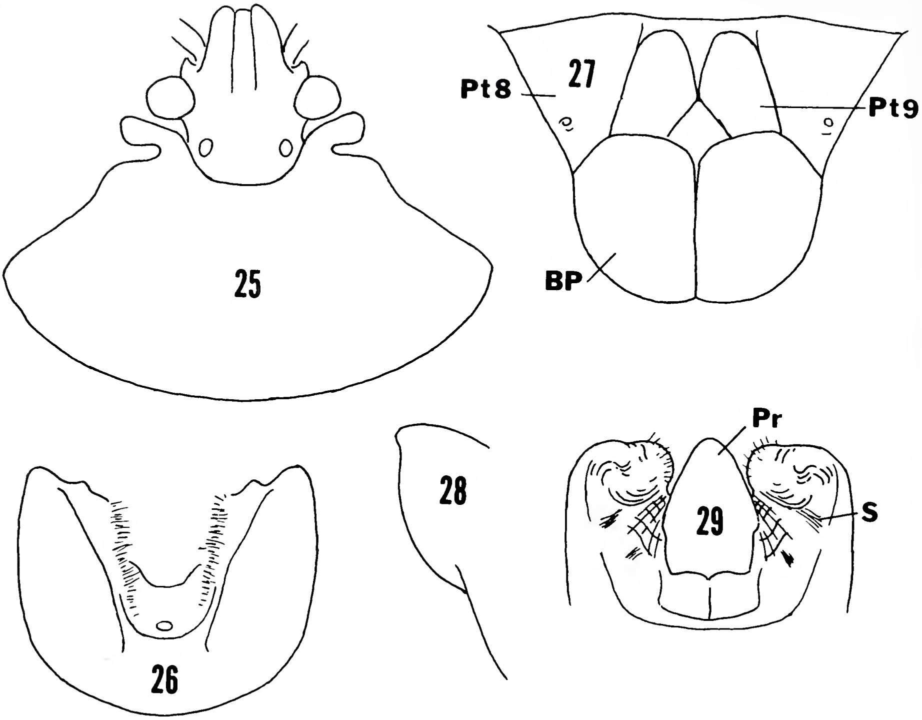
Distribution. Bolivia, Brazil (Amazonas), Peru.

Comments. The ♂ lectotype and ♀ paralectotype were examined.

Lincus parvulus (Ruckes), **New Combination**
(Figs. 30–33)

Minilincus parvulus Ruckes, 1958, pp. 15–17, fig. 2.

Diagnosis. Entire vertex of head tumescent. Second antennal segment subequal to first and third in length. Distance across ocelli from lateral margin of each slightly greater than interocular distance. Width and length of eyes from dorsal view subequal. Juga a little longer than tylus, their lateral margins sigmoid, briefly parallel between concavity above antennifers and apex (Fig. 30). Pronotal lobes small; emargination caudad of lobe reaching mesad about



Figs. 25–29. *Lincus securiger*. 25. Head and pronotum. 26. Pygophore, caudal view, proctiger omitted. 27. Genital plates, caudoventral view; basal plate (BP); 8th paratergite (Pt8); 9th paratergite (Pt9). 28. Posterior margin of pygophore, lateral view. 29. Genital cup, dorsal view, setal tufts (S), proctiger (Pr).

as far as lateral limit of eyes. Anterolateral margins of pronotum weakly sinuous, notably reflexed. Posterior margins of basal plates convex (Fig. 31); surface of basal plates smooth. Emargination of pygophore sinuously V-shaped (Fig. 32).

Length about 9 mm.

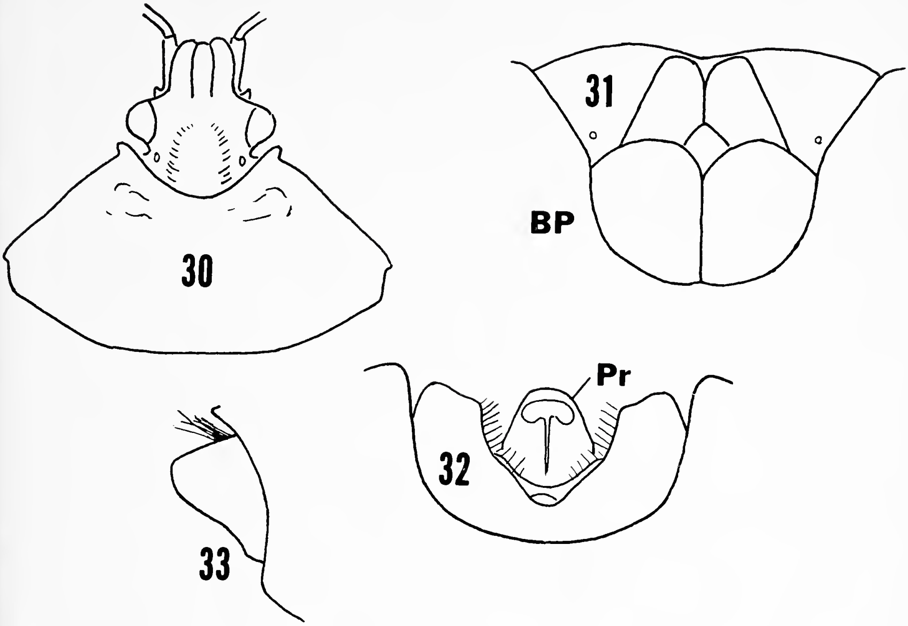
Distribution. Peru and Brazil (Acre).

Comment. The much swollen vertex and rather small size together are diagnostic.

The holotype and allotype were examined.

Lincus singularis, new species
(Figs. 34, 35)

Description. Dark brown to fuscous with humeri, 3 basal spots on scutellum and one on disk of each corium, mesial macule on each connexival



Figs. 30–33. *Lincus parvulus.* 30. Head and pronotum. 31. Genital plates, caudoventral view; basal plates (BP). 32. Pygophore, caudoventral view; proctiger (Pr). 33. Same, lateral view.

segment with enlarged continuation on lateral border of corresponding sternite, and vermiform markings on abdominal venter, all yellowish brown.

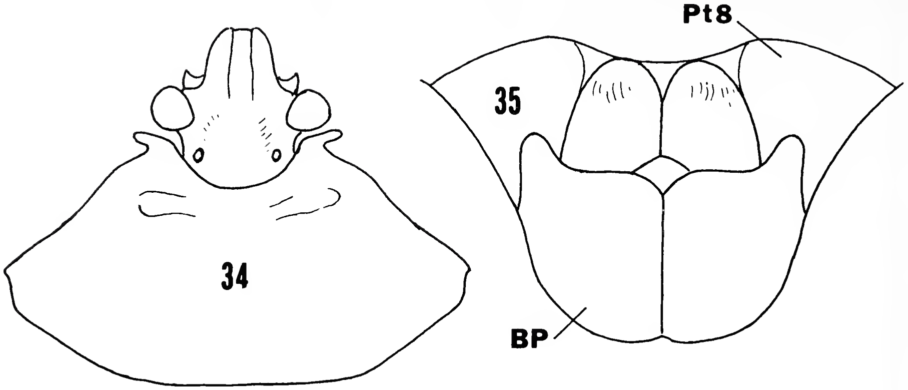
Vertex of head tumid (Fig. 34). Juga little longer than tylus, their lateral margins subparallel above antennifers. Antennal segments 0.8, 0.8, 1.1, 1.5, 2.0 mm in length. Distance across ocelli and interocular width equal, 1.25 mm. Eyes from dorsal view as long as wide, 0.6 mm. Width of head across eyes 2.4 mm, length 2.2 mm. Rostral segments 2–4 about 2.7, 2.2, 2.0 mm long.

Anterior and posterior margins of pronotal lobes subparallel, each lobe extending laterad of corresponding eye by 0.3–0.4 width of eye; emargination caudad of lobes extending mesad of lateral limit of eye by about 0.2 width of eye. Anterolateral pronotal margins moderately sinuous. Disk with moderately rugose band between humeri. Pronotal width across humeri 6.3 mm, length at meson 2.8 mm.

Scutellum 4.0 mm wide at base, 5.2 mm long. Basal angles scarcely foveate.

Lateral angle of basal plates strongly produced, projecting beneath 8th paratergites (Fig. 35); 9th paratergites reflexed apically.

Length 12.6 mm.



Figs. 34, 35. *Lincus singularis.* 34. Head and pronotum. 35. Genital plates, caudoventral view; basal plates (BP); 8th paratergites (Pt8).

Distribution. Peru.

Holotype. ♀, labeled (a) "Chauchamayo, Peru" (b) "From F. H. Rosenburg". Deposited in U.S. National Museum. Type no. 76690.

No paratypes.

Comment. The basal plates of this species are unique within the genus.

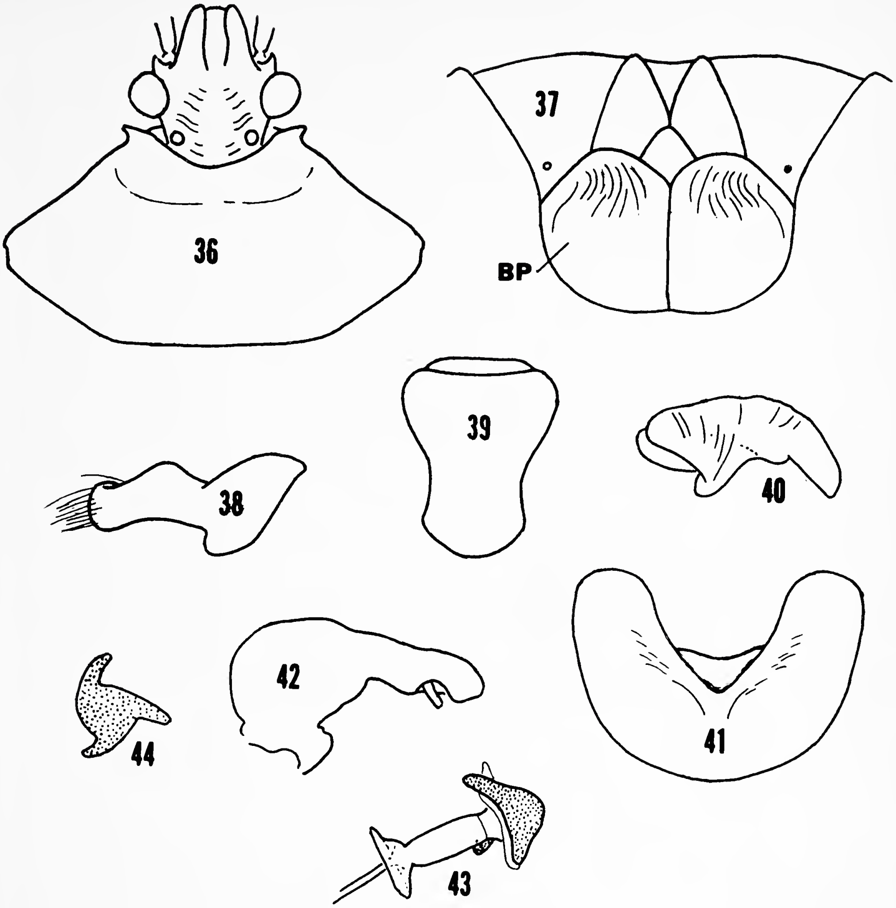
Lincus tumidifrons, new species
(Figs. 36–44)

Description. Fuscous above with some of interstitial rugae yellowish brown; similarly colored macule on humeri, 3 along base of scutellum, marginal macule in middle of each connexival segment. Rostrum, legs, basal band on last antennal segment and sternites yellowish brown, latter with fuscous punctures; remainder of venter fuscous.

Entire vertex strongly convex (Fig. 36). Antennal segment 2 short, usually about two-thirds length of 1 and 3, latter 2 segments subequal in length; length of segments 0.8–0.9, 0.5–0.6, 0.8–0.9, 2.0–2.3, 2.6–2.8. Distance across ocelli from lateral margin of each subequal to interocular width, 1.25–1.4 mm. Width and length of eye from above subequal, 0.65 mm. Width of head across eyes 2.3–2.7 mm length 2.3–2.6 mm. Juga little longer than tylus, their lateral margins sigmoid.

Pronotal lobes extending little if at all laterad of eyes, narrowly rounded apically. Disk rugose. Anterolateral margins weakly sinuous. Width across humeri 5.7–6.3 mm, mesial length 2.3–2.8 mm.

Scutellum shallowly foveate in each basal angle. Disk similar to pronotum in rugosity. Basal width 3.5–4.1 mm, length 4.1–5.0 mm.



Figs. 36–44. *Lincus tumidifrons.* 36. Head and pronotum. 37. Genital plates, caudoventral view; basal plates (BP). 38. Paramere. 39. Proctiger, dorsal view. 40. Proctiger, lateral view, apex to right. 41. Pygophore, caudal view, proctiger omitted. 42. Aedeagus, basal plate omitted. 43. Distal parts of spermatheca (bulb stippled). 44. Spermathecal bulb, terminal view.

Posterior margin of basal plates with pronounced submarginal impression (Fig. 37).

Mesial emargination of pygophore broad, V-shaped (Fig. 41).

Length about 11–13.7 mm.

Distribution. Panama, Trinidad, Venezuela.

Holotype. ♀, labeled “Las Cumbres, Panamá, 9°06’ N, 79°32’ W, Lt. trap. 2-V-75. Col: Henk Wolda”. Deposited in U.S. National Museum. Type no. 76686.

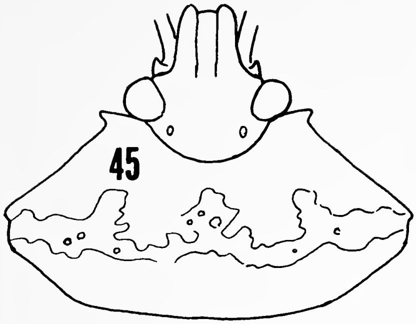
Paratypes. 10♀♀, 6♂♂. Same data as holotype except date "16-VI-76" (♀ HDE), "11-VII-76" (♀ LHR) and "7-X-75" (♀ LHR) "Barro Colorado—C. Z., Lights, Weir/SM-I, 7-XII-1977, Coll. H. Wolda" (♂ HDE); same data except "Weir SM-I-III, 3-9-IX-1975" (♂ LHR); "Barro Colorado Isl., Canal Zone—Lt. trap, 9-VI-76, Col: D. Engleman" (♀ HDE); same data except "23-VI-77, Wolda" (♀ HDE); (a) "Panama Canal Zone, Barro Colorado Is., 9°10' N, 79°50' W" (b) "8-VII-1977, H. A. Hespenheide" (♀ HDE); "Panama, dist. Chepo, Altoa de Maje, 17 May 75 at lights, Stockwell-Engleman" (♀ HDE); "Panamá; Pmá Pr., Altos (Isla) de Majé, 9°08' N, 78°49' W, 15 May '76, Stockwell" (♂ HDE); "Barro Colorado Isl., Canal Zone—Lt. trap 8-IX-76. Col: D. Engleman" (♀ UNAM); "Cabima Pan., May 17-11, August Busck" (♂ UNAM); same data except "May 20.11" (♂ USNM); (a) "Venezuela, on orchid" (b) "Inspect. H., D. C. 6.27.40" (♀ USNM); (a) "Venezuela, on orchid packing" (b) "Inspect. H., Wash. D. C. VII-11-35" (♀ USNM); "Trinida: W.I. Simla, Arima Valley. II-18-1966. B. Heineman" (♂ LHR).

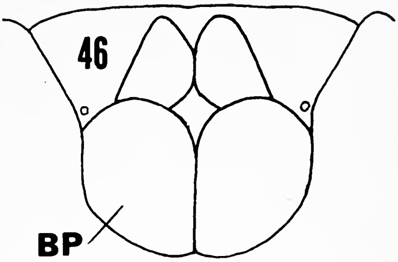
Comment. A female from Peru that is probably this species is omitted from the type series because its identity is uncertain. The juga of this specimen are nearly contiguous apically and the basal plates are less impressed than in females of the type series.

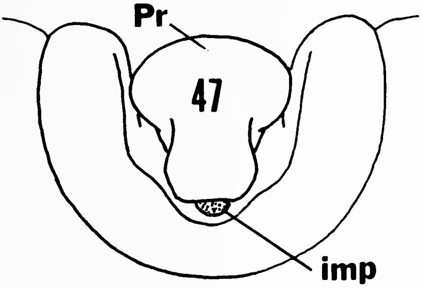
Lincus anulatus, new species
(Figs. 45–48)

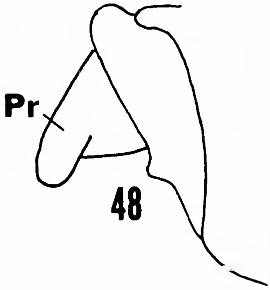
Description. Mostly dark to fuscous, occasional yellowish clay colored with fuscous punctation; sparsely punctate transverse fascia connecting humeri irregular, of varying size, contrasting yellowish brown in dark specimens as is macule on disk of each corium, marginal macule in middle of connexival segments, mesial spot at base of scutellum and sometimes at basal angles, small scattered patches on venter, macule on lateral margins of each sternite corresponding with macule on connexival segment, rostrum and legs excepting small spots and bands: broad preapical femoral band, one of comparable width at apex of tibiae and broader band near base of tibiae all fuscous; tibial bands occasionally obscure; humeri, connexival macules and apex of femora sometimes rufous.

Antennal segments 0.5–0.7, 0.6–0.8, 0.7–0.9, 1.0–1.5, 1.4–1.9 mm in length; basal segment nearly reaching to slightly exceeding apex of head. Rostral segments 2–4 about 1.8–2.6, 1.6–2.3, 1.5–2.2 mm in length; apex reaching middle of penultimate sternite to apex of abdomen. Eyes as wide as anterior–posterior diameter from dorsal view, width of each half or somewhat less of interocular distance. Interocular distance slightly greater (usually 0.5 mm) than distance between lateral limits of ocelli. Juga a little longer than tylus, their lateral margins parallel between concavity above antennifers









Figs. 45–48. *Lincus anulatus.* 45. Head and pronotum. 46. Genital plates, caudoventral view; basal plates (BP). 47. Pygophore, caudal view; proctiger (Pr). 48. Same, lateral view; proctiger (Pr), impression (imp).

and convexity at apices (Fig. 45). Width of head across eyes 2.0–2.1 mm, length 1.7–2.0 mm.

Pronotal lobe small, subacute, directed anterolaterad, usually projecting laterad of eye by distance equal to 0.2–0.4 width of an eye, rarely shorter; emargination caudad of lobe varying in depth, reaching lateral limit of eye or failing to do so by distance equal to 0.2 width of an eye. Anterolateral margins of pronotum usually slightly sinuous, sometimes markedly so (♂), occasionally straight or slightly concave. Pronotal width at humeri 4.6–5.3 mm, mesial length 1.9–2.2 mm.

Scutellum 2.7–3.3 mm wide at base, 3.3–4.0 mm long. Fovea in basal angles inconspicuous.

Posterior margin of basal plates obtusely angulate (Fig. 46). Ninth paratergites suboval.

Rim of pygophoral emargination produced posteriorly on each side just dorsad of mesial circular impression at bottom of emargination (Figs. 47, 48).

Length 9.2–10.3 mm.

Distribution. Brazil (Amapá, Amazonas, Mato Grosso, Pará) and Panama.

Holotype. ♀, labeled "Brazil, Mato Grosso: Lat. 12°13' and Long. 55°37' Sinop, October 1974. M. Alvarenga". Deposited in the American Museum of Natural History. The left antennae is aberrant, having 4 segments.

Paratypes. 1♂, 3♀♀. "Panama, Colon Prov. Sta. Rita Ridge, 18–26 VI 76 at lights, Engleman-Thurman" (♀ LHR); "Benjamin Constant, Amazonas, Brasil, 18–28-IX-1962, K. Lenko—col." (2♂♂ MZSP); "Sta. Isabel do Pará, PA Brasil, 30 III 1962, J. Bechyné col." (♀ MZSP), (a) "Jei Amapá, Serra Novio, X Bicelli col." (b) "--arape Sucuriji" (Hyphen indicating illegible letter) (c) "Coleção J. Lane" (♂ NZSP).

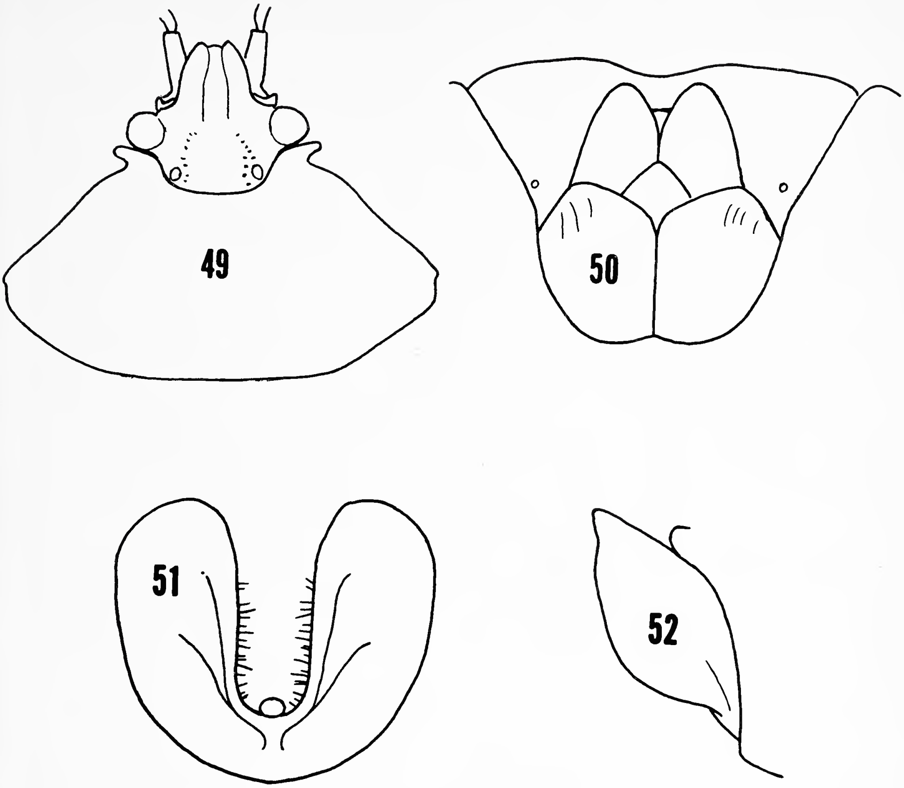
Comments. The annulated femora and tibiae are diagnostic, although faint or even obscured in discolored specimens.

There appears to be sexual dimorphism with respect to the anterolateral margin of the pronotum. In the males this margin is clearly sinuous; in the females it is at most weakly sinuous. The pronotal lobe is more weakly developed in males than in females.

Lincus repizcus, new species
(Figs. 49–52)

Description. Dorsum dark brown becoming fuscous on anterior disk of pronotum, head and connexiva, mottled with yellowish brown rugae and small macules of same color: one on each humerus, mesially at base of scutellum, on disk of each corium and on margin in middle of each connexival segment. Antennae dark brown excepting brownish yellow mesial surface of first segment and basal third of last segment. Rostrum and legs brownish yellow excepting superior surface of tibia, broad diffuse incomplete subbasal tibial band and similar subapical femoral band darker. Venter yellowish brown with punctures and surrounding area brown to fuscous; head, evaporative areas and plura above coxae fuscous; mesial impunctate abdominal vitta brown; yellow macule on lateral margins of each sternite includes lateral trichobothrium.

Head 2.3–2.4 mm wide across eyes, 2.0–2.1 mm long. Antennal segments 0.7–0.8, 0.8, 0.9, 1.4, 1.6–2.0 mm in length; first segment clearly surpasses apex of head (Fig. 49). Eyes from dorsal view 0.55 mm wide, anterior–posterior diameter 0.5–0.6 mm. Interocular width 1.3 mm; distance across ocelli 1.2 mm. Greatest diameter of each ocellus 0.25 mm. Juga a little longer than tylus, their lateral margins tapering sinuously toward apex. Base of tylus



Figs. 49–52. *Lincus repizcus.* 49. Head and pronotum. 50. Genital plates, caudoventral view. 51. Pygophore, caudal view. 52. Same, lateral view.

slightly tumescent. Vertex of head convex, not tumescent, its lateral margins delineated on each side by densely punctate band of punctures that envelopes ocellus. Ventrally on each side a narrow but markedly elevated brown ridge runs from base of head to base of antennifer at mesial limit of eye. Rostral segments 2–4 about 2.2–2.6, 1.8–2.0, 1.7–1.9 mm in length.

Pronotal lobes nearly parallel-sided, extending laterad of eye by 0.2–0.3 width of eye; emargination caudad of lobes reaching mesad of lateral limit of eye by about 0.1 width of eye. Width of pronotum across humeri 5.5–5.7 mm, mesial length 2.4–2.5 mm; anterolateral margins slightly sinuous; disk rugosely punctate.

Scutellum 3.4–3.5 mm wide at base, 4.3–4.5 mm long. Fovea in each basal angle black, triangular, with one large and a few small punctures. Punctures in basal disk forming transverse vermiform rows separated by ruga.

Greatest width and greatest length of basal plates subequal, about 1 mm (Fig. 50).

Pygophoral emargination U-shaped, its margins entire (Fig. 51). Posterior pygophoral margin convex in profile (Fig. 52).

Length about 11 mm.

Distribution. Peru.

Holotype. ♂, labeled (a) "Valle Chanchamayo (Peru) 800 M, 13-VIII-1951, Leg. Weyrauch" (51 of the year written over other numbers) (b) "EKW4632" (c) "ex col. Weyrauch" (d) "coleccion Fundacion M. Lillo, 4000 S. M. Tucumán, Tucumán, Argentina". Deposited in Fundacion Miguel Lillo, Tucumán, Argentina.

Paratype. ♀, labeled (a) "Pucallapa, Peru. 6-6-1956. Jose M. Schunke, Coll." (b) "J. C. Lutz Collection, 1961" (USNM).

Lincus discessus Distant
(Figs. 53–56)

Lincus discessus Distant, 1900, pp. 688–689.

Diagnosis. Pronotal lobe on each side extending laterad of eye by less than 0.2 width of eye, curving to rounded apex. Incision between lobes and anterolateral pronotal margins shallow, scarcely extending mesad as far as lateral limit of corresponding eye. Antennal segments 2 and 3 subequal in length. Juga projecting beyond tylus but not markedly convergent (Fig. 53). Interocular width and distance across ocelli subequal; width of each eye about 0.42 of interocular width. Posterior margin of each basal plate unevenly convex, bending most at posterolateral angle of 9th paratergites; latter briefly contiguous mesially (Fig. 54). Pygophore without projections extending into mesial emargination from border, contour of emargination interrupted only at dorsal corners by sulcus formed by diagonal lamina entad of posterior pygophoral surface (Fig. 55). Posterior pygophoral surface concave in profile (Fig. 56).

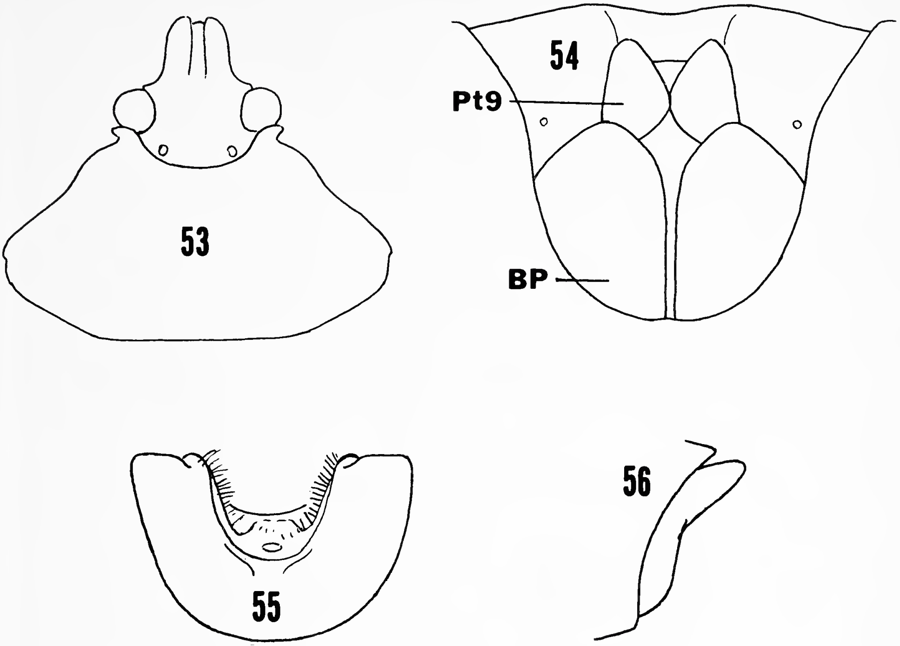
Length 9.3–11.5 mm.

Distribution. Costa Rica, Guyana.

Comment. The holotype, a female was examined.

Lincus varius, new species
(Figs. 57–59)

Description. Dorsum dark brown to fuscous with small brownish yellow macule on each humerus, on disk of each corium, mesially at base of scutellum and marginally in middle of each connexival segment; some rugae of pronotum and scutellum and all appendages brownish yellow, the 3 basal antennal segments darker than last 2 segments. Venter fuscous with some

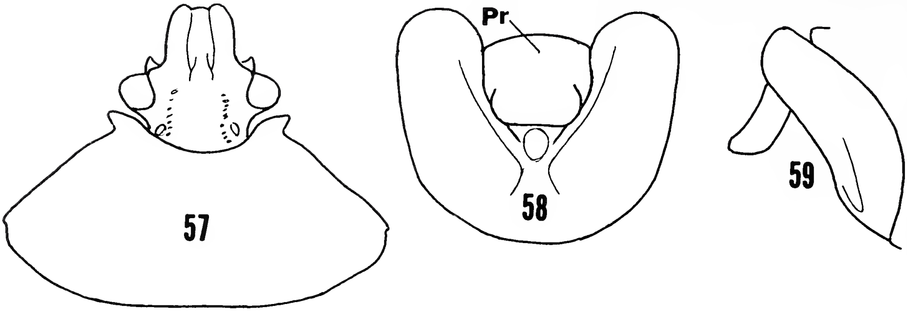


Figs. 53–56. *Lincus discessus.* 53. Head and pronotum, antennifers omitted. 54. Genital plates, caudoventral view; basal plates (BP); 9th paratergites (Pt9). 55. Pygophore, caudal view. proctiger omitted. 56. Same, lateral view.

rugae and broad somewhat discontinuous callus along lateral margins of abdomen brownish yellow; calli extend mesad to include mesial trichobothrius; punctation inconspicuous.

Head 2.3 mm wide across eyes, 2.2 mm long. Antennal segments 0.7, 0.7, 1.1, 1.4, 2.0 mm in length; first segment reaching apex of head. Eyes from dorsal view 0.45–0.5 mm wide, anterior–posterior diameter 0.6 mm, their width 0.35–0.40 of interocular width. Distance across ocelli from lateral limit of one to lateral limit of other 1.2 mm; greatest diameter of each ocellus 0.25 mm. Juga slightly longer than tylus, their lateral margins subparallel between concavity above antennifers and apex of head (Fig. 57). Tylus tumescent at base. Vertex of head convex but not tumescent, its lateral margins defined on each side by densely punctate band which envelopes ocellus. Ventrally on each side a slightly elevated narrow ridge runs from base of head to base of antennifer at mesial limit of eye, this ridge contrastingly brownish yellow on fuscous surface. Rostral segments 2–4 about 2.8, 2.1, 2.0 mm long.

Pronotal lobes subtriangular, extending laterad of eye by 0.2–0.3 width of



Figs. 57–59. *L. varius.* 57. Head and pronotum. 58. Pygophore, caudal view; proctiger (Pr). 59. Same, lateral view.

eye; emargination caudad of lobes reaching mesad as far as lateral limit of eye or nearly so. Width of pronotum across humeri 6.4 mm, mesial length 2.3 mm; anterolateral margins slightly sinuous, disk somewhat rugosely punctate with weak ruga on meson.

Scutellum 3.4 mm wide at base, 4.4 mm long. Triangular black fovea in basal angles with few punctures. Most punctures in scutellum arranged in transverse vermiform rows.

Pygophoral emargination a bowed V from caudal view (Fig. 58). Posterior margin of pygophore sinuously linear from lateral view (Fig. 59).

Length about 11.5 mm.

Distribution. Peru.

Holotype. ♂, labeled (a) "Satipo, Peru. III. 10. 1941. P. Paprzycki" (b) "J. C. Lutz Collection. 1961" Deposited in U.S. National Museum. Type no. 76691.

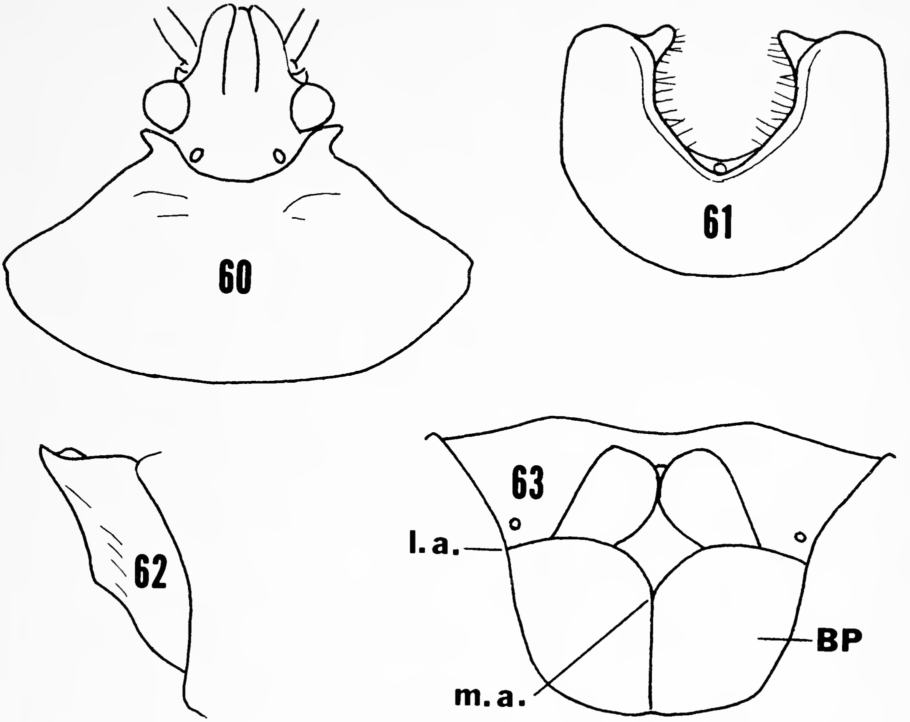
No paratypes.

Comments. This is one of 7 species with relatively small eyes. The pale, calloused band along the lateral margins of the abdominal venter and the parallel sided juga is a combination that distinguishes the species.

Lincus modicus, new species
(Figs. 60–63)

Description. Fuscous with castaneous or ochraceous macule on each humerus, mesially at base of scutellum and on disk of each corium. Basal band on last antennal segment and tarsi ochraceous. Rostrum brown.

Antennal segments 0.6–0.7, 0.8, 0.9–1.0, 1.2, 1.6 mm in length. Head little wider than long, 2.1 mm across eyes, 2.0 mm long. Width and anterior–posterior diameter of eyes subequal, about 0.5 mm, less than half interocular width. Interocular width 1.1–1.15 mm, slightly greater than distance across



Figs. 60–63. *Lincus modicus.* 60. Head and pronotum. 61. Pygophore, caudal view, proctiger omitted. 62. Pygophore, lateral view, proctiger omitted. 63. Genital plates, caudoventral view; basal plates (BP); lateral angle (l.a.); mesial angle (m.a.).

ocelli from lateral margin of one to lateral margin of other, 1.05 mm. Juga longer than tylus, apically convergent (Fig. 60).

Pronotal lobe on each side extending laterad about as far as lateral limit of eye, with anteromesial and posterolateral margins tapering to narrowly rounded apex, slightly reflexed apically. Incision between lobe and anterolateral margin of pronotum not extending mesad as far as middle of eye. Pronotal disk strongly punctate, rugosely so laterally. Width across humeri 5.2–5.4 mm, mesial length 2.2–2.3 mm.

Scutellum 3.2–3.3 mm wide at base, 3.9–4.0 mm long. Large black fovea in each basal angle containing several small punctures. Disk rugosely punctate basally. Connexiva entirely fuscous.

Posterior margin of basal plates broadly rounded mesially, otherwise subtruncate (Fig. 63). Greatest width of each plate (1.0 mm) exceeding greatest length (0.9 mm).

Large projection at dorsal corners of broadly U-shaped emargination in pygophore directed cephalad and dorsomesad (Fig. 61). From lateral view these projections visible above rim of genital cup (Fig. 62).

Length about 10.7–11 mm.

Distribution. Ecuador.

Holotype. ♀, labeled "Ecuador, Pastaza: Cuisimi, on Rio Cuisimi, 150 km SE Puyo, 350 m, May 15–31, 1971. B. Malkin". Deposited in the American Museum of Natural History.

Paratypes. Same labeling as holotype (12♂♂, 5♀♀ AMNH; 2♂♂, 2♀♀ LHR).

Lincus leviventris, new species
(Figs. 64, 65)

Description. Dark brown, appendages for most part lighter, with yellowish brown macule on each humerus, mesially at base of scutellum, on disk of each corium and marginally at middle of connexival segments.

Head 2.5 mm wide across eyes, 2.4 mm long. Antennal segments 0.8, 0.8, 1.1, 1.6 mm long (last segment missing); first segment reaching apex of head. Width and anterior–posterior diameter of eyes from dorsal view equal, about 0.55 mm and about 0.45 of interocular width. Interocular width 1.4 mm; distance across ocelli about 0.1 less than interocular width. Juga longer than tylus, their lateral margins subparallel between concavity above antennifers and apex of head (Fig. 64). Rostral segments 2–4 about 2.9, 2.1, 2.1 mm long.

Pronotal lobes extending laterad of eye by 0.1–0.3 width of an eye, tapering to obtuse apex; emargination caudad of lobe extending about as far mesad as lateral limit of eye. Width of pronotum across humeri 5.9 mm, mesial length 2.5 mm; anterolateral margins sinuous; disk rugosely punctate.

Scutellum 3.6 mm wide at base, 4.4 mm long. Triangular black fovea in basal angles containing a few strong punctures. Basal disk rugosely punctate.

Abdominal venter inconspicuously punctate, smooth excepting some wrinkles along sutures.

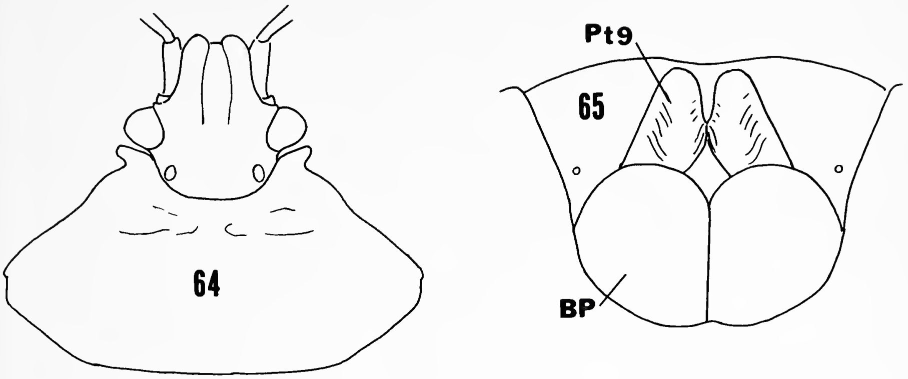
Greatest length of each basal plate 1.1 mm, greatest width 1.0 mm; posterior margin evenly convex; lateral angle anterior to mesial angle formed by junction of basal plates when viewed caudoventrally (Fig. 65). Ninth paratergites reflexed as narrow perpendicular ridge where they meet; surface convex with broad longitudinal ridge nearer mesial than lateral margins (Fig. 65).

Length about 12 mm.

Distribution. Peru (Cuzco). Known only from holotype.

Holotype. ♀, labeled (a) "Pilcopata" (2nd and 3rd letters uncertain) "Cuzco. 9-8-64" (b) "trampa de luz" (c) "CUZCO" (d) "1592". Deposited in Museu Nacional, Rio de Janeiro, Brazil. No paratypes.

Comments. This species is one of 7 whose interocular width is more than



Figs. 64, 65. *Lincus leviventris*. 64. Head and pronotum. 65. Genital plates, caudoventral view; basal plates (BP); 9th paratergites (Pt9).

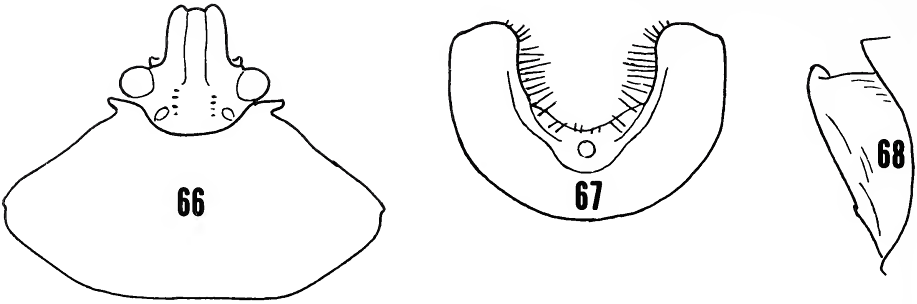
twice the width of an eye, i.e., it belongs in the "small eyed" group of species. Within this group it is one of 5 species bearing on each side a low ridge on the ventral surface of the head behind the eyes, and among these 5 only this species and *L. modicus* have the abdominal venter almost uniformly dark. The genital plates of these 2 species differ.

Lincus manchus, new species
(Figs. 66–68)

Description. Yellowish brown with darker punctures; humeri, narrow diffuse border on anterolateral pronotal margins, basal third of coria, apex of scutellum, lateral ventral margins of thorax and abdomen, all rufous; large discal macule on each corium, basal 0.4 of last antennal segment, tarsi and abdominal venter (excepting last sternite) between spiracular lines yellowish or brownish yellow, latter with brown punctures on each side of wide impunctate mesial area.

Head 2.0 mm wide across eyes, 1.8 mm long. Antennal segments 0.7, 0.6, 1.0, 1.2, 1.7 mm long; first segment reaching apex of head. Width and anterior–posterior diameter of eyes from dorsal view about 0.45 mm; width of an eye 0.4–0.45 of interocular width. Interocular width 1.1 mm, distance across ocelli subequal; ocelli relatively large, greatest diameter of each 0.35 of distance between them. Juga slightly longer than tylus, their lateral margins subparallel between concavity above antennifers and apex of head (Fig. 66). Vertex flat, delimited on each side by densely punctate depressed band that basally flows around ocellus. Rostral segments 2–4 about 2.1, 1.9, 1.8 mm in length.

Pronotal lobes extending laterad of eye by 0.4–0.5 width of eye, sides



Figs. 66–68. *L. manchus.* 66. Head and pronotum. 67. Pygophore caudal view, proctiger omitted. 68. Same slightly exserted, lateral view.

subparallel, narrowly rounded at apex; emargination caudad of lobes reaching mesad nearly to lateral limit of eyes. Width of pronotum across humeri 4.9 mm, mesial length 2.1 mm. Anterolateral margins sinuous, notably reflexed. Coarsely punctate disk with narrow irregular callus along meson.

Scutellum 3.0 mm wide at base, 3.7 mm long. Pale mesial line on basal disk. Punctation similar to that on pronotum.

Mesial emargination of pygophore U-shaped from caudal view; area around circular impression at base of emargination slightly raised (Fig. 67). Profile of pygophore nearly linear (Fig. 68).

Distribution. Bolivia. Known only from holotype.

Holotype. ♂, labeled (a) "Tumupasa, Boliv. Dec. W. M. Mann." (b) "Mulford Biological Exploration. 1921–1922." Deposited in the U.S. National Museum. Type no. 76693.

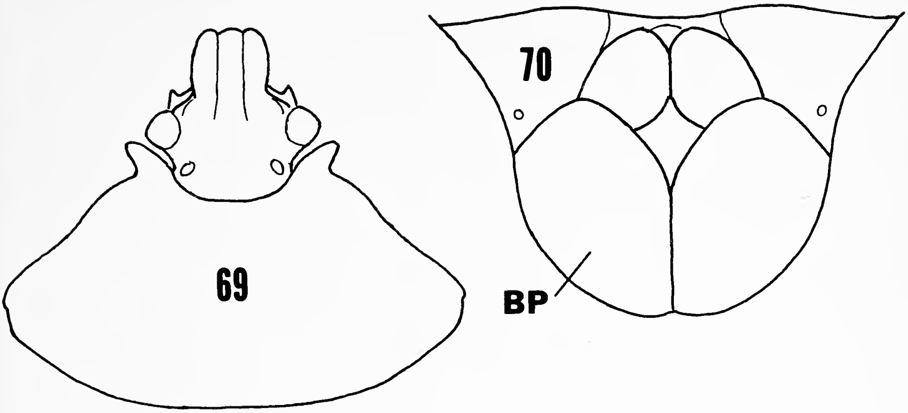
Comment. The small eyes, absence of a pair of ridges on the venter of the head between the base of the head and base of the antennifers, and large ocelli are a diagnostic combination.

The holotype may be somewhat callow and as a consequence unusually light in color.

Lincus armiger Breddin
(Figs. 69, 70)

Lincus armiger Breddin, 1908, pp. 26–27, fig. 4.

Diagnosis. Eyes relatively small, width of one eye about 0.4 of interocular width. Juga as long as tylus, their lateral margins somewhat constricted above antennifers (Fig. 69). Vertex evenly convex between ocelli; surface of juga shallowly excavated; base of eyes from ocelli to ommatidia somewhat polished; eyes not elevated above adjacent part of head; sides of head laterad of concavity in lateral margin of juga sloping to antennifers and visible from



Figs. 69, 70. *Lincus armiger*. 69. Head and pronotum. 70. Genital plates, caudoventral view; basal plates (BP).

above. Anterolateral margins of pronotum sinuous; pronotal lobes extending laterad of eyes by about one-half width of eye, triangular, narrowly rounded apically; emargination behind lobes extending no farther mesad than lateral limit of eyes. Basal plates with depressed area along posterolateral margins (Fig. 70); second gonocoxae convex. Length 10 mm.

Distribution. Bolivia. Known only from holotype.

Comments. The small eyes together with the form of the head distinguishes this species.

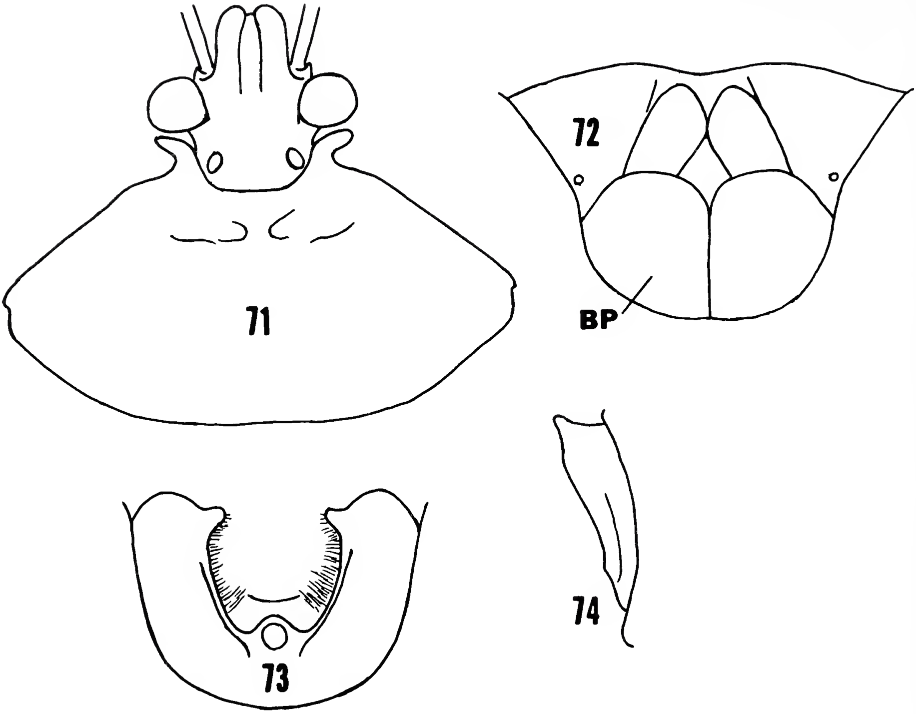
The female holotype, in the Naturhistorisches Museum Wien, was examined.

Lincus breddini, new species
(Figs. 71–74)

Description. Mostly fuscous with ochraceous macule on each humeral angle, mesially at base of scutellum and on disk of each corium. Last 2 segments of antennae, rostrum and tarsi also ochraceous.

Antennal segments 0.7–1.0, 1.0–1.4, 1.0–1.5, 1.4–1.8, 1.9–2.3 mm in length. Rostral segments 2–4 about 2.9, 2.2, 2.1 mm in length. Head 2.6–2.9 mm wide across eyes 2.3–2.6 mm long. Eyes wider by about 0.05 mm than their anterior–posterior diameter. Distance across ocelli from lateral margin of one to lateral margin of other usually slightly greater (0.1 mm or less) than interocular width. Width of eye (0.75–0.9 mm) more than half of interocular width (1.15–1.3 mm). Juga longer than tylus, apically convergent and occasionally contiguous (Fig. 71).

Pronotal lobes extending laterad approximately to lateral limit of eyes,



Figs. 71–74. *Lincus breddini.* 71. Head and pronotum. 72. Genital plates, caudoventral view; basal plates (BP). 73. Pygophore, caudal view, proctiger omitted. 74. Same, lateral view.

longer than wide, usually somewhat reflexed but not expanded apically, their anteromesial and posterolateral margins subparallel. Incision caudad of lobes extending mesad at least as far as middle of eye. Pronotal disk rugose. Width across humeri 6.2–7.4 mm, mesial length 2.3–2.6 mm.

Basal width of scutellum 3.8–4.5 mm, length 4.7–5.6 mm. Large black fovea in each basal angle containing several small punctures. Disk rugose except apically. Apex slightly reflexed on each side.

Posterior margin of basal plates truncately rounded (Fig. 72).

Mesial emargination of pygophore from caudal view with large projection near dorsal margin directed obliquely dorsomesad and somewhat cephalad (Fig. 72). Profile of pygophore irregular (Fig. 74).

Length about 12.2–14.3 mm.

Distribution. Surinam.

Holotype. ♀, labeled "Museum Leiden. Suriname. Mapane area, Blakka Watra, 26. V. 1960. Ph. v. Doesburg, Jr.". Deposited in the Rijksmuseum van Natuurlijke Historie. The left antenna is deformed, there being only 3 segments, with the basal 2 segments formed normally.

Paratypes. 4♀♀, 8♂♂. Same data as holotype (♂, ♀ LHR; ♂, 3♀♀ RNH); handwritten label "Brownsweg, 8 juni '61", remainder uncertain (♀ RNH); handwritten label "Suriname 28. VI. 1938", remainder uncertain (♀ RNH); same labeling except date "16. VIII. 1938" (♂ RNH) and "13. X. 1938" (♂ RNH); "Museum Leiden. Suriname exp. 1948–1949" with additional handwritten data of which only "14. x. '48" is clearly decipherable (♂ RNH); "Suriname, Faglust op Erthyrina, 28. VI. 1938, Ge[--]les".

Comments. The species is named for Gustav Breddin who, among his numerous contributions to pentatomid taxonomy, described the majority of species previously recognized in the genus *Lincus.*

Lincus lamelliger Breddin
(Figs. 75–78)

Lincus lamelliger Breddin, 1908, pp. 34–35, figs. 19, 20.

Diagnosis. Pronotal lobe on each side extending laterad of eye nearly 0.4 width of eye, about as long as wide at base, broadly rounded apically (Fig. 75); anterolateral pronotal margins somewhat sinuous. Width of each eye about 0.6 of interocular width. Juga exceeding tylus, their lateral margins briefly subparallel anterior to antennifers. First antennal segment about 0.6 length of second. Posterior margin of basal plates broadly rounded (Fig. 78). Dorsal margin of pygophore from caudal view shallowly notched adjacent to large mesial emargination (Fig. 76); profile of pygophore concave (Fig. 77).

Length about 10.2–10.8 mm.

Distribution. Colombia, French Guiana, Surinam.

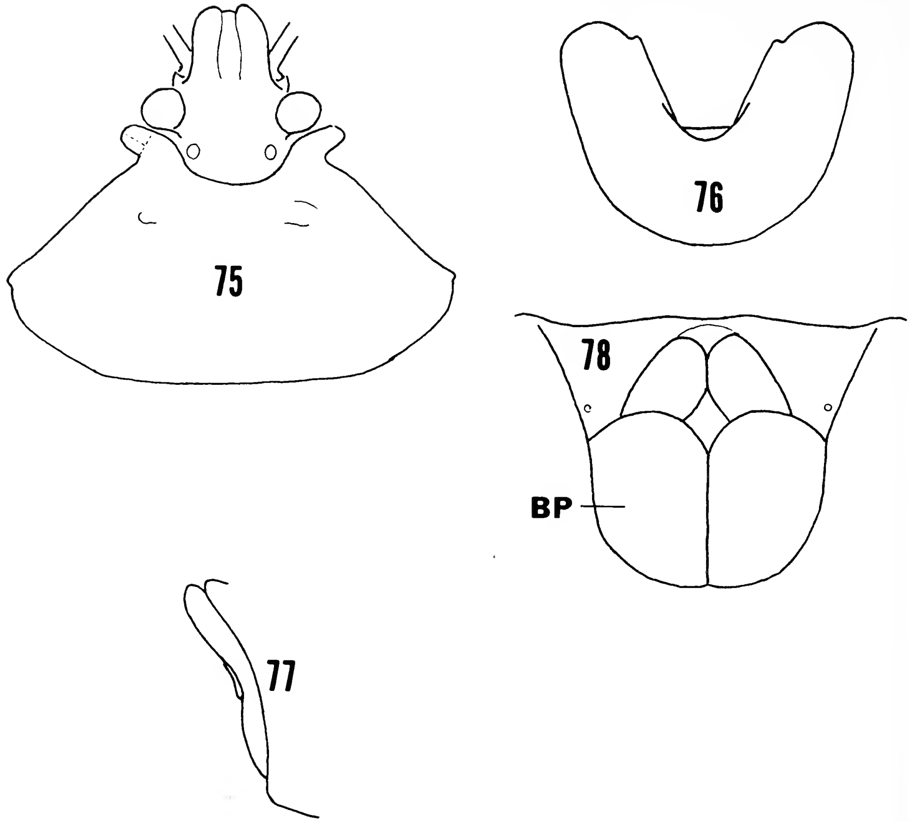
Types. Of 2 syntypes one remains in the Naturhistorisches Museum Wien. This female labeled "Colomb. Sign.", is designated lectotype.

Comment. The basal width and length of the pronotal lobes are subequal in this species; this is not true for other species of the "big eyed" group.

Lincus lobuliger Breddin
(Figs. 79–82)

Lincus lobuliger Breddin, 1908, pp. 27–29, figs. 5–8.

Diagnosis. Pronotal lobes variable in length, extending laterad nearly to lateral limit of corresponding eye, or longer and projecting laterad of eye as much as 0.4 width of eye (Fig. 79); incision caudad of lobes extending mesad of lateral limit of corresponding eye by about 0.2 width of eye; anterolateral pronotal margins sinuous. Width of each eye about 0.6 of interocular width. Juga exceeding tylus, their lateral margins anterior to anteocular concavity tapering slightly to apex. First antennal segment about 0.8 as long as second. Genital plates as in Figure 82. Dorsal margin of pygophore from caudal view



Figs. 75–78. *Lincus lamelliger.* 75. Head and pronotum. 76. Pygophore, caudal view, proctiger omitted. 77. Same, lateral view. 78. Genital plates, caudoventral view; basal plates (BP).

bearing on each side a small projection at edge of setose area along mesial emargination (Fig. 80); posterior pygophoral margin in profile strongly convex subdorsally (Fig. 81).

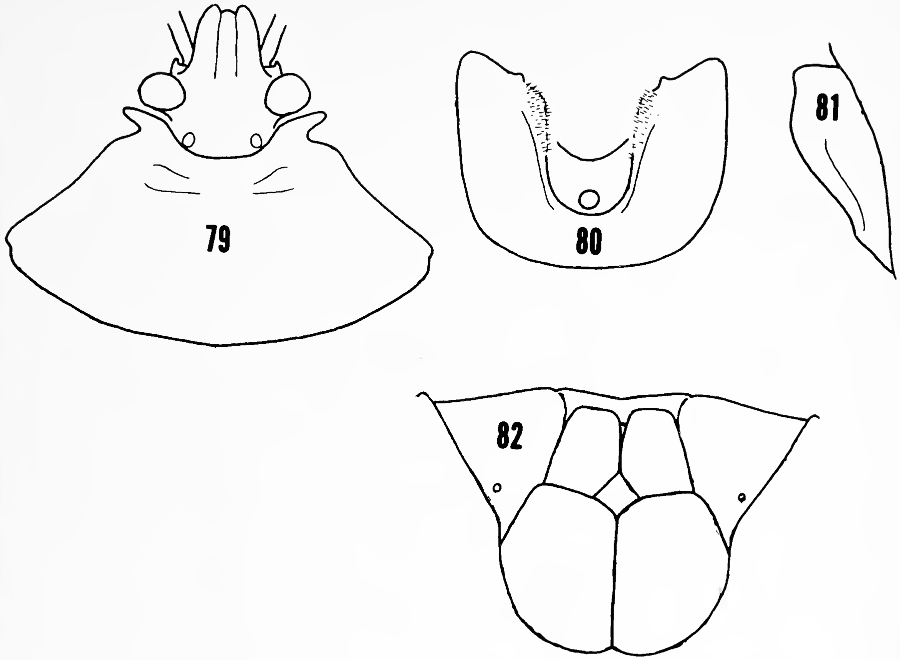
Length about 9.4–12.0 mm.

Distribution. Brazil (Bahia, Espirto Santo, Rio de Janeiro).

Types. Of the syntype series of 2 females and 1 male, only the male was located and examined. This specimen, in the Naturhistorisches Museum Wien, is designated lectotype.

Lincus rufospilotus (Westwood)
(Figs. 83–86)

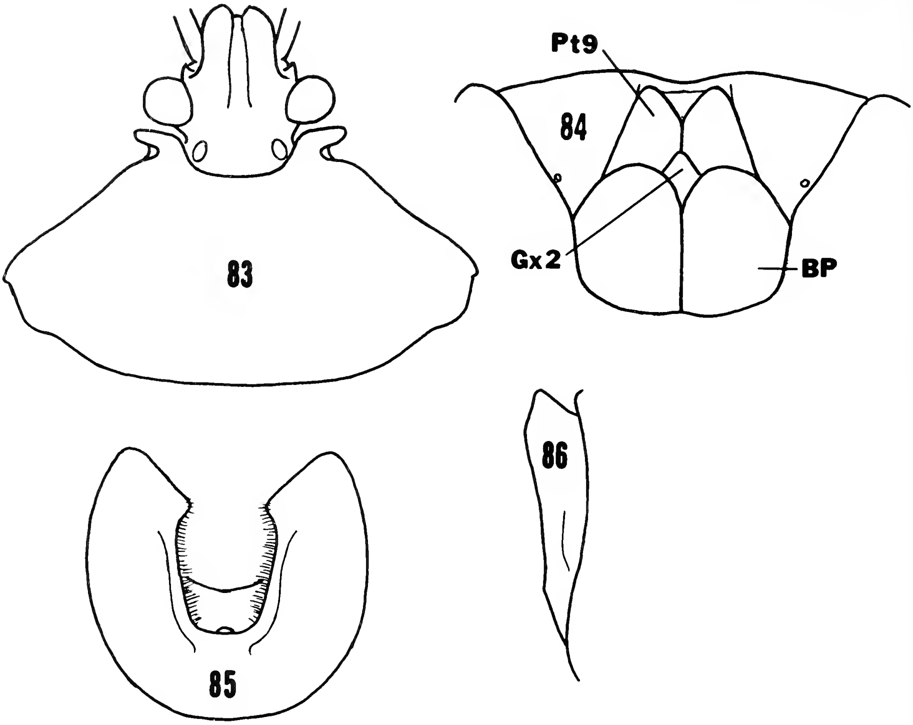
Pentatoma rufospilota Westwood, 1837, p. 44.
Ochlerus rufospilota: Dallas, 1851, p. 157.



Figs. 79–82. *Lincus lobuliger*. 79. Head and pronotum. 80. Pygophore, caudal view, proctiger omitted. 81. Same, lateral view. 82. Genital plates, caudoventral view.

Ochlerus villis Walker, 1867, p. 196 (synonymized by Distant, 1899).
Lincus rufospilotus: Stål, 1867, p. 254; Distant, 1899, p. 423.
Lincus erythrospilus Stål, 1872, p. 14 (replacement name).
Lincus cultiger Breddin, 1908, pp. 35–36, figs. 21–23. **New Synonymy.**

Diagnosis. Pronotal lobe on each side extending no further laterad of eye than 0.2 width of eye, narrowly round and often reflexed apically (Fig. 83). Incision between posterior margin of lobes and anterolateral pronotal margins not reaching as far mesad as middle of eyes. Distance across ocelli slightly greater than interocular width. Width of each eye about 0.1 greater than one-half of interocular width, slightly greater than anterior–posterior diameter of eye from dorsal view. Antennal segments 2 and 3 subequal in length; segments 4 and 5 lighter in color than basal 3 segments, neither annulated. Juga projecting beyond tylus, their lateral margins parallel between anteocular concavity and apex. Posterior margin of basal plates broadly rounded; greatest width of each plate about 0.8 of greatest length (Fig. 84). Large mesial emargination in pygophore from caudal view U-shaped below tubercles protruding into emargination at its dorsal limit; rim of emargination continuing for short distance ventrad of emargination (Fig.



Figs. 83–86. *Lincus rufospilotus.* 83. Head and pronotum. 84. Genital plates, caudoventral view; basal plates (BP); 9th paratergites (Pt9); 2nd gonocoxae (Gx2). 85. Pygophore, caudal view, proctiger omitted. 86. Same, lateral view.

85); dorsal pygophoral margin on each side of emargination slanting evenly dorsolaterad to rounded dorsolateral corners. Posterior surface of pygophore sinuously linear in profile (Fig. 86).

Large species, 11.5–15 mm in length.

Distribution. Northern Brazil, Colombia, Guyana, Peru and Surinam.

Comments. The holotypes of *Pentatoma rufospilata, Ochlerus vilis* and *Lincus cultiger* were examined.

Stål (1872) gave no reason for renaming the species but he presumably believed that *Pentatoma rufospilota* was preoccupied.

Lincus vallis, new species
(Figs. 87–89)

Description. Dark castaneous to fuscous with ochraceous macule on each humeral angle, mesially at base of scutellum and on disk of each corium. Basal fourth of last antennal segment and mottling on venter also ochraceous.

Antennal segments 0.7, 0.8, 1.3, 2.1, 2.0 mm long. Head 2.4 mm wide across eyes, 2.1 mm long. Eyes slightly wider (by 0.05–0.1 mm) than anterior–posterior diameter, the width of each equal to or slightly greater than half interocular distance. Distance across ocelli 1.1 mm, 0.1 mm less than interocular width. Juga longer than tylus, their lateral margins converging sinuously toward apex (Fig. 87). Rostral segments 2–4 about 2.5, 2.2, 2.0 mm long.

Pronotal lobes extending laterad of eyes by about 0.2 width of eye, about twice as long from base of incision to apex as wide, parallel sided or slightly expanded subapically; incision behind lobes reaching mesad well past lateral limit of corresponding eye but not reaching middle of eye. Disk rugose. Anterolateral margins sinuous. Width at humeri 5.9 mm, mesial length 2.5 mm.

Scutellum 3.7 mm wide at base, 4.4 mm long. Fovea in each basal angle triangular, black. Disk rugose except apically.

Length about 11.7 mm.

Mesial emargination of pygophore from caudal view U-shaped, with setose projection directed mesad from dorsal limit of emargination (Fig. 88). Dorsal pygophoral margin on each side of emargination sloping dorsolaterad. Rim of emargination disappearing at level with bottom of emargination. Posterior surface of pygophore sinuously linear in profile (Fig. 89).

Distribution. Peru. Known only from holotype.

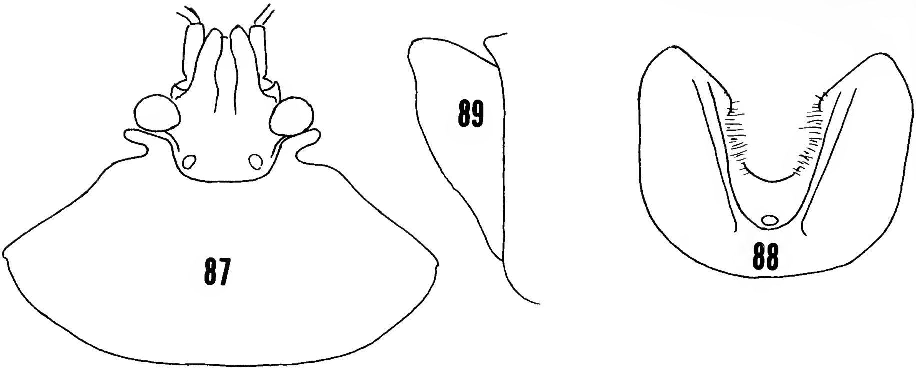
Holotype. ♂, labeled "Tingo Maria, Huan. Peru. Nov. 21, 1946. Alt. 670 m." Deposited in the U.S. National Museum. Type no. 76695.

Comments. This species is similar to *L. rufospilotus* but differs in having antennal segment 3 about 1.5 times as long as segment 2, the basal fourth of the last antennal segment pale, the distance across the ocelli less than the interocular width, and the produced rim along the mesial pygophoral emargination disappearing at a level even with the bottom of the emargination.

Lincus dentiger Breddin
(Figs. 90–93)

Lincus dentiger Breddin, 1904, p. 154; Breddin, 1908, pp. 24–26, figs. 1, 2 (redescription); Gaedike, 1971, p. 84 (type).

Diagnosis. Pronotal lobes on each side extending laterad of eye by less than 0.2 width of eye, tapering to narrowly rounded apex. Incision between lobe and anterolateral pronotal margin of pronotum extending mesad about as far as lateral limit of eye. Antennal segments 2 and 3 subequal in length. Juga not or scarcely exceeding tylus (Fig. 90). Interocular width and distance across ocelli subequal, about twice width of one eye. Posterior margin of basal plates broadly and evenly rounded. Each 9th paratergite subtriangular (Fig. 93). Emargination in pygophore from caudal view constricted midway



Figs. 87–89. *Lincus vallis.* 87. Head and pronotum. 88. Pygophore, proctiger omitted, caudal view. 89. Same, lateral view.

in dorsoventral direction, cordiform ventrad of constriction, widening uniformly dorsad of constriction (Fig. 91); pygophoral profile as in Figure 92.

Length about 9.5–10 mm.

Distribution. Ecuador, Surinam.

Comments. The type, a female from Ecuador, was examined. Both sexes were seen from Surinam.

Lincus styliger Breddin
(Figs. 94–99)

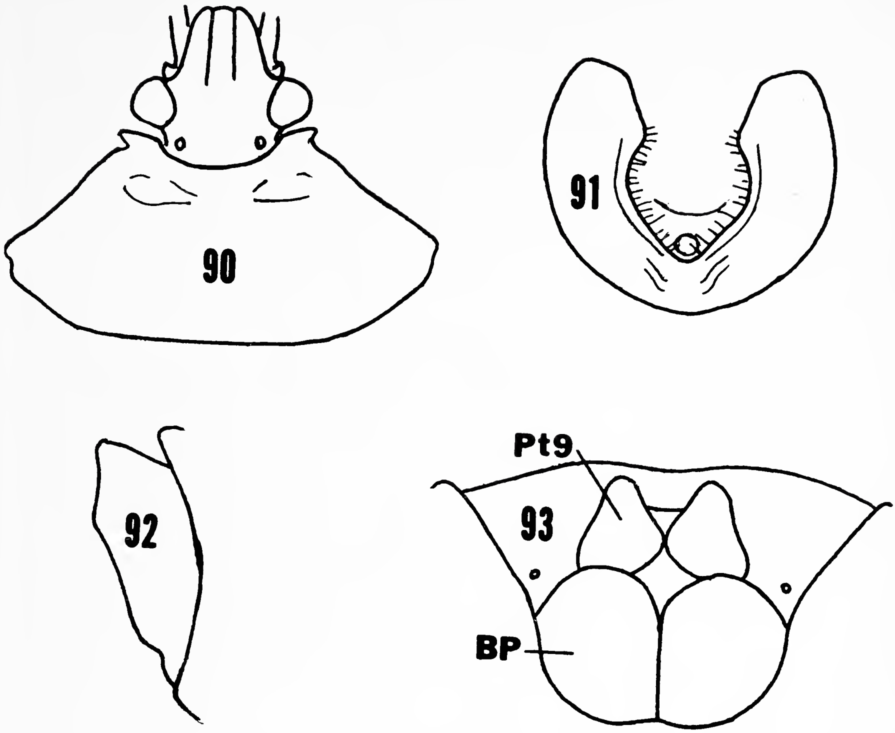
Lincus styliger Breddin, 1908, p. 31, figs. 12, 13.

Diagnosis. Pronotal lobe on each side extending laterad of eye by nearly one-half width of eye; length of each lobe from base of emargination almost twice width of lobe at this point; apex narrowly rounded (Figs. 94, 95); anterolateral margins of pronotum sinuous. Width of each eye about 0.6 of interocular width. Juga exceeding tylus slightly, their lateral margins converging slightly toward apex. First antennal segment about 0.8 length of second. Basal plates subtriangular with uniformly convex posterolateral margin (Fig. 96). Mesial emargination of pygophore V-shaped; dorsal margin of pygophore from caudal view notched about midway between mesial emargination and dorsolateral corners (Fig. 97), this notch resulting from inflection of posterior rim of genital cup on each side into a small dorsolateral lobe and large plate mesoventrad of this lobe (Fig. 99). Posterior pygophoral surface convex in profile (Fig. 98).

Length 11.5–12.5 mm.

Distribution. Colombia, Peru.

Types. The 2 syntypes were not located. Of a pair of specimens in the



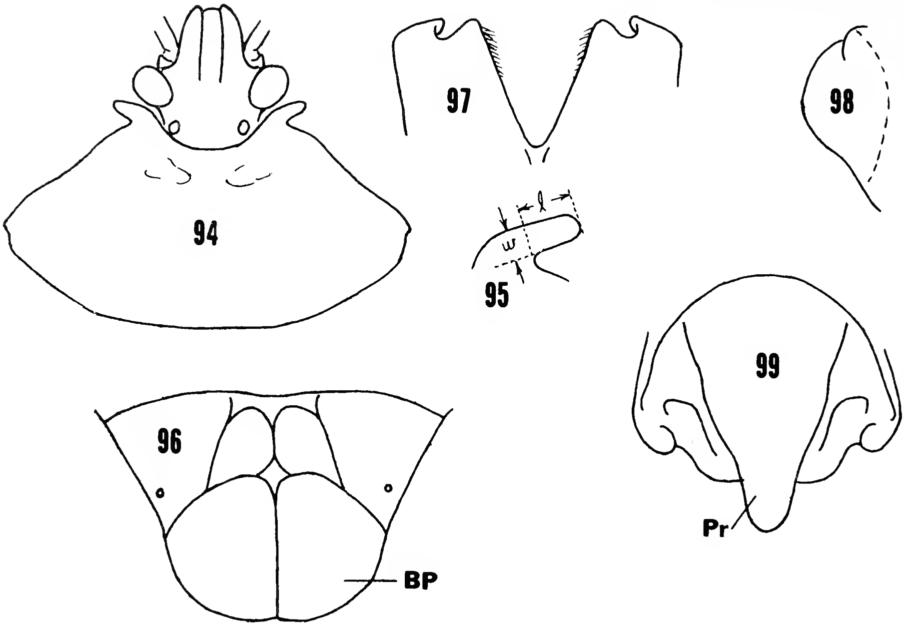
Figs. 90–93. *Lincus dentiger.* 90. Head and pronotum. 91. Pygophore, caudal view, proctiger omitted. 92. Same, lateral view. 93. Genital plates, caudoventral view; basal plates (BP); 9th paratergites (Pt9).

Akademie der Landwirtschaftswissenschaften der DDR, a male labeled "Peru, Amer.", with the abdomen and pygophore both carded, is designated the voucher specimen.

Lincus laminatus, new species
(Figs. 100–103)

Description. Fuscous to dark brown with following light brown to yellowish brown: macule on humeri, on base of scutellum mesially and on disk of each corium; calloused marginal line or macule expanding from middle of connexival segments to form broken submarginal band on abdominal venter; many interstitial areas of venter.

Head 2.5 mm wide across eyes, 2.0 mm long. Distance between lateral limits of ocelli (1.15 mm) slightly greater than interocular width (1.10 mm). Width of eyes (0.7 mm) greater than anterior–posterior diameter (0.6 mm)



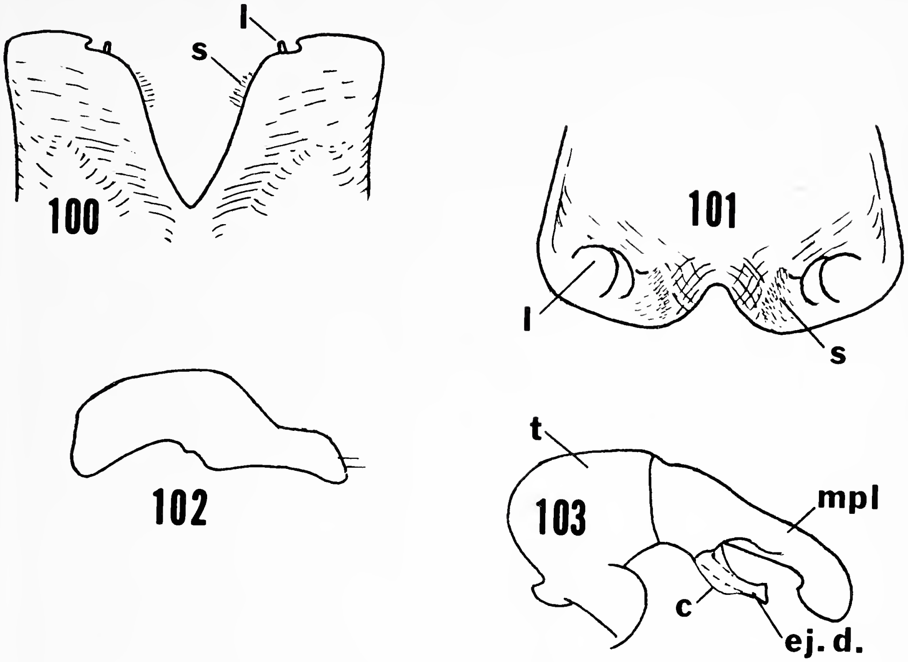
Figs. 94–99. *Lincus styliger*. 94. Head and pronotum. 95. Pronotal lobe. 96. Genital plates, caudoventral view; basal plate (BP). 97. Dorsal margin and mesial emargination of pygophore, caudal view, proctiger omitted. 98. Same, lateral view, probable anterior limit of exposure indicated by broken line. 99. Genital cup, dorsal view; proctiger (Pr).

from dorsal view. Juga exceeding tylus, their lateral margins parallel between concavity above antennifers and convexity at apices.

Pronotal lobes long, narrow, their anteromesial and posterolateral margins subparallel, extending laterad of eye by distance equal to 0.2 width of an eye; emargination caudad of lobes reaching mesad of lateral limit of eye by distance equal to 0.2 width of eye. Anterolateral margins of pronotum quite sinuous. Width of pronotum at humeri 7.1 mm, mesial length 3.1 mm.

Scutellum 4.3 mm wide at base, 5.3 mm long; fovea in basal angles with large deep puncture; apex weakly reflexed on each side.

Pygophoral emargination V-shaped; dorsal margin of pygophore stepped down toward mesial emargination and riser of step recessed (Fig. 100). Posterodorsal border of genital cup with 2 laminae on each side of emargination near dorsal margin and dorsad of patch of dense stout setae (Fig. 101); part of dorsal laminae visible above dorsal pygophoral margin from caudal view, and some of setae visible in mesial emargination. Posterior surface of pygophore deeply impressed between rim of mesial emargination and lateral border of pygophore. Parameres as in Figure 102. Aedeagus as in Figure 103; membranous conjunctiva enveloping much of ejaculatory



Figs. 100–103. *Lincus laminatus.* 100. Dorsal margin and mesial emargination of pygophore, caudal view, proctiger omitted; lamina (l); setae (s). 101. Posterodorsal border of genital cup; lamina (l); setae (s). 102. Paramere. 103. Aedeagus, lateral view; conjunctiva (c); ejaculatory duct (ej.d.); median penial lobes (mpl); theca (t).

duct, remainder of aedeagus heavily pigmented and sclerotized; median penial lobes elongate.

Length about 11.5 mm.

Distribution. Peru. Known only from holotype.

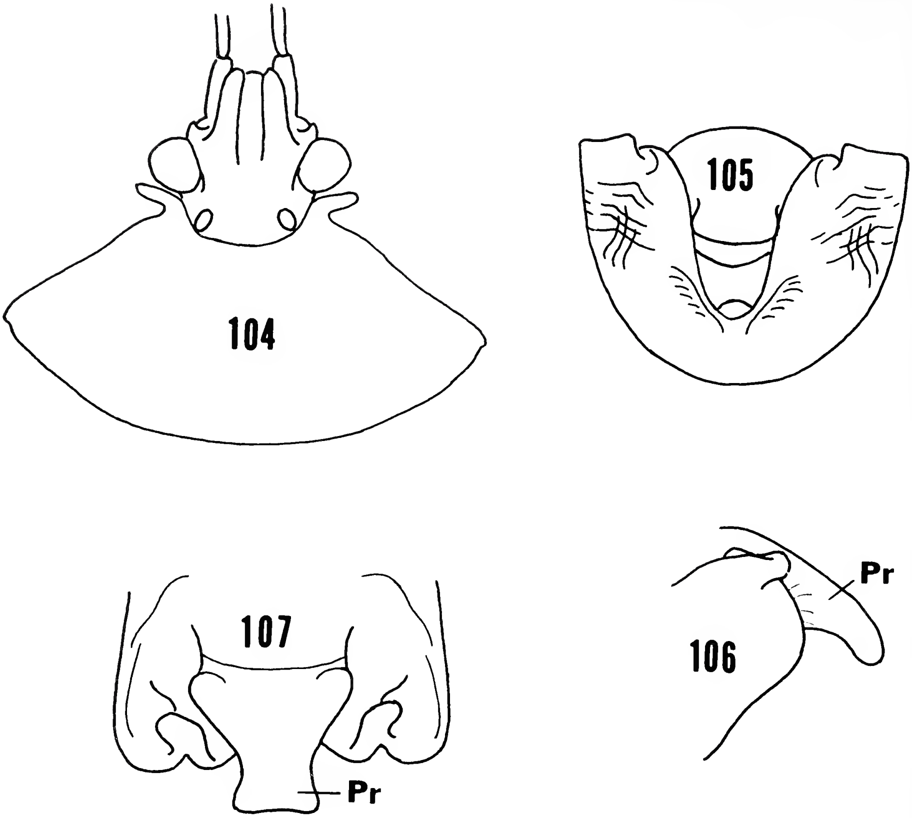
Holotype. ♂, labeled "PERU: Loreto Prov. Amazon Safari Camp. Rio Manón NNW Iquitos, ca. 3° 42′ S 73° 14′ W." Deposited in American Museum of Natural History. The holotype is completely without appendages.

No paratypes.

Comments. This species is much like *L. styliger,* differing in the male genitalia and in the parallel lateral margins of the juga.

Lincus substyliger, new species
(Figs. 104–107)

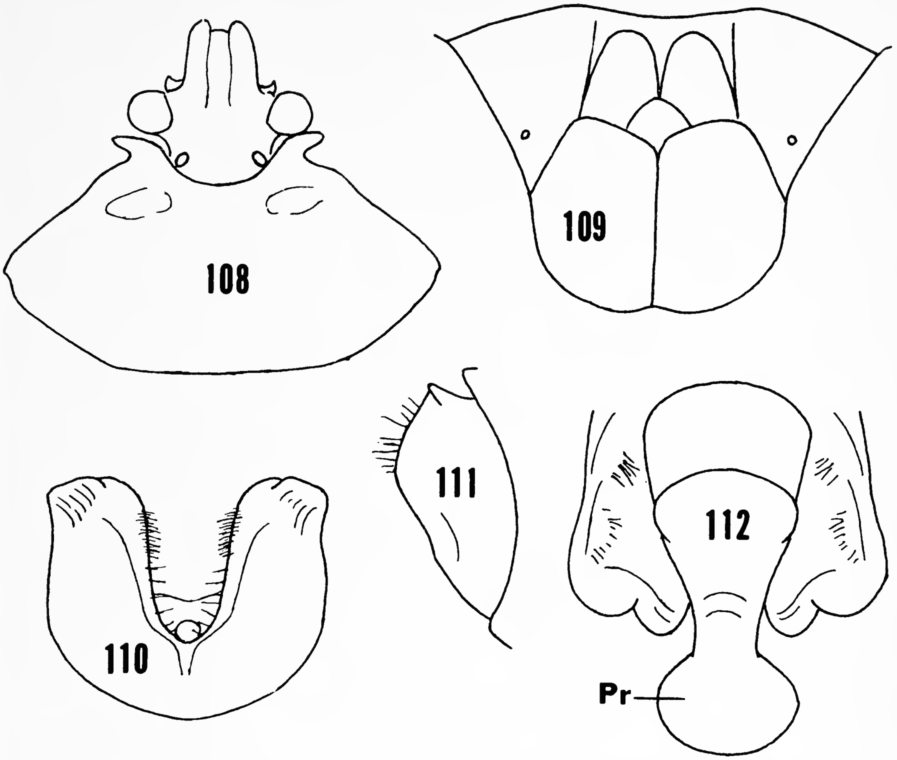
Description. Dorsum fuscous with humeral angles and macule on disk of each corium reddish orange; basal fourth of last antennal segment yellowish. Venter fuscous to dark castaneous.



Figs. 104–107. *Lincus substyliger.* 104. Head and pronotum. 105. Pygophore, caudal view, proctiger omitted. 106. Same, profile. 107. Same, dorsal view; proctiger (Pr).

Antennal segments 0.8, 0.8, 1.1, 1.4, 1.9 mm long; basal segment extending slightly beyond apex of head. Rostral segments 2–4 about 2.5, 2.0, 2.0 mm long. Anterior–posterior diameter of eyes and width from dorsal view subequal, about 0.6–0.65 mm. Interocular width 1.1 mm. Distance across ocelli 1.2 mm; greatest diameter of each ocellus about 0.25 mm. Juga slightly longer than tylus, their lateral margins subparallel between anteocular concavity and apex. Width of head across eyes 2.4 mm, length 2.1 mm. Vertex normally convex.

Pronotal lobes parallel-sided, longer than wide, extending laterad of eyes by 0.1–0.2 width of an eye; incision caudad of lobes reaching mesad from lateral limit of corresponding eye by 0.3–0.4 width of eye. Width of pronotum across humeri 5.6 mm, mesial length 2.3 mm. Disk rugosely punctate. Anterolateral margins weakly sinuous (Fig. 104).



Figs. 108–112. *Lincus subuliger.* 108. Head and pronotum. 109. Genital plates, caudoventral view. 110. Pygophore, caudal view, proctiger omitted. 111. Same, lateral view. 112. Genital cup; proctiger (Pr).

Scutellum 3.5 mm wide at base, 4.4 mm long. Fovea present in each basal angle.

Pygophoral emargination narrowly U-shaped from caudal view, notched at junction with dorsal margin where rim continues into genital cup and flattens into lamina inclined anterodorsad (Figs. 105, 106). Apex of proctiger flattened and expanded, attaining width about one-fourth greater than width of proctiger at base of expansion.

Length about 11.5 mm.

Distribution. Colombia. Known only from the holotype.

Holotype. ♂, labeled (a) "Colombia: Road Bogota-Villavicencio. June 29, 1965. 1500 M." (b) "P. & B. Wygodzinsky, Collectors." Deposited in the American Museum of Natural History.

No paratypes.

Comments. The pygophore of this species is similar to that of *L. styliger,* especially in having a lamina within the genital cup on each side of the mesial emargination near the dorsal margin of the cup. The most conspicuous difference between these two species with respect to the male genitalia is that the proctiger of *L. styliger* is neither flattened nor expanded apically.

This species resembles *L. subuliger* in having the apex of the proctiger flattened and expanded, although in *L. subuliger* the expansion is much greater, about three-fourths wider than the proctiger at the base of the expansion. The rim of the mesial pygophoral emargination of *L. subuliger* continues into the genital cup as a low ridge on each side of the emargination and does not enlarge into a lamina as it does in this species.

Lincus subuliger Breddin
(Figs. 108–112)

Lincus subuliger Breddin, 1908, p. 33, figs. 17, 18.

Diagnosis. Pronotal lobes extending laterad of eyes by 0.2–0.4 width of eye, longer than wide at base (Fig. 108). Width of each eye about 0.55 of interocular width; distance across ocelli subequal to interocular width. Juga exceeding tylus, their lateral margins subparallel anterior to concavity above antennifers. First and second antennal segments subequal in length. Basal plates diagonally truncated apically (Fig. 109). Mesial emargination of pygophore narrowly U-shaped; posterolateral corners of pygophore bent posteriorly (Fig. 110); profile of pygophore quite convex (Fig. 111); proctiger expanded and flattened apically into small paddle (Fig. 112).

Length about 11–11.5 mm.

Distribution. Colombia, Venezuela.

Comments. Breddin's type, which was examined, is a female from an unknown locality.

The proctiger of this species is remarkable for its apical expansion.

DEPOSITION OF PARATYPES

AL	Akademie der Landwirtschaftwissenschaften
HDE	H. Dodge Engleman collection
LHR	author's collection
MZSP	Museu de Zoologia de São Paulo
RNH	Rijksmuseum van Natuurlijke Historie
USNM	U.S. National Museum

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91(1), 1983, pp. 48–56

ON THE BIOLOGY AND FOOD PLANTS OF *LYGAEUS TURCICUS* (FABR.) (HEMIPTERA: LYGAEIDAE)[1]

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Abstract.—The food plant of *Lygaeus turcicus* (F.) is shown to be the false sunflower, *Heliopsis helianthoides* (L.) (Sweet) (Asteraceae) rather than species of milkweeds (Asclepiadaceae). The literature is reviewed and the records of *L. turcicus* on milkweeds are believed to pertain to *Lygaeus kalmii* Stål. Laboratory rearing records are summarized for *L. turcicus* on seeds of *Heliopsis helianthoides, Asclepias syriaca* L. and sunflowers. Nymphs of all five instars and the egg are described. The nymphs are compared and contrasted with those of *Lygaeus kalmii.*

For many years I have been puzzled by the scarcity of *Lygaeus turcicus* (F.) in New England and the upper midwest despite the abundance of its supposed food plant, the large milkweed, *Asclepias syriaca* L., and the abundance upon this plant of the closely related milkweed bug, *Lygaeus kalmii* Stål. Although on two occasions specimens were taken in late summer on this milkweed, I have never encountered a breeding population in the northeast. The scarcity of *turcicus* could have several causes: 1) it is at the northern periphery of its range in the northeast; 2) it does not breed in the northern states, but rather migrates north in the summer, as is the case with *Oncopeltus fasciatus* (Dallas) (Dingle, 1965); 3) it is outcompeted by *Lygaeus kalmii*; or, 4) it is associated with some plant other than *Asclepias syriaca* L. With the last thought in mind, I have spent considerable time in the field observing other milkweed plants, but without finding a specimen of *L. turcicus.*

It has been apparent for sometime (see Slater, 1964) that many records of *L. turcicus* actually refer to *L. kalmii* and others cannot, in the absence of specimens, be assigned to either species. Indeed some authors, e.g., Heidemann (1894), have considered the two to be synonymous; this is certainly not the case as both adults and nymphs differ in a number of ways.

Uhler (1872) stated that eggs were deposited on *Asclepias.* In 1878 he noted that records in the T. W. Harris collection suggested that adults and nymphs were present on *Asclepias syriaca.* Provancher (1886) reported tak-

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[1] This work was supported in part by a grant from the National Science Foundation.

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ing it on *Asclepias cornuti* Dcne. (=*A. syriaca*). Townsend (1887), in a detailed paper treating the life history of what he called *turcicus,* quoted from Uhler's (1878) paper to demonstrate that in Michigan *turcicus* was taken on *Asclepias syriaca* as early as 1832 (Harris collection) and that "larvae" were present. Townsend also noted however that *turcicus* was seldom found in Michigan "on any other plant than *A. tuberosa* although sometimes on *A. syriaca.*" He does mention an individual specimen taken on ragweed, "a tall weed," and a flowering almond, but considered these accidental occurrences. In 1891 Townsend again reported *turcicus* feeding on *A. tuberosa* L. and seemed to have little doubt that this was the principal food plant.

There are numerous later records on milkweeds. Robertson (1891) reports *turcicus* on flowers of *A. cornuti* and *A. incarnata* L., Blatchley (1895) reports adults and nymphs on *A. cornuti,* Morrill (1910) states that *Asclepias* is the natural food and, as recently as 1944, Froeschner reports it on flowers of *Asclepias tuberosa.* Nymphs are recorded as present several times suggesting that milkweeds are the host plants and that the preferred host may be the butterfly weed, *A. tuberosa.* I have attempted to take *turcicus* from the orange butterfly weed on a number of occasions without success, although *Lygaeus kalmii* occurs there.

It is true that other plants have been associated with *turcicus.* Morrill (1910) reports it on cotton (this record apparently repeated by Hargreaves, 1948) and on alfalfa in Texas. Banks (1912) lists it from *Ceanothus* in Virginia (record repeated by Barber, 1912, 1923, and Torre-Bueno, 1946, among others). Blatchley (1926) lists it from flowers of *Rhus hirta* (L.) Sudw. Robertson's (1929) compendium of plant associations lists it on flowers of 26 species of plants, only three of which are milkweeds. None of these nonmilkweed records give any indication that immature stages were present and therefore do not suggest a breeding host relationship.

Several references establishing *Lygaeus kalmii* Stål as breeding on various species of milkweeds can be found in the literature (Simanton and Andre, 1936; see Slater, 1964, for references), and it has been reared in the laboratory on dry milkweed seeds in a manner similar to *Oncopeltus fasciatus* (Dallas). The paucity of recent records of *L. turcicus* on milkweeds, coincident with the increase of records of *L. kalmii,* strongly suggests that the earlier records of *turcicus* might in part, or entirely, refer to *L. kalmii.* (See following article by Wheeler for *kalmii* food plants.)

The establishment of the principal food plant of *L. turcicus* came quite unexpectedly; the manner in which this question was resolved emphasizes strongly the importance of, and need for, enthusiastic amateurs in American entomological study.

In 1979 the Rev. James M. Sullivan of St. Louis, Missouri sent me a letter expressing his pleasure with the recent publication of my book with Dr. R. M. Baranowski (Slater and Baranowski, 1978). Rev. Sullivan stated that for many years he had been collecting host plant records of various Hemiptera, and he included sample pages for several species, one of which was *Lygaeus turcicus*. The Sullivan records indicated that *turcicus* did not breed upon milkweeds but rather on the composite *Heliopsis helianthoides* (L.) Sweet, the false sunflower. Rev. Sullivan generously made available his entire file on *turcicus,* and to him is due the credit for establishing the definitive host plant.

The Sullivan records list *turcicus* from 18 species of plants in eight families. Of 49 records 28 are from *H. helianthoides,* and 11 of the remaining 21 are from other composites (Asteraceae). *H. helianthoides* was the only plant upon which copulation was observed and the only plant upon which nymphs were taken; his records included all collections made later than June 30. There was only a single record of *turcicus* occurring on a milkweed—adults taken on the inflorescence of *Asclepias incarnata.*

The most compelling of the Sullivan records for *L. turcicus* on *H. helianthoides* are summarized:

1. September 5, 1976—nymphs of various instars feeding.
2. September 8 to September 29, 1976—nymphs present and molting to later instars on same plants during period.
3. September 15, 1976—eight nymphs present, one reared to adult.
4. Records of adults copulating June 30, 1972, July 30, 1973, August 28, 1974 and August 9, 1977.
5. More than 50 specimens July 25, 1979.
6. Six records of feeding from June through August of several years.

On August 15, 1982 A. G. Wheeler, Jr. (pers. comm.) took many adults and first, second and third instar nymphs on *H. helianthoides* in Randolph County, West Virginia (Route 219 midway between Valley Head and Mingo).

In July and August 1979 Rev. Sullivan sent specimens of *L. turcicus* from St. Louis, Missouri. They were carried through four generations in this laboratory entirely upon the dried seed heads of *H. helianthoides* with almost no mortality.

As noted below *turcicus* was reared successfully for more than one generation on dried sunflower seeds and also upon seeds of *Asclepias syriaca.* Specimens were reared both in the open laboratory and in an environmental chamber. Growth was more rapid on milkweed seeds than upon sunflower seeds.

Thus it appears that *L. turcicus* utilizes *Heliopsis helianthoides* as its principal and possibly only breeding host. However, it certainly is capable, in the laboratory at least, of completing its life cycle on other plants, including milkweeds. This is not really surprising, as in the laboratory *Oncopeltus fasciatus* has been successfully maintained upon both sunflower and peanut seeds, although there is no evidence that it ever breeds upon these plants in the field. The choice of host plants in the field depends upon many factors, not merely the ability of the insect to survive and reproduce on a given plant. Slater and Wilcox (1973) suggest that many essentially host specific Lygaeidae tend to colonize other plants; occasionally such attempts are successful for a generation or two, and in some cases a "better" host may be selected, which, in time, becomes the primary plant upon which the insect breeds.

While there is no firm evidence that *L. turcicus* breeds upon any other plant than *H. helianthoides,* the number of Rev. Sullivan's records from other composites suggests that under favorable conditions some of these species may serve as hosts.

What is clearly evident is that *L. turcicus* is not a milkweed bug. It is unfortunate that Robertson (1929) apparently did not distinguish *turcicus* from *kalmii.* To my knowledge he is the only previous author to report *turcicus* from *H. helianthoides.* Many of his records are from composites, suggesting that he did, in part, have *turcicus* before him. (Robertson worked at Carlinville, Illinois not far from the St. Louis area.)

The scarcity of *L. turcicus* in the north, compared with populations in the middle Mississippi valley area, suggests that its breeding range may be more southern than previously thought, with a late summer movement northward in favorable years. Northern records should be carefully checked to attempt to test this hypothesis.

LABORATORY REARING

Eggs of *L. turcicus* were obtained from St. Louis County, Missouri, July 25, 1979. The insects were maintained for two generations in plastic containers with dry seeds of *H. helianthoides* and a water source. At this time fresh seed heads were introduced together with dried seeds, and individual egg masses were isolated in petri dishes. The colonies were first maintained at room temperatures and later placed in a rearing chamber at 75°F with a 16-hour day cycle for most of their development.

When seed heads of *H. helianthoides* were introduced into a colony, insects of all instars sought them actively. Young nymphs moved deep into the heads and were almost invisible despite the bright red color of the abdomen. Eggs were laid in clumps or loose masses of 15 to 50, preferentially upon cotton but sometimes loosely in the litter on the floor of the rearing cages.

Individual nymphs were not isolated, but colonies were examined daily and notes on egg laying, copulation, molting and death of adults recorded. While this method is less accurate than isolating individuals, the large number of observations taken from 35 colonies, some of which were maintained through several generations, has yielded data that is probably a reasonably reliable expression of the life cycle. The duration of the first stadium is appreciably shorter than that of stadia II, III, and IV, the latter three stadia

Table 1. Summary of laboratory rearing of *Lygaeus turcicus* (F.) reared on *Heliopsis helianthoides* (L.) Sweet.

	N	Mean	Median	Range	SD
Copulation to egg laying	17	5.06	5.5	3–8	1.56
Adult emergence to copulation	13	6.92	7	5–10	1.61
Egg laying to hatching	34	7.24	8	6–10	1.13
Instar I to instar II	35	3.77	4.5	2–7	1.19
Instar II to instar III	45	6.93	7	4–11	1.88
Instar III to instar IV	51	7	7	3–11	1.93
Instar IV to instar V	52	6.62	7.5	4–12	1.83
Instar V to adult	73	9.47	11	4–19	3.15
Adult longevity	34	60.91	59	26–97	19.31

are of equal length, and the duration of the fifth stadium is the longest (Table 1, Fig. 1). This life cycle agrees with those of many other hemipterans. The longevity of the adults is extremely variable but can be as long as three months.

In addition to the colonies maintained on *Heliopsis helianthoides,* similar colonies were established on commercial sunflower seeds and dried seeds of *Asclepias syriaca. Lygaeus turcicus* is capable of completing its life cycle on both of these food sources. Although these colonies were observed only sporadically on milkweeds, the length of the life cycle and the mortality appeared similar to colonies reared on *Heliopsis.* Where only sunflower seed was available, mortality was increased, the individual nymphs were smaller, and the duration of individual stadia appeared more erratic.

In several crosses attempted between *Lygaeus kalmii* and *Lygaeus turcicus,* no mating was observed and no fertilized eggs were produced.

IMMATURE STAGES

Nymphs of *Lygaeus turcicus* are readily distinguishable from those of *Lygaeus kalmii.* In the latter species the abdomen is conspicuously longitudinally striped with red and pale yellow. There is a broad, median, red stripe and an even broader red stripe somewhat laterad of midway between meson and each lateral margin. The intervening area is pale yellow with a "sprinkling" of tiny red dots; the lateral margins are broadly white. In *turcicus* the abdomen has the appearance of being nearly uniformly red rather than striped. However, as noted in the descriptions that follow, there is a tendency for early instars to have obscure stripes. In such cases *kalmii* nymphs can readily be distinguished by having a very conspicuous transversely elongate-elliptical black spot in the center of the sub-lateral red stripe on each ab-

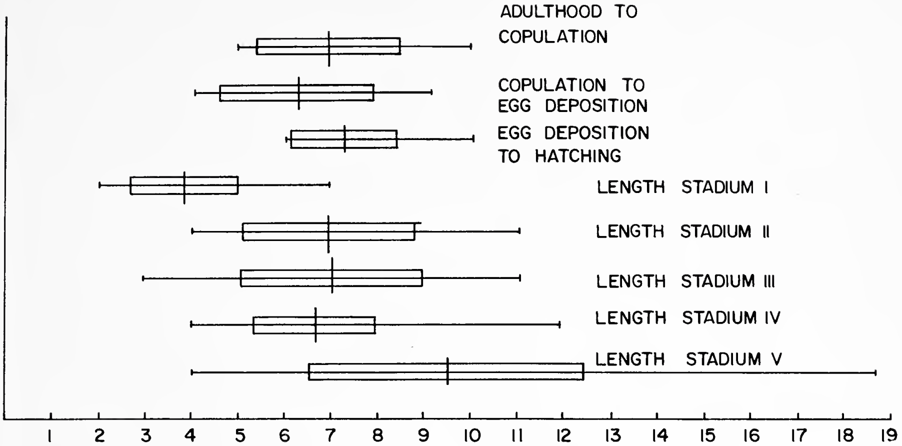

Fig. 1. Length of life cycle of *Lygaeus turcicus* (F.) reared on *Heliopsis helianthoides* (L.) Sweet.

dominal tergum from segments two through six. In *turcicus* this area is undifferentiated in color. These dark spots, plus the darkened areas around the abdominal scent glands, give nymphs of *kalmii* a striking spotted appearance.

The labium is much longer in *turcicus* than in *kalmii.* In *kalmii* the labium reaches only the metacoxae in early instars and only between the mesocoxae in later instars. In *turcicus* the labium reaches well onto the abdomen as late as the fourth instar, and even in the fifth instar it attains the posterior end of the metacoxae.

DESCRIPTION OF *Lygaeus turcicus* NYMPHS

Fifth instar. Coloration bright orange-red with strongly contrasting chocolate brown to black coloration as follows: a broad comma-shaped area that curves antero-laterad on each pronotal calli area, a small paler spot on posterior pronotal margin on either side of midline, meso- and metathoracic wing pads, antero-lateral corners of scutellum, elliptical areas around abdominal scent gland openings between terga 4–5 and 5–6, a mesal patch on tergum 8 and sterna 7 and 8, all appendages (but distal ends of femora paler). Dorsal coloration of head chiefly dull reddish brown. Vertex with a speckled, longitudinal, dark stripe on either side of midline, darkened anteriorly on tylus along inner margins of juga. Head below orange posterior to antennal bases, dark brown anteriorly.

General form typical for genus. First antennal segment exceeding apex of tylus. Labium attaining posterior ends of metacoxae. Length head 1.56[2], width 1.88, interocular space 1.31. Length pronotum 1.12, width 2.44. Length mesothoracic wing pads 2.94. Length abdomen 5.50. Length labial segments I 1.00, II 0.94, III 0.94, IV 0.88. Length antennal segments I 0.44, II 1.12, III 0.94, IV 1.38. Total length 9.44.

Fourth instar. General form and color as in instar five but dark coloration reddish brown rather than chocolate brown to black. Labium extending well onto second abdominal sternum. Length head 0.88, width 1.31, interocular space 0.81. Length pronotum 0.56, width 1.44. Length wing pads 0.88. Length abdomen 2.56. Length labial segments I 0.75, II 0.75, III 0.69, IV 0.62. Length antennal segments I 0.38, II 0.75, III 0.62, IV 1.00. Total length 5.50.

Third instar. Similar to instar four. Head markings as noted in instar five but much more strongly contrasting. Abdomen tending to show a narrow, darker, longitudinal orange stripe and shading to darker orange laterally. Lateral abdominal margins with a narrow white stripe present. Length head 0.94, width 1.12, interocular space 0.78. Length pronotum 0.50, width 1.25. Length wing pads 0.38. Length abdomen 1.56. Length labial segments I 0.62, II 0.62, III 0.62, IV 0.62. Length antennal segments I 0.31, II 0.56, III 0.62, IV 0.75. Total length 4.50.

Second instar. Very similar to instar three. Thoracic terga each marked with an irregular transverse dark "dash." Abdomen laterally with a broad pale yellow to translucent white border. Length head 0.66, width 0.76, interocular space 0.51. Length pronotum 0.32; width 0.90. Length abdomen 1.73. Length labial segments I 0.42, II 0.42, III 0.42, IV 0.42. Length antennal segments I 0.20, II 0.37, III 0.37, IV 0.56. Total length 3.05.

First instar. Head and thorax brown, strongly contrasting with bright red abdomen, each thoracic tergum marked with a nearly black transverse dash, similar to instar II. Abdomen nearly uniformly red except for pale margins. (Abdominal coloration variable; some nymphs have abdomen pale yellowish flecked with red and a darker reddish central longitudinal stripe.) Legs and antennal segments I–III pale brown, antennal segment IV suffused with reddish. Labium extending to middle of abdomen. Length head 0.59, width 0.56, interocular space 0.39. Length pronotum 0.20, width 0.56. Length abdomen 1.02. Length labial segments I 0.34, II 0.34, III 0.34, IV 0.34. Length antennal segments I 0.15, II 0.29, III 0.27, IV 0.49. Total length 1.81.

Egg. Smooth, glabrous, broadly elliptical with ten short subtruncate chorionic processes around anterior pole. Length 1.34, width 0.76.

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[2] All measurements are in millimeters.

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THE SMALL MILKWEED BUG, *LYGAEUS KALMII* (HEMIPTERA: LYGAEIDAE): MILKWEED SPECIALIST OR OPPORTUNIST?

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Abstract.—*Lygaeus kalmii* Stål, the small milkweed bug, often is considered a milkweed specialist. A review of recent literature and observations of nymphs and adults on composites (Asteraceae) and plants of other families in Missouri, Pennsylvania, and West Virginia show that *L. kalmii* uses various food sources. The feeding strategies of this lygaeid are briefly compared with those of *Oncopeltus fasciatus* (Dallas), a lygaeine restricted to milkweeds and related plants, and the Palearctic *Lygaeus equestris* (L.), which prefers asclepiads but feeds on plants of numerous families.

Relatively few North American insects have been thoroughly studied, and when a particular species is considered biologically well known, further investigation may be stifled. Any misconceptions about the habits of that species often are perpetuated in the literature and are difficult to rectify.

Any large, strikingly colored insect, especially a common one, is apt to convey the impression "well studied." Indeed, aposematic species of the lygaeid genera *Oncopeltus* and *Lygaeus* have long been characterized as milkweed feeders and are now known to sequester and store cardenolides (cardiac glycosides) from their hosts (Duffey and Scudder, 1972; Scudder and Duffey, 1972). *L. kalmii* Stål, known in the United States by the approved common name small milkweed bug, sometimes has been assumed representative of the specialized fauna associated with the Asclepiadaceae. Caldwell (1974) considered its utilization of resources similar to that of *O. fasciatus* (Dallas), a definite milkweed specialist, although he acknowledged the biology of *L. kalmii* was not as well known. Dailey et al. (1978) referred to both lygaeine species as "milkweed-specific."

Several species of *Lygaeus,* however, seem to furnish examples of hard-to-correct biological misconceptions. *L. turcicus* F., a close relative of *kalmii,* has been considered a milkweed bug although specific observations were lacking. Published records from *Asclepias* spp. are unreliable because many

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observers did not distinguish *turcicus* from *kalmii.* Slater (1983, this issue) has shown that *turcicus* feeds mainly on composites, especially ox-eye [*Heliopsis helianthoides* (L.) Sweet], rarely, if ever, developing on milkweeds.

Slater's paper, which I had the opportunity to review, prompted me to reevaluate my collections of *L. kalmii* from various composites, considered merely fortuitous when first made in 1977. Recent papers by Isman et al. (1977), Hunt (1979), and Duarte and Calabrese (1982) also led me to reappraise the habits of *L. kalmii.* Isman et al. found adults of *kalmii* collected from *Asclepias* spp. in California varied widely in their cardenolide content; they suggested that some of the adults might have developed on hosts lacking these compounds. In Michigan, Hunt described *kalmii* as an opportunist that feeds on various food sources, especially when milkweed pods are unavailable. After determining that the chromosome number and sex determination mechanism of populations in west Texas differed from those previously recorded, Duarte and Calabrese suggested *L. kalmii* might represent a sibling complex.

Herein I summarize my records of *L. kalmii* taken on plants other than milkweeds. Through the courtesy of the Rev. James M. Sullivan, who has made extensive collections of Hemiptera-Heteroptera (see Slater, 1983), I am able to refer to his observations of *kalmii* on various plants in Missouri. My Pennsylvania and West Virginia observations and those made in Missouri refer to the subspecies *angustomarginatus* Parshley (see Slater and Knop, 1969). On the basis of these observations tentative conclusions are drawn regarding the feeding strategies of this lygaeid.

OBSERVATIONS ON COMPOSITES

In late July 1977 I collected an adult and a 5th-instar nymph on the seed heads of yarrow, *Achillea millefolium* L. (Asteraceae = Compositae), in Adams County, Pennsylvania. Adults and a 5th instar were observed on heads of yarrow on a return visit to this site in mid-August 1982. At about this time I found 5 nymphs (instars III–V) and adults on heads of yarrow growing in an old field on Dolly Sods, a wilderness area at approximately 4,000 ft. (1,219 m) in Tucker County, West Virginia. Milkweeds were not observed in the vicinity (40–50 m) of either collecting site.

I found a larger population of *L. kalmii* associated with *Senecio vulgaris* L. growing in isolated colonies in an otherwise weed-free nursery in Somerset County, Pennsylvania. On 14 July 1982 about 10 mating pairs were observed on inflorescences and seed heads (dried capitula); many more adults were found beneath the plants. A thorough examination of the nursery beds and nearby hedgerows did not reveal any milkweeds or the association of *kalmii* with other composite or weed species. Two weeks later adults were common on the ground beneath *S. vulgaris*; 2 adults, a 3rd, and a 5th instar were collected on mature heads. On 19 August no nymphs were observed, but 3 adults were taken on fruiting heads and others were observed beneath *Senecio.*

During July and August I collected small numbers of late instars, usually only 1 or 2 individuals, on fruiting heads or inflorescences of *Centaurea maculosa* Lam., *Conyza canadensis* (L.) Cronq., and *Erigeron strigosus* Muhl. Adults only were collected on seed heads of *Ambrosia artemesiifolia* L., *Chondrilla juncea* L., *Daucus carota* L., and *Eupatorium perfoliatum* L.

In Missouri the Rev. Sullivan has observed *L. kalmii* visiting flowers in succession, apparently taking nectar from *Eupatorium altissimum* L. and *Solidago graminifolia* (L.) Salisb. In early March an adult was taken on the fresh receptacle of dandelion, *Taraxacum* sp., and in April on a dandelion flower and in gravel beneath the plants. During July–October adults were observed on inflorescences or old flower heads of *Cirsium altissimum* (L.) Spreng., *Eupatorium rugosum* Houtt., *Lactuca saligna* L., *Solidago altissimum* L., and *Tragopogon dubius* Scop.; apparent feeding took place on several of the plants. In October a mating pair was found on the dried heads of *Helianthus annuus* L. In the literature a mating pair is known from goldenrod, *Solidago* sp. (Procter, 1946), and on goldenrod Balduf (1943) observed an adult feeding on a dead honeybee. Maw (1976) swept *L. kalmii* from *Cirsium* and *Taraxacum.*

Lygaeus kalmii ON PLANTS OF OTHER FAMILIES

Occasionally I found nymphs of *L. kalmii* on nonmilkweed plants other than composites. Thirty or more nymphs (instars II–V) and a smaller number of adults were observed in August on mature inflorescences of buckwheat, *Fagopyrum sagittatum* Gilib. (Polygonaceae). The small field, well removed from milkweed and nearly weed free except for a few plants of common ragweed, *Ambrosia artemesiifolia,* was bordered by a pure stand of ragweed. No nymphs or adults, however, were observed or swept from ragweed. Smaller numbers of nymphs (1 or 2 individuals of instars III–V) were taken during August on *Hypericum punctatum* Lam. (Hypericaceae = Guttiferae) and on or under *Euphorbia* spp. (Euphorbiaceae) growing in isolated colonies in ballast along railroad tracks. In Missouri, the Rev. Sullivan observed 2 adults in early September on fruits of *Euphorbia* sp. He also observed probable feeding in late August on the calyx of *Campanula americana* L. (Campanulaceae) and 3 adults beneath these plants; in mid-October he found an adult with its rostrum inserted in a capsule of *Scrophularia marilandica* L. (Scrophulariaceae). In mid-September he collected an adult from an unripe fruit of *Datura stramonium* L. (Solanaceae).

DISCUSSION

The observations here summarized, and the studies of Hunt (1979), suggest that *L. kalmii* is not as intimately associated with Asclepiadaceae as stated in much of the literature and thus not a milkweed specialist in the sense of *Oncopeltus fasciatus.* Caldwell (1974) contrasted the migratory strategies of these lygaeines, noting that *kalmii* remains in its habitat year round rather than engaging in migratory flights. According to Caldwell, it flies to new habitats only when food or mates are scarce; he referred to its tracking of new milkweed stands as "more opportunistic" than in *O. fasciatus.*

L. kalmii also may be more an opportunist in its utilization of food resources. Adults obtain nectar from flowers in early spring and later in the season, sometimes "moving systematically from nectary to nectary" (Hunt, 1979). In late summer and fall *L. kalmii* may feed on seeds and other structures found on old flower heads.

L. kalmii also uses milkweeds for reproduction, and various asclepiads may represent preferred hosts. The similarity in distribution of *kalmii* and *Aclepias syriaca* L. and *A. speciosa* Torr. (Slater and Knop, 1969) suggests a dependence on these plants if not an extensive coevolutionary history.

But the finding of nymphs on various composites and on plants of unrelated families suggests that *L. kalmii* develops also on nonmilkweed hosts. The observation of 1 or a few late instars on other plants may be based on nymphs that have ascended after completing most of their development elsewhere. It is known that nymphs feed on fallen seeds of their hosts and that 5th instars may climb plants at metamorphosis (Hunt, 1979). It is likely, however, that the nymphs found on *Senecio vulgaris* and buckwheat completed their development on those plants.

The evidence indicates that *L. kalmii* reproduces on plants other than Asclepiadaceae or the related Apocynaceae, perhaps "getting by" before milkweed pods are formed. Hunt found that this multivoltine lygaeid was not common on milkweed in southern Michigan until late June and not abundant until July or August. She characterized *kalmii* as an opportunistic forager which preferred milkweeds but fed on a succession of angiosperms when asclepiads were scarce or unavailable. It is not clearly stated, however, whether this foraging involved adults only or if nymphs occurred on nonmilkweed hosts.

Assuming reproduction takes place on plants other than milkweeds, my observations and Hunt's may help explain the relatively few nymphs Dailey et al. (1978) collected on milkweed in Ohio (152 compared to 1,021 adults). Nymphs may have fed on fallen milkweed seeds, but it is possible that they developed on plants of other families. Feeding on nonmilkweed hosts may also explain the differences in cardenolide content that Isman et al. (1977) found in field-collected *L. kalmii* in California.

Observations of *L. kalmii* on composites and other plants unrelated to the Asclepiadaceae and Apocynaceae suggest a comparison with the Palearctic lygaeine *L. equestris* L. This species, although preferring the asclepiad *Cynanchum vincetoxicum* (L.) Pers., feeds on a succession of hosts throughout the season. It has been observed on more than 60 plant species in 37 families; nymphs have been associated with 13 species in 11 families (Solbreck and Kugelberg, 1972). Another milkweed-associated lygaeine that is known to develop on composites is *Spilostethus pandurus* var. *elegans* (Wolff) in South Africa (Slater and Sperry, 1973). A lygaeine perhaps preferring seeds of Asteraceae and feeding on some of the same composite genera as *L. kalmii* (e.g., *Achillea, Senecio*) is the widely distributed *Neacoryphus bicrucis* (Say) (Solbreck and Pehrson, 1979).

Careful field studies are needed to determine the similarity in feeding strategies between *L. kalmii* and *L. equestris*. Such work will help determine whether oviposition occurs a considerable distance from potential food plants (as Kugelberg, 1977, has reported for *L. equestris*), whether the occurrence of nymphs on aerial portions of plants reflects only a shortage of seeds on the ground, the extent to which feeding preferences vary throughout the geographic range, whether resource utilization changes during development (as Puchkov, 1956, has discussed for various phytophagous Heteroptera), and whether feeding on nonmilkweed plants represents a recent shift in the host spectrum similar to the use of oleander (*Nerium oleander* L.—Apocynaceae) by *Oncopeltus fasciatus* in Florida (Klausner et al., 1980).

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A NEW SPECIES OF CLERADINI (HEMIPTERA: LYGAEIDAE: RHYPAROCHROMINAE) FROM THE CENTRAL AFRICAN REPUBLIC AND GHANA

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Abstract.—*Navarrus ater,* a new Ethiopian species, is described in a formerly monotypic genus known only from the Oriental Region and New Guinea. Characters are presented to distinguish *N. ater* from *N. phaeophilus,* the type species of the genus. A dorsal view drawing of the holotype of *N. ater* is provided.

Members of the little-known hemipteran tribe Cleradini are nest inquilines found principally in the nests of rodents where they feed on vertebrate blood. In such a specialized habitat these insects are not commonly collected. Indeed, some species are known only from the limited material of the original description. A majority of the genera in this tribe are currently monotypic.

The cleradine genus *Navarrus* was described by Distant in 1901, with *Rhyparochromus phaeophilus* Walker, 1872 as the type species. To date *Navarrus* has remained monotypic, with *N. phaeophilus* known to occur broadly in the Oriental Region and in New Guinea. The present paper extends the distribution of *Navarrus* into the Ethiopian Region by describing *N. ater,* a new species from the Central African Republic and Ghana. In the following description all measurements are in mm and the Villalobos color chart (Palmer, 1962) has been used as a standard.

Navarrus ater, new species

Virtually entire body surface dark blackish brown; scutellum subtly darker, almost true black; tarsi, lateral pronotal carina and lateral hemelytral carina appearing lighter, between blackish brown and sepia; subproximal one-third antennal segment IV dark tawny, segment IV dark on distal two-thirds and in very narrow band at proximal end.

Body subshining save for dull granular evaporative area surrounding metathoracic scent gland auricle and adjacent strip along posterior margin mesopleuron. Pronotum, scutellum, clavus, and corium evenly covered with

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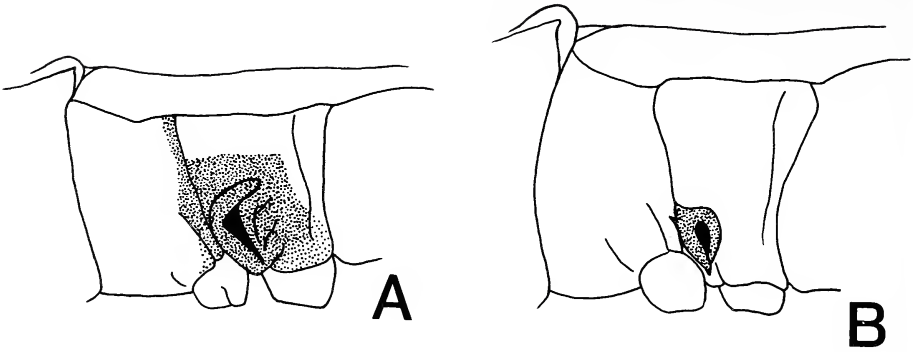

Fig. 1. Metathoracic scent gland auricles and evaporative areas of: (A) *Navarrus ater* and (B) *N. phaeophilus.*

small shallow punctures; punctures larger and deeper on head and lateroventral aspects of pro- and mesothorax; abdomen impunctate, marked lateroventrally on sterna II and III (first two visible) with large finely textured areas representing a diffuse stridulitrum. Abdomen sparsely clothed with slender recumbent posteriorly directed hairs; similar distally directed hairs on legs and antennae; head including eyes with short anteriorly directed hairs, some stout and bristle-like; each puncture on pronotum, scutellum and hemelytra containing a very short minute scale-like hair.

Head very short and broad, slightly declivent from flat vertex; tylus narrow, appearing markedly so with antenniferous tubercles short to nonexistent; eyes large, seeming to rest on anterior pronotal angles; postocular distance negligible; ocelli at posterior margin of head; length head 0.56; width 0.90; interocular distance 0.46. Pronotum shield-like, not noticeably bilobed, declivent from posterior margin; transverse impression obsolete; no collar apparent on anterior lobe; a broad continuous lateral carina running from anterior angle to just short of posterior margin; humeral angle elevated and knob-like, extending posteriorly a short but distinct distance beyond lateral carina; posterior pronotal margin straight across base of scutellum; length pronotum 1.00; width posterior margin across humeral angles 1.64; greatest width including carinae 1.78. Length scutellum 0.90; width 0.94. Hemelytron vaguely sinuate laterally, with a broad lateral carina; length corium 2.58; distance apex corium to apex membrane 0.34; length claval commissure 0.50; distance apex clavus to apex corium 1.16. Labium extending between mesocoxae; length labial segments I 0.30, II 0.26, III 0.82, IV 0.26; bucculae long extending most of head length, with a broad U-shaped juncture at level of proximal one-third labial segment II. Antennae with segments relatively stout; length antennal segments I 0.24, II 0.40, III 0.26, IV 0.68. Fore femur slightly incrassate, armed on anterior edge of ventral surface with three very

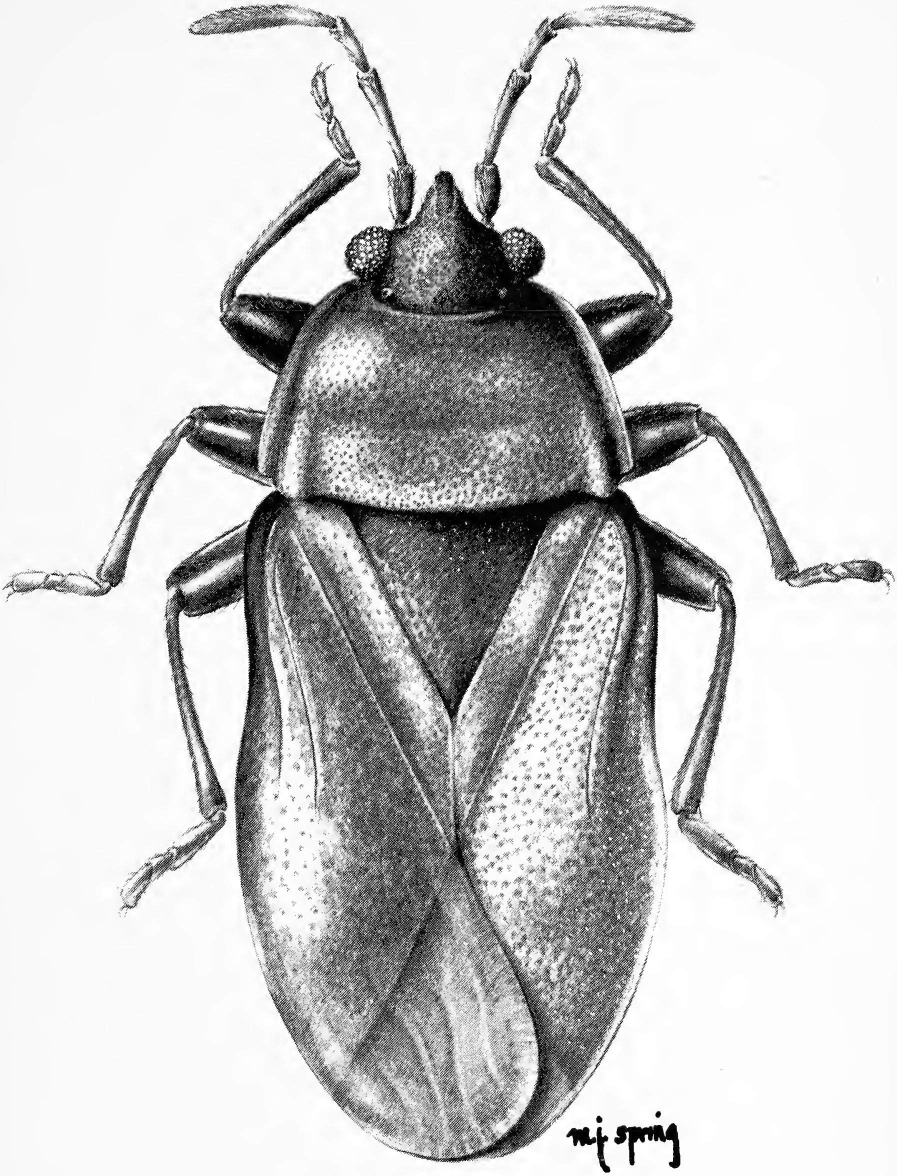

Fig. 2. *Navarrus ater,* new species. Holotype, dorsal view.

minute broad spines each with a stout apical bristle; meso- and metafemora also relatively swollen; metafemur with several fine denticles on posterior surface aligned to strike textured areas on abdomen, these two surfaces probably constituting a stridulatory apparatus. Metathoracic scent gland auricle large elongate crescent-shaped and arched posteriorly (Fig. 1a). Total length 4.44.

Holotype. ♀, CENTRAL AFRICAN REPUBLIC: La Maboke 6–9.VI.1973 (Linnavouri). In American Museum of Natural History, New York.

Paratypes. CENTRAL AFRICAN REPUBLIC: Same data as holotype, 1♀. GHANA: Tafo 10.X.1967 (UV trap) (D. Leston), 1♀. In J. A. Slater and B. J. Harrington collections.

The paratype from Ghana is somewhat lighter (more toward chestnut) than the holotype and paratype from the Central African Republic.

N. ater and *N. phaeophilus* have a very similar general habitus with a broad ovoid body shape, a distinct shelf-like and reflexed lateral pronotal carina, an obsolete pronotal transverse impression, and a broad short head that is not prolonged at all in the postocular region.

N. ater can be easily distinguished from *N. phaeophilus* by its uniform dark coloration. *N. phaeophilus* is lighter with the ground color ranging between chestnut and tawny. In *N. phaeophilus* the hemelytral membrane is largely fuscous but proximally marked at the midline with a distinct light colored macula contiguous to the claval commissure. *N. phaeophilus* also has a small rounded scent gland auricle with the evaporative area confined to the auricle itself (Fig. 1b) in contrast to the large crescent-shaped auricle of *N. ater* which is surrounded by a broad evaporative area that extends onto the posterior margin of the mesopleuron (Fig. 1a). Additionally, *N. ater* apparently has a stridulatory apparatus while there is no evidence of one in *N. phaeophilus.*

Such striking morphological differences might suggest separate generic status for *N. ater.* However, without male specimens for examination and pending a comprehensive generic-level reevaluation of the tribe Cleradini that will shed more light on whether the features shared by *N. ater* and *N. phaeophilus* represent synapomorphies or symplesiomorphies, it seems preferable to be conservative and describe this new species as a member of the genus *Navarrus.*

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OVERWINTERING EGG MASS ADAPTATIONS OF THE EASTERN TENT CATERPILLAR, *MALACOSOMA AMERICANUM* (FAB.) (LEPIDOPTERA: LASIOCAMPIDAE)[1]

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Abstract.—Experiments were designed to determine the role of the spumaline covering eastern tent caterpillar egg masses as an adaptation for overwintering. The ability of the spumaline to absorb water from the environment is a direct function of temperature and water concentration in air. Egg mass temperatures may be significantly higher than ambient temperatures. The spumaline covering egg masses of this species may act to ameliorate low overwintering temperatures and to prevent desiccation by absorbing as much moisture from surrounding air as possible.

The survival success of overwintering insects is achieved by many adaptations which overcome or compensate for extremes and fluctuations in winter conditions. In the temperate regions adaptations like the presence of cryoprotectants, low supercooling points and reduced metabolic activity (dormancy) are examples of physiological adaptations. More subtle but equally important to survival are microenvironmental adaptations, such as location of hibernacula and external protective structures.

Malacosoma americanum (Fab.), the eastern tent caterpillar, overwinters as a pharate larva inside its egg shell. Egg masses are laid on branches of suitable hosts in early summer. Complete embryonation occurs within 3–4 weeks. These mature embryos remain dormant from late July to April of the following year (Mansing, 1974). Characteristically the egg masses of all North American species (except *M. tigris*) are covered with a froth called spumaline. This material which is produced in accessory glands is deposited by the ovipositing female on top of the newly laid eggs. Very little is known about this material. Hodson and Weinman (1945) described important features of the spumaline on eggs of *Malacosoma disstria* such as its ability

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[1] This research was completed at the Department of Entomology of the University of Massachusetts, Amherst, Massachusetts.

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to absorb atmospheric moisture and elucidated the role of spumaline in the eclosion process.

This investigation examines, in further detail, the adaptive role of the spumaline of overwintering *Malacosoma americanum* egg masses in modulating environmental temperature and humidity.

MATERIAL AND METHODS

All tent caterpillar egg masses examined were collected from black cherry trees (*Prunus serotina* Ehrh.) located in Amherst, Massachusetts (42°23′N, 72°32′W) during the months of January–April 1979.

Hygroscopic properties of spumaline. To test water absorption capabilities of egg masses, field collected egg masses were exposed to three different temperatures: 0°C, −5°C, −10°C and five different saturation deficits per temperature for a total of 15 treatments, replicated 3 times each with 9 egg masses per replicate. Before being used in experiments any egg mass sections not covered by spumaline were covered with wax. All egg masses were placed in a controlled temperature chamber at 5°C until experiments began.

Our initial attempts to establish the hygroscopicity of the spumaline at low temperatures and high saturation deficits resulted in water loss to the surrounding environment. Therefore, subsequent experiments used desiccated egg masses, which resulted in better determination of expected water gain. Water absorption of the spumaline is expressed in terms of percent weight gain of egg mass (previously desiccated to a constant weight) maintained in humidity chambers for 24 hr. The humidity chambers consisted of closed glass containers (105 × 76 × 76 mm) where egg masses were suspended with zinc wire above a given aqueous sulphuric acid solution (Solomon, 1951). Vapor pressures for corresponding sulphuric acid solutions at temperatures ranging from 0°C to 235°C can be calculated with the aid of "International Critical Tables" (Washburn, 1928). Unfortunately, simulation of common mid-winter conditions requires creation of saturation deficits at temperatures lower than 0°C. To obtain vapor pressures for solutions below 0°C, extrapolations were made from correlations of $\log_e$ vapor pressure vs. temperature. In all correlations performed the Pearson's correlation coefficient was $r = 0.999$ ($P < 0.001$). Saturation deficits (SD) were calculated from the formula:

$$\mathrm{SD}_t = e_s - e \qquad \text{(Rosenberg, 1974)}$$

where e_s is the saturation vapor pressure at temperature t°C and e is the actual vapor pressure, both in mm Hg.

Insulative properties of the spumaline. To determine the effect of the spumaline layer on the temperature of egg masses in the field, temperature measurements were made of egg masses on trees with a thermocouple probe

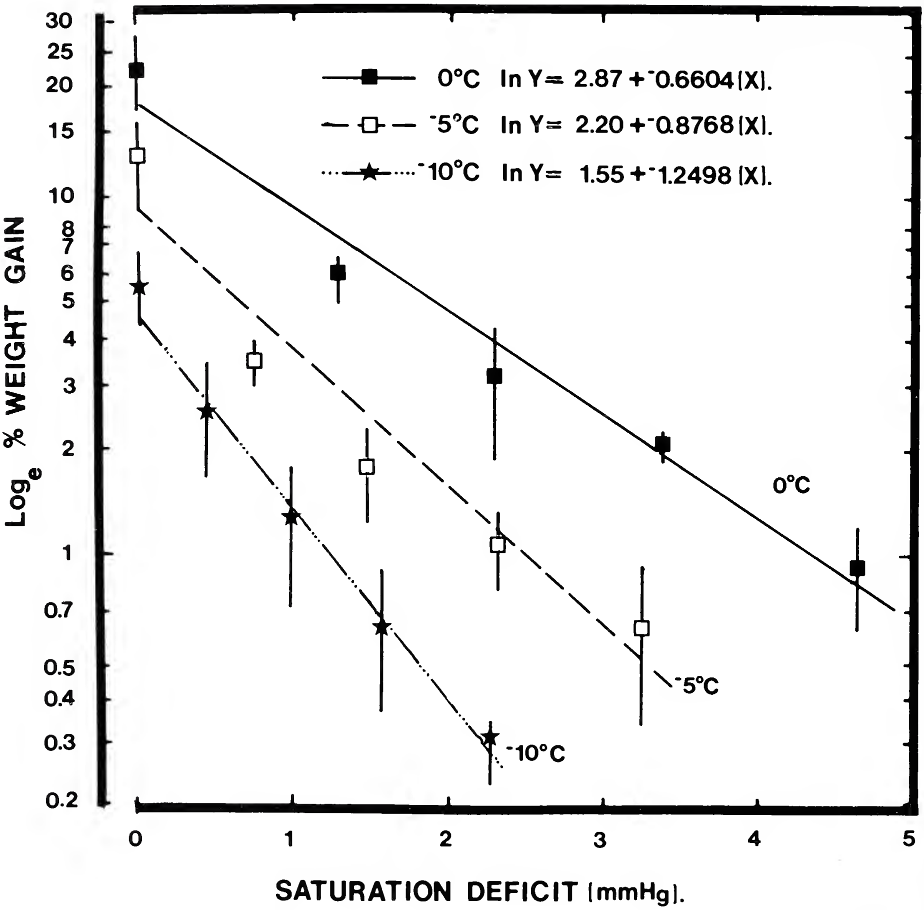

Fig. 1. Log$_e$ of percent of weight gain of *Malacosoma americanum* (Fab.) exposed to different absolute humidities −10°C, −5°C and 0°C for 24 hr (mean and SD).

and a cryothermometer model Bat-5 (Bailey Instrument Co.). For each egg mass the information recorded included type of day (e.g., cloudy or sunny), temperature inside the spumaline (but above the eggs themselves) and ambient temperature (temperatures were taken to the nearest 0.5°C).

Egg masses stored in the laboratory for two weeks at 11°C and 9.8 g/m^2 absolute humidity were utilized to study the reflectance spectrum of the chorion and spumaline. Study of reflectance spectrum is an important tool in determining how different light wavelengths behave on media and thus their energy trapping characteristics. The spectrum was measured with a Shimadzu Spectronic 210 UV Spectrophotometer equipped with an integrating sphere 200 UV attachment for measuring solid materials.

Table 1. Differences between air temperature and egg masses of *Malacosoma americanum* on clear days.

Air temperature range (°C)	Mean temperature difference: under the spumaline and air (°C)	Number of egg masses examined
9 to 5	+1.6	29
4 to 0	+2.7	47
−1 to −5	+3.0	122
−6 to −10	+3.5	73
−11 to −20	+6.0	67

RESULTS

Water absorption decreased logarithmically with increasing saturation deficit (Fig. 1), i.e., the less water in the environment the less water the spumaline absorbs at all the temperatures tested. The regression analyses of water absorption at ($r^2 = -0.99$, $P < 0.01$), −5°C ($r^2 = -0.98$, $P < 0.01$) and −10°C ($r^2 = -0.99$, $P < 0.001$), show that water absorption is a direct function of temperature and water concentration. Examination of the regression equations' slopes reveals an inverse relationship between temperature and the magnitude of the slope, furthermore, the slope of the −10°C regression line is significantly larger ($t = 3.86$, $P < 0.0005$). These two facts agree with a fundamental characteristic of hygroscopic materials where decreasing temperatures mark a corresponding increase in any material's ability to absorb water (Hodson, 1937).

Although water uptake occurs at the air-spumaline interface, it may also occur at the chorion-spumaline interface since the chorion also is hygroscopic (Hodson and Weinman, 1945; and pers. obs.). A differential response to temperature and/or humidity at each interface could account for the nonlinear nature of the water absorption curves. In addition, it was also observed that immediately after rainfall, and at temperatures higher than 10°C, field collected spumaline contains so much water that it can be literally squeezed out. This illustrates the extent of spumaline's hygroscopicity at high absolute humidity (characteristic of higher temperatures). (Also see Hodson and Weinman, 1945.)

Preliminary field measurements of temperature differences between egg masses and ambient showed that although marked temperature differences are observed on clear sunny days these disappeared during cloudy days even when measurements are taken on the same egg mass. Thus, Table 1 presents a summary of data for egg masses measured on clear days only. It was observed that differences varied inversely with environmental temperature. In some specific comparisons, egg masses were up to 12°C warmer than air

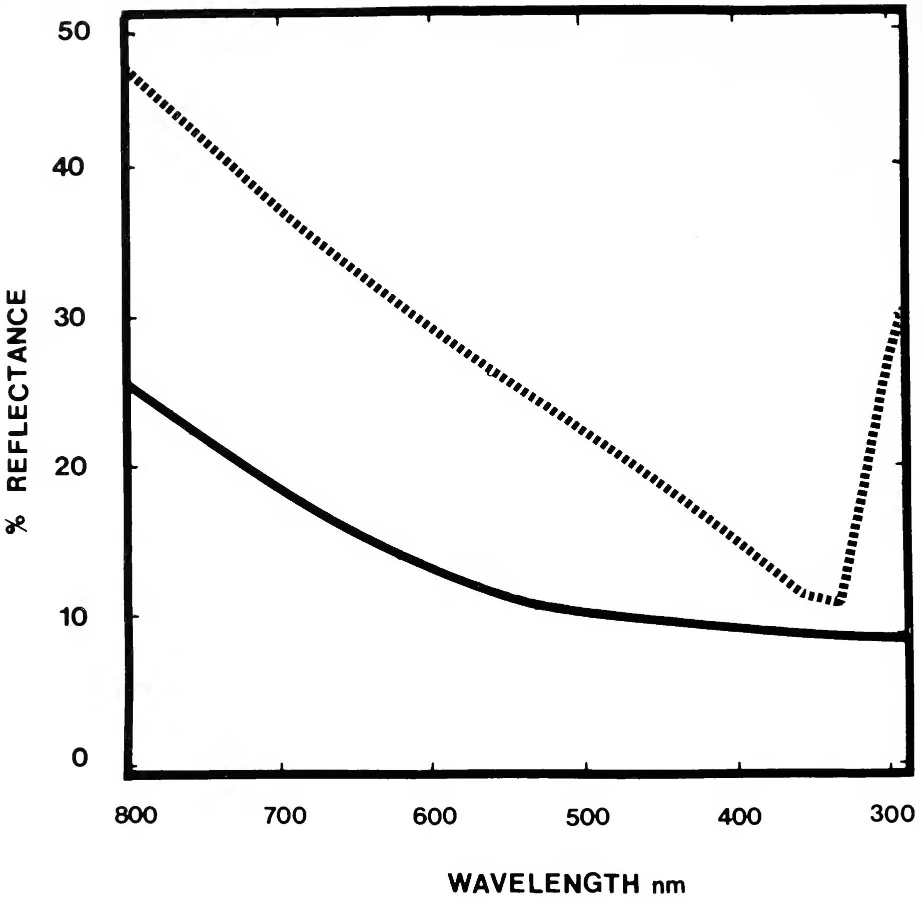

Fig. 2. Percent reflectances of the chorion (·····) and the spumaline (——) of egg masses held at 9.8 g/m^3 absolute humidity and 11°C.

temperature. These differences are in concert with differences of up to 5°C on an egg mass of *M. disstria,* during one cold and clear February day found by Wellington (1950). This observation points at the importance of solar radiation.

The reflectance spectrum of the spumaline and the chorion is presented in Figure 2. The percent reflected light decreased with decreasing wavelength with a reflectance minimum at 342 nm, in the near ultraviolet region for both structures. The fact that the spumaline consistently had high reflectance values at the infrared (IR) region of the spectrum suggests that: as short high energy wavelength radiation penetrates the chorion and spumaline some of its energy is reemitted as IR, which in turn is trapped in the spumaline, due to its large reflectivity. Thus a greenhouse effect is probably created between the chorion and the air-spumaline interface. This effect would maintain egg mass temperatures above those in the air on days when the UV component of incident light is large (i.e., on sunny clear days).

DISCUSSION

The hibernacula of many insects occur under or within snow cover, bark, leaf litter or soil. These substrates provide relatively small temperature fluctuations and excellent insulative qualities (Holmquist, 1931). On the other hand, the overwintering stage of *Malacosoma americanum* in its arboreal habitat is exposed to wide environmental fluctuations and low temperatures. Under these conditions, species like those of *Malacosoma* tend to have cold-hardy overwintering stages (MacPhee, 1964). Several physiological mechanisms of cold-hardiness in *Malacosoma* have been reported namely the presence of high cryoprotectant levels and low supercooling points (Hanec, 1966; Mansingh, 1974). However, although important these are not the only ways to compensate for climatic extremes. The egg masses of many overwintering arthropods are often protected from cold environments by materials provided by the maternal parent. The eggs of the gypsy moth can withstand temperatures of −50°C if the masses are covered by the hair placed on them by the female, but die at −19°C if the hairs are removed (Kulagin, 1897, cited in Danks, 1978). Similarly, the egg sac of *Floridia bucculenta* protects eggs from desiccation and flooding (Schaefer, 1976). In *Malacosoma* the presence of the spumaline appears to serve two purposes: to ameliorate environmental temperatures and to prevent desiccation. The spumaline insures the capture of the water when the humidity is high and serves as an interphase for slow evaporation when air moisture is low. Extremely dry winters seldom occur in the natural range of *M. americanum* where precipitation is usually high. The suggestion of Hodson and Weinman (1945) that the spumaline of *M. disstria* was essential for its winter survival appears to apply equally well to *M. americanum.*

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MELANISM IN *PHIGALIA TITEA* (CRAMER) (LEPIDOPTERA: GEOMETRIDAE): A FOURTEEN-YEAR RECORD FROM CENTRAL MASSACHUSETTS

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Abstract.—The melanic morph of *Phigalia titea* (Cramer), "*deplorans*" (Franclemont, 1938), comprised 18.7 percent of 3,906 specimens collected at various light sources at a single location in central Massachusetts between 1968 and 1981. There were no discernible trends in melanic frequency over that period. Three different light sources (incandescent, fluorescent and mercury vapor) yielded similar estimates of melanic frequency. There was a decline in melanic frequency late at night (after 2300 hours), and an increase in melanic frequency during the second half of the flight season. The implications of these results are briefly discussed.

This report summarizes information on the incidence of melanism in *Phigalia titea* (Cramer) (Lepidoptera: Geometridae) as determined by light-source collecting at a single location in Leverett, Franklin County, Massachusetts from 1968–1981. Previous papers have dealt with part of this period (1968–1973) (Sargent, 1971, 1974), and the present paper extends and elaborates on the overall record.

LOCALITY AND METHODS

Male *P. titea* were collected at several light sources about my home in Leverett. (Female *P. titea* have only rudimentary wings, do not fly, and are not included in any of the recorded data.)

My home is located in an extensive, mixed deciduous woodland dominated by 40-year-old oaks (*Quercus alba* L. and *Q. velutina* Lam.) and hickories (*Carya ovata* (Mill.) and *C. glabra* (Mill.)). Other trees with substantial representation include birches (*Betula papyrifera* Marsh. and *B. lenta* L.), pine (*Pinus strobus* L.) and hemlock (*Tsuga canadensis* L.). Understory shrubs include mountain laurel (*Kalmia latifolia* L.), viburnums (esp. *Viburnum acerifolium* L.) and blueberries (inc. *Vaccinium corymbosum* L. and *V. vacillans* Torr.), reflecting an acidic soil. The area shows little evidence of air-borne pollution, as epiphytic lichens are common on tree trunks that are themselves not noticeably darkened by soot.

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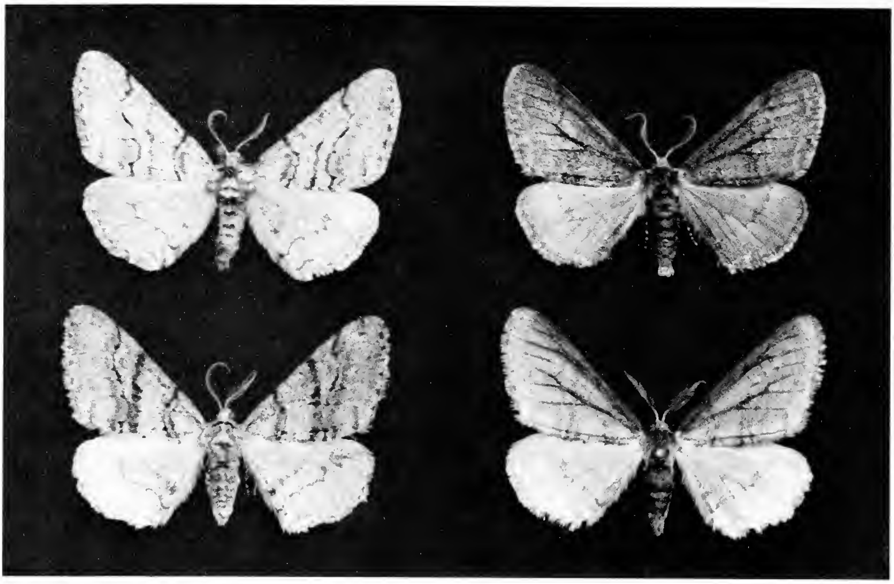

Fig. 1. The typical (left) and melanic (right) morphs of *P. titea.* The upper specimens are representative of the Leverett population. The lower specimens are an unusually dark typical (left) and an unusually light melanic (right). Approximately life-size.

Four incandescent spotlights (Westinghouse outdoor projector, 150-watt), a fluorescent blacklight tube (General Electric F15T8 BL, 15-watt), and a medium-pressure, mercury-vapor discharge lamp (Atlas MB/U, 125-watt) were all used at various times, and these light sources were carefully distinguished in the records. Generally, the lights were checked on several occasions during the night, and the time, as well as the numbers of typical and melanic *P. titea* present, were recorded. An effort was made to capture all of the assembled moths on each visit to a light in order to minimize the possibility of counting individuals on more than one occasion. The capture moths were sacrificed, except for some that were color-marked and released as part of a mark/recapture study during 1969 and 1970 (see Sargent, 1971).

Most collected *P. titea* were easily assignable to one of two morph categories: "typical" (light gray ground with strongly contrasting black lines), or "melanic" (="*deplorans*", Franclemont, 1938) (blackish overall, with only a trace of the black lines). Occasional specimens, especially worn individuals, were somewhat intermediate, but these were assigned to one or the other category on the basis of whether the scales on the abdomen were light gray ("typical") or blackish ("melanic") (Fig. 1).

(The division of specimens into only two categories on the basis of appearance is undoubtedly an oversimplification in terms of reflecting the underlying genetic and/or environmental bases of melanism in this species.

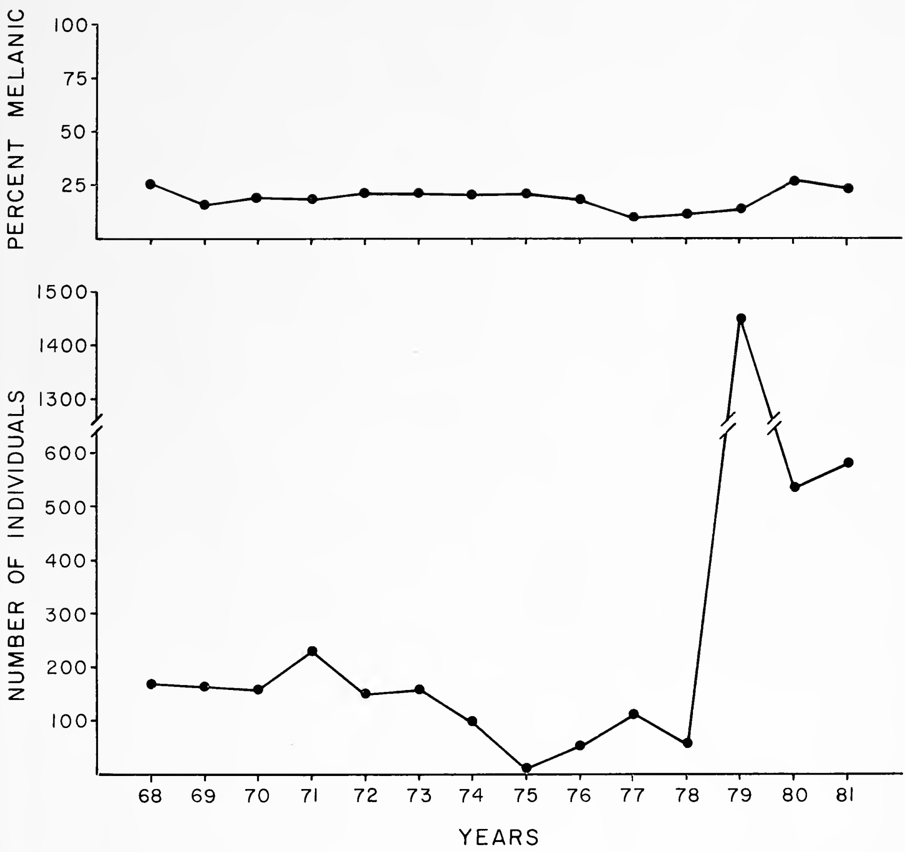

Fig. 2. The total numbers of *P. titea* taken at light sources in Leverett, Massachusetts for the years 1968–1981 (below), and the percentage melanic for each of these yearly samples (above).

However, given our lack of knowledge regarding these underlying factors, and further uncertainty regarding the effects of wear on phenotypic appearance, it seems pointless to attempt a finer classification at this time.)

RESULTS

A total of 3,906 *P. titea* was taken at the various light sources over the 14-year period, 1968–1981. Of that total, 730 individuals, or 18.7 percent, were melanic. The yearly sample sizes varied considerably, but the corresponding percentages of melanics were relatively constant, and there were no long-term trends of either increasing or decreasing melanic frequency (Fig. 2).

Light sources. The three different light sources used in this study (incan-

Table 1. The numbers of typical and melanic individuals of *P. titea* taken at various light sources during periods of simultaneous operation.

Year	Light sources	Numbers Typical	 Melanic	P*
1971	Spotlights	118	24	>0.50
	Blacklight	71	17	
1979	Spotlights	652	110	>0.70
	Blacklight	574	92	
1972	Spotlights	22	5	>0.40
	Blacklight	41	15	
	Mercury vapor	54	12	

* Probabilities based on chi-square contingency tests.

descent spotlights, fluorescent tube, and mercury vapor bulb) were apparently sampling identically, as the frequencies of typical and melanic *P. titea* taken were not significantly different when compared for any of the sources during periods of simultaneous operation (Table 1).

Time of night. In a previous paper (Sargent, 1971), I suggested that melanic *P. titea* might occur at their highest frequency during the early hours of the evening. That suggestion was not supported by the more extensive data reported here (Table 2). However, there was a decline in the frequency of melanics taken late at night (after 2300 hr) (chi-square, 2 × 3 contingency test = 5.94; $P \cong 0.05$), suggesting that melanics may have a somewhat different daily flight period (shorter, if not earlier) than typicals.

Seasonal effect. No seasonal effects were discernible in the data reported previously with respect to the proportions of typical and melanic *P. titea* taken (Sargent, 1971). Analysis of the current data reveals, however, that significantly more melanics were taken over the second half of the season each year ($^{370}/_{1,768}$, 20.9%) than were taken over the first half of the season ($^{354}/_{2,079}$, 17.0%) (chi-square 2 × 2 test, $P < 0.002$) (Fig. 3B). This effect is

Table 2. The numbers of typical and melanic individuals of *P. titea* taken at various times of night (based on data from nights when sampling was repeated no less than hourly) for the six years when *P. titea* was most abundant at the Leverett location.

Time of night	Numbers Typical	 Melanic	% melanic
<2100 hr	586	141	19.4
2100–2300 hr	560	148	20.9
>2300 hr	267	45	14.4

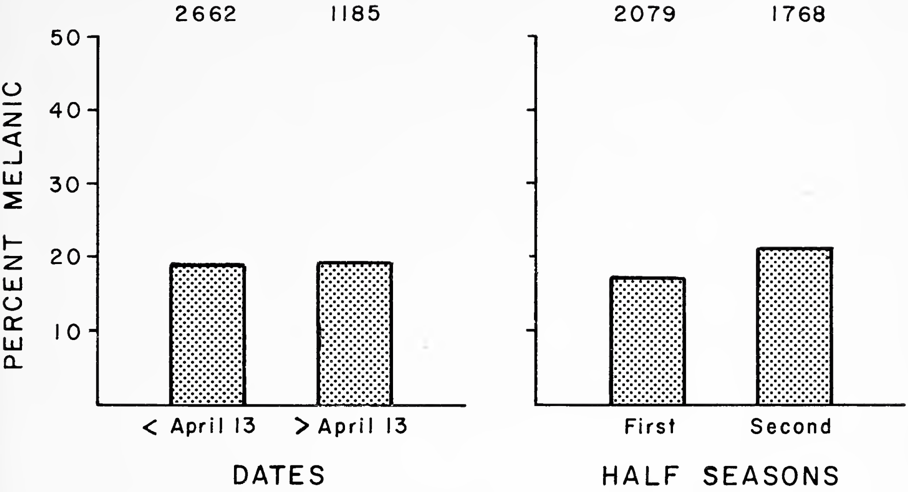

Fig. 3. The percentage of melanic individuals of *P. titea* taken before and after April 13 (left) and during the first and second half of the flight season (right), summed for the years 1968–1981 in Leverett, Massachusetts. The total numbers of individuals taken are given above the bars.

not apparent when the data are analysed by calendar dates (Fig. 3A), suggesting that the seasonal effect is not based on differential responses of the two morphs to extrinsic environmental factors (e.g., temperature, daylength), but rather reflects some intrinsic difference between the morphs with respect to either their physiology (e.g., development rates, longevity) or their susceptibility to predation.

DISCUSSION

Aside from a single, very early record from West Roxbury, Massachusetts (Minot, 1869), melanic *P. titea* were first reported from most localities in eastern North America from about 1915–1960 (Owen, 1962). Minot described his early specimen as a new species, *P. strigataria,* but Franclemont (1938) correctly identified the melanic as a morph of *P. titea,* naming it "*deplorans*". Interestingly, by 1962, "*deplorans*" had not been noted in certain industrial areas (e.g., Pittsburgh, Chicago) where melanic *Biston cognataria* (Guenée) had already become quite common, and at that time it was estimated that "*deplorans*" made up no more than 10 percent of any *P. titea* population in North America (Owen, 1962). Few other data are available until the present records which indicate that the melanic frequency of *P. titea* in central Massachusetts has remained stable at close to 20 percent of the population for the past 14 years.

I have previously pointed out that the area in which these records have been obtained shows little discernible evidence of industrial air pollution, and Owen (1962) noted that *P. titea* was unusual in that the initial reports of melanism were not from industrial centers. Thus, the bases for melanism in *P. titea* remain obscure, although similar problems exist with respect to explaining melanism in the closely related *P. pilosaria* (Schiff.) in Britain (Lees, 1971, 1981). It seems certain that factors other than selective predation based on crypsis are involved in these cases, as they seem to be in *Biston* in both the rural central Appalachians in this country (West, 1977) and southern Britain (e.g., Steward, 1977).

Evidence for different daily flight periods for the typical and melanic morphs of a species has not, to my knowledge, been reported previously. Such a difference would be detected only if sampling were carried out as here with *P. titea,* i.e., at intervals throughout the daily flight period of the species, with all of the moths collected at each sampling time. The significance of the apparently earlier flying of melanics than of typicals in *P. titea* is not immediately apparent, though it may be related in some way to the differences one would expect to find in the warming and cooling characteristics of dark, as opposed to light, insects (see e.g., Watt, 1968).

A tendency for melanics to become more common later in the season, as reported here for *P. titea,* has been reported for other species as well. Thus, Bishop, Cook and Muggleton (1978) described an abrupt increase in the frequency of the melanic "*nigra*" morph of *Gonodontis bidentata* Clerk towards the end of the season at two locations in northwest England. These authors attributed this effect to a later emergence of the "*nigra*" morph. Increasing melanic frequency over the season has also been reported in *Cleora repandata* L. in the Scottish Highlands, though in this case the effect has been attributed to selective predation favoring the melanics (Kettlewell, 1973, p. 86).

There is some evidence to suggest that melanics may have slower development rates than typicals in some species (e.g., *Spodoptera exigua* Hubn. (Poitout, 1973), and *Biston betularia* (Kettlewell, 1973, p. 85)). There is no evidence on this point for *P. titea,* but Lees (pers. comm.) has detected no differences between the development rates of typical and melanic *P. pilosaria* in his extensive rearing of that species.

Another factor that could lead to higher melanic frequencies later in the season is an increased viability of melanics relative to typicals in the adult stage. I am aware of no studies on adult viabilities in an industrial melanic species, though there is evidence for a greater viability of the larvae of melanics in certain cases (e.g., *Menophra abruptaria* Thunb. (Onslow, 1921), and *Cleora repandata* (Ford, 1940)). Kettlewell (1973, p. 78), however, found the evidence for differential viability of larvae of the morphs in industrial melanic species "unconvincing", and the matter needs further investigation.

The possibility remains that the increased frequency of melanic *P. titea* later in the season is due to selective predation that favors the melanics. If this were so, it seems unlikely that it would be based on crypsis, as the area in which these studies were conducted is, as previously noted, visibly rural. Furthermore, experimental tests have shown that melanic *P. titea* prefer light backgrounds (Sargent, 1969), a tendency that would seemingly place them at a cryptic disadvantage.

Other possible bases for differential predation on the morphs of *P. titea* should be explored. Whittle et al. (1976) obtained evidence that bats take more typical than melanic *B. betularia,* and this possibility should not be overlooked in *P. titea,* particularly in light of the evidence that melanics of this species may fly earlier in the evening or for a shorter period of time than typicals. Other matters that should be investigated include the relative palatabilities of typical and melanic *P. titea* to potential predators, and the possibility of behavioral differences between the morphs in reacting to predator attacks.

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THE DIPTERA BREEDING ON SKUNK CABBAGE, *SYMPLOCARPUS FOETIDUS* (ARACEAE)

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Abstract.—The larvae of 19 species of flies belonging to 7 families were found to feed in the rotting portions of leaves, petioles, and flowers of skunk cabbage. Among flies bred from this plant, drosophilids were by far the most numerous, but there is considerable geographic and seasonal variation in composition and abundance of the fauna. The sex ratio of one species, a *Bryophaenocladius* sp. (Chironomidae), reveals it to be parthenogenetic. The breeding biology of the flies, with particular reference to other dipteran-aroid relationships, is reviewed.

Symplocarpus foetidus is a common perennial plant of wet lowland areas in eastern North America. Inflorescences appear in early spring, the leaves expand about one month later, and seeds are formed in the fall, when the above-ground portion of the plant dies back. This species forms established patches that may vary in size from a few square meters to several hectares. *Symplocarpus foetidus* would thus seem to be an "apparent" plant to potential consumers, and as such one might expect it to be protected by "quantitative" defenses (sensu Feeny, 1976). It is: the tissues contain barbed crystals of calcium oxalate, which may deter a variety of herbivores (B. Meeuse, pers. comm.). An herbivore that would cope with this defense, however, would be rewarded with a predictable supply of food. Hence, specialization of some herbivore species on *S. foetidus* might be expected to evolve.

Although a few Coleoptera, Psocoptera and Collembola breed in skunk cabbages, the majority of insects bred from the plant are a variety of dipterans. We have never seen visible signs of serpentine or blotch mines, chewing areas, or petiole girdling which might be indicative of insect activity. All flies in this study were bred from rotting portions of plants and most likely fed on bacteria harbored therein. This does not, however, rule out the possibility that diptera may be the cause of decay in the portions of some plants. We show here that *Symplocarpus foetidus* is probably the major breeding site of the Holarctic species *Scaptomyza graminum.* Another significant finding is that *Drosophila recens,* previously thought to breed exclusively in mushrooms, also utilizes *Symplocarpus* as well.

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METHODS

One collection of 22 flowers (including the spathe and spadix) was made from two *Symplocarpus* patches on Deer Isle, Maine on June 28, 1982. Three collections of 37, 27, and 28 plants were made on May 14, June 25, and August 6, 1982, respectively, at Chenango Valley State Park, Chenango, New York. Only flowers were collected in May, since rotting or damaged leaves were not found. Rotting and damaged petioles and leaves, all from different plants, comprised the specimens thereafter, as spathes were uncommon. Portions of plants were bagged and transported to the laboratory, where they were placed on damp sand (except for the Maine collections, which were placed on Instant *Drosophila* medium [Carolina Biol. Suppl. Co.]) in 200 ml plastic containers covered with cardboard tops. To prevent drying, the specimens were misted every other day with water. Adult insects were aspirated as they emerged and were preserved in 70 percent ethanol prior to identification.

Insects were identified using the following references: Wheeler (1960) and Strickberger (1962) for *Drosophila,* Wheeler (1952) for Drosophilidae other than *Drosophila,* Johannsen (1952) for Chironomidae and Ceratopogonidae, Saether (1973) for *Bryophaenocladius* sp., and Quate (1960) for Psychodidae. *Scaptomyza* 'sp. *A*' appears to be a new species and will probably be described later. Voucher specimens are deposited in the Cornell University collection, Ithaca, New York. Our identification of *Dasyhelea* was confirmed by Dr. Willis W. Wirth and the ephydrid and chloropids were identified by Drs. W. N. Mathis and C. W. Sabrosky, respectively, all of the Systematic Entomology Laboratory of the U.S. Department of Agriculture.

RESULTS AND DISCUSSION

The most conspicuous aspect of the breeding records (Tables 1 and 2) is the complete absence of parasitic Hymenoptera: from a total of 1,132 potential dipteran hosts reared (an average of 10 flies per plant part), not one parasite emerged. This contrasts with the number of parasitic braconids and cynipids bred from mushrooms containing Diptera also growing at the Chenango Valley site (Grimaldi, 1983). Carson et al. (1980) also bred numerous small wasps from another primary dipteran breeding site, the aroid *Calocasia esculenta* in Papua New Guinea.

Not so surprising is the seasonal variation in abundance of some flies, since insect populations generally fluctuate in abundance seasonally. For instance, none of the nematocera present during the spring and early summer breed in *Symplocarpus* in late summer in New York. In contrast, *Scaptomyza graminum* abundance increases almost four-fold towards late summer. *Drosophila recens,* which is the most common fly in the spring collection, is virtually nonexistent in the later collections. Of particular interest is the

Table 1. Drosophilidae reared from *Symplocarpus foetidus* (N = 672).

Species	Numbers		
	Males	Females	Total
Chenango Valley, New York, May 1982: flowers, 37 plants			
Drosophila recens Wheeler	62	84	146
Scaptomyza graminum Fallén	11	15	26
Drosophila affinis-subgroup	5	15	20
Scaptomyza sp. *A*	8	4	12
Drosophila putrida Sturtevant	6	4	10
Drosophila falleni Wheeler	7	2	9
Drosophila palustris Spencer	1	4	5
Chymomyza amoena Loew	2	3	5
			233
Chenango Valley, New York, June 1982: leaves and petioles, 27 plants			
Scaptomyza graminum	42	36	78
Drosophila palustris	1	6	7
Scaptomyza sp. *A*	2	1	3
			88
Deer Isle, Maine, June 1982: flowers, 22 plants			
Drosophila quinaria Loew	17	20	37
Drosophila busckii Coquillett	2	3	5
Drosophila recens	1	1	2
			44
Chenango Valley, New York, August 1982: leaves and petioles, 28 plants			
Scaptomyza graminum	137	144	281
Scaptomyza sp. *A*	7	12	19
Scaptomyza paravittata Wheeler	3	4	7
			307

geographic variation of species breeding in skunk cabbages. *Drosophila quinaria,* which is common in *S. foetidus* in Rochester, New York and Deer Isle, Maine (Jaenike, 1978) is not present in the Chenango Valley population. In the latter area, *D. recens* is the predominant species of *Drosophila* bred from this plant.

The Araceae appears to be a pivotal resource in the ecological diversity of the Drosophilidae. The niche is typical of *Scaptomyza,* which are leaf miners. We have bred a large number of *S. graminum* (=*S. borealis* [Wheeler, 1981]) from skunk cabbages (this study and Jaenike, 1978). This drosophilid has, however, been found, occasionally, to use some non-araceous resources, such as *Stellaria aquatica* (Caryophyllaceae) in Japan (T. Okada, pers. comm.), *Nasturtium officinalis* (Cruciferae) (Wheeler, 1952), *Petasites officinalis* (Compositae), *Brassica campestris, B. oleracea, B. rapa* (Cruciferae), and

Table 2. Non-drosophilid Diptera reared from *Symplocarpus foetidus* (N = 460).

Family	Species	Numbers		
		Males	Females	Total
Chenango Valley, New York May 1982: flowers, 37 plants				
Psychodidae	*Psychoda satchelli* Quate	29	52	81
	Psychoda alternata Say	2	4	6
Chloropidae	*Tricimba lineella* (Fallén)			94
	Elachiptera costata (Loew)			11
				192
Chenango Valley, New York, June 1982: leaves and petioles, 27 plants				
Psychodidae	*Psychoda satchelli*	33	35	68
Ceratopogonidae	*Dasyhelea oppressa* Thomsen	31	36	67
Chironomidae	*Bryophaenocladius* sp.	0	29	29
Chloropidae	*Tricimba lineella*			2
				166
Deer Isle, Maine, June 1982: flowers, 22 plants				
Psychodidae	*Psychoda satchelli*	12	11	23
Ceratopogonidae	*Dasyhelea opressa*	9	3	12
Chloropidae	*Elachiptera costata*			18
Ephydridae	*Athyroglossa granulosa* (Cresson)			5
				58
Chenango Valley, New York, August 1982: leaves and petioles, 28 plants				
Cecidomyiidae	*Dyodiplosis* sp.	19	22	41
Ephydridae	*Athyroglossa granulosa*			3
				44

Aquilegia vulgaris (Ranunculaceae) (Frost, 1923). Stalker (1945) has bred *S. graminum* from *Trifolium pratense* leaves, but mentions this is not a major resource since so few individuals were reared. Stalker also found that *S. graminum* in Rochester, New York, like the flies bred in this study, are most abundant throughout the summer and early fall as found by sweep netting in open areas. In addition, R. Lacy (pers. comm.) has bred 13 individuals of *S. graminum* from a very extensive collection of mushrooms. Our data show that a major larval resource of *Scaptomyza graminum,* perhaps the most abundant species of its genus, is *Symplocarpus foetidus.*

In the *Drosophila quinaria* species group, some members, such as *D. quinaria* and *D. magnaquinaria,* specialize on aroids (Jaenike, 1978; Wheeler, 1954; this study). Other species in the group (such as *D. falleni, D. phalerata,* and *D. transversa*) breed in a diversity of mushrooms (Jaenike, 1978; Lacy, 1982; Grimaldi, 1983; Shorrocks, 1980). *Drosophila recens* and *D. limbata* are intermediate, breeding in both mushrooms and aroids. *D. limbata* has been bred from *Arum maculatum* fruits (Schatzmann, 1977) and from *Russula* mushrooms (Burla and Bächli, 1968) in Switzerland. *D. recens* commonly breeds in mushrooms, but utilizes *Symplocarpus* in the spring before mushrooms are fruiting.

Although the bulk of dipteran-aroid relationships in the tropics has yet to be investigated, Heed (1957) gives an indication of the potential importance of this relationship in structuring Neotropical drosophilid communities. Approximately one-quarter of the 222 species of Drosophilidae collected in El Salvador can be found in "aroid swamps," of which *Xanthosoma* is a characteristic plant. In Papua New Guinea, Okada and Carson (1979) and Carson and Okada (1980) have found that several aroids are a "veritable zoological garden" for drosophilids. Four drosophilid species were reared from *Colocasia esculenta,* and 13 different species reared from *Alocasia macrorrhiza.* The larvae of most of these species feed on spathes and spadices, and are quite monophagous. *Drosophila aproclinata,* for example, breeds only in decaying staminate portions of *Alocasia hollrungii* spadices. Like most of the *Drosophila* breeding in *Symplocarpus,* Carson and Okada found the New Guinea *Drosophila* limited to breeding in the flowers. It appears that throughout the world the Araceae have repeatedly been invaded by Drosophilidae.

For some drosophilids, *Symplocarpus foetidus* is just an incidental resource. For example, only 20 individuals of the extremely abundant *Drosophila affinis* subgroup were bred in this study. *Drosophila putrida, D. falleni, D. busckii,* and *Chymomyza amoena* are also, judging from their numbers bred from other substrates and caught in banana traps, just incidental rearings.

Another interesting parallel between New Guinea aroid-breeding flies and the kind we have bred are the Psychodidae. For a family with larvae generally breeding in detritus (Quate, 1960) such as compost and decaying organic matter (Johannsen, 1934), aroids are an unusual niche. But, about one-third of the non-drosophilid Diptera in *Symplocarpus foetidus* are *Psychoda.* Carson and Okada (1980) also found several psychodids breeding in *Calocasia esculenta.* Quite unusual for cecidomyiids are our records for *Dyodiplosis* sp. in *Symplocarpus.* Decaying vegetation may not be an unusual niche for *Dyodiplosis* since it occasionally is found in some of our mushroom rearings.

Symplocarpus is not an unusual niche for the other nematocera and the ephydrid and chloropids bred in this study. Ephydridae and Chloropidae are commonly associated with wet areas, many members of both these families boring the stems of plants. Although ceratopogonids and chironomids are almost entirely aquatic groups, *Dasyhelea* and *Bryophaenocladius,* which were bred from skunk cabbages, are among the more derived, terrestrial forms. *Dasyhelea oppressa* is common in bleeding exudates of Elm (*Ulmus*) trees in New York (Thomsen, 1937). At least three *Dasyhelea* species breed in cacti (Wirth and Hubert, 1960). Other ceratopogonids are quite terrestrial, larvae of *Forcipomyia argenteola* group species commonly breeding in decaying portions of banana stems, cacao pods, and *Calathea* and *Heliconia* bracts in the Neotropics (Wirth, 1982). *Bryophaenocladius,* together with *Smittia* and *Pseudosmittia,* belongs to a related group of Orthocladiinae, some members of which Johannsen (1937) records as breeding in and among plant roots. Parthenogenesis occurs repeatedly in the Chironomidae, but is most frequent primarily in only the Orthocladiinae among the eight subfamilies usually recognized. In the Orthocladiinae, species belonging to 8 genera, including *Bryophaenocladius,* are known to be obligately or facultatively thelytokous (Scholl, 1960). Oliver et al. (1972) used emergence trap data to show female-biased sex ratios occur in three additional genera of this subfamily.

Most Diptera raised in this study, with the exception of some drosophilids (and possibly chloropids), probably breed in plant matter other than decaying *Symplocarpus.* Nematocera breed in detritus, on the whole, with several of the species mentioned here adding the bacterial flora of decayed skunk cabbage to their diet.

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NOTES AND COMMENTS

PREDATION OF *PROSIMULIUM MIXTUM/FUSCUM* (DIPTERA: SIMULIIDAE) COPULATING PAIRS BY *FORMICA* ANTS (HYMENOPTERA: FORMICIDAE)

A comprehensive description of black fly predators, both vertebrate and invertebrate, was given by Davies (Davies, D. M. 1981. Pages 139–158 *in:* M. Laird (ed.), Blackflies. Academic Press, New York). While most predation of black flies by Hymenoptera occurs by sphecid and vespid wasps, five species of formicids have been observed preying upon black flies. Peterson (Peterson, B. V. 1960. Can. Entomol. 92:266–274) lists *Formica fusca* L., *F. obscuripes* Forel and *Myrmica brevinodes* Emery. Peterson and Davies (Peterson, B. V. and D. M. Davies. 1960. Can. J. Zool. 38:9–18) list *Lasius neoniger* Emery and *Myrmica emeryana* Forel. Of these only *L. neoniger* and *M. emeryana* were observed preying upon adult black flies.

On 5 May 1982, I observed large numbers of *Formica subnuda* Emery preying on newly emerged *Prosimulium* males that were unwilling or unable to fly when disturbed (air temp. = 18°C). The newly emerged males were presumably drying their wings on the rocks and vegetation adjacent to the Saranac River, Franklin Co., New York. On 12 and 13 May I observed predation of mating pairs of *Prosimulium mixtum/fuscum* by *Formica podzolica* Fraenkcoeur at a site 0.8 km upstream from the initial site. While approaching this particular site, I had located a large swarm (estimated at 60 m × 8 m × 10 m high) of male *Prosimulium* black flies (at 3:00 p.m., ambient temperature = 24°C, RH = 37%) swarming in the leeward (3 km/hr W) shaded sides of 2 20-m hemlocks (*Tsuga canadensis*) and 1 25 m quaking aspen (*Populus tremuloides*) whose leaves had opened about 30–50 percent. *Prosimulium mixtum/fuscum* adults were dropping onto the road surface *in copula* and remained attached for 0–5.75 min. Quite often the larger female dragged the copulating male behind her as she walked along the sandy road. A marauding ant randomly traversed the road until it crossed the trail of a mating pair or came within 3–4 cm of an immobile pair. The ant then turned abruptly in the same direction that the mating pair had travelled, increased its pace, followed the same path the flies had taken and, within 3–4 seconds of locating the pair, immobilized one or both of the flies. On four separate occasions other ants that had been 20 cm or more from a copulating pair when it crossed the flies' trail responded similarly. Shorter hunting trails were more common.

The *F. subnuda* that I observed on 5 May were attacking only the male flies since the females had not yet emerged. The *F. podzolica* that were observed on 12 and 13 May showed no apparent preference for the male or female black fly. A few ants were observed dragging both male and female carcasses that were still *in copula.* More frequently, an ant was successful in killing only one fly. The other fly would either remain wounded and separate immobilized from the mate or fly off unscathed.

Once an ant obtained its victim, it quickly turned back toward the colony. With the captured fly (flies) supported by the ant's mandibles, the ant completely ignored the trail of other mating pairs and other flies. On two occasions, ants with flies clasped in their mandibles walked directly over mating flies, which having been disturbed, separated and flew off. The *F. podzolica* colony (ca. 40 cm diam) was in a loose sand area about 1.5 m off the vehicular access zone on the south side of the road. On 13 May, ants from within the colony were also observed to be discarding *Prosimulium* carcasses from the colony interior to the area just outside (3–4 cm) the access holes. Since adult flies had been emerging since 3 May, the duration of time within the colony for these discarded *Prosimulium* is uncertain.

The author is indebted to Dr. John Simeone, SUNY College of Environmental Science and Forestry, Syracuse, New York and to Dr. William Brown, Department of Entomology, Cornell University, Ithaca, New York for identification of the ant specimens. I would also like to thank Dr. Charlie Morris, NYS Department of Health, SUNY College of Environmental Science and Forestry, Syracuse, New York for reviewing the ms.—*Dennis J. White, New York State Department of Health, Saranac Lake, New York 12983.*

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THE FIRST OCCURRENCE OF *CATORHINTHA MENDICA* STÅL IN NEW ENGLAND (HEMIPTERA: COREIDAE)

The spread of the coreid bug *Catorhintha mendica* Stål from the Great Plains eastward is, as noted by Hoebeke and Wheeler (1982) one of the few well documented cases of such a range extension known in the Hemiptera.

On August 7, 1982 I collected a series of eight adults of this species from a small patch of the host plant, *Mirabilis nyctaginea* (Michx.) MacMill.

growing adjacent to the spillway of the large flood control dam in Mansfield Center, Connecticut.

The collecting site is several miles from any railroad and the plants occurred within a two square meter area. Hoebeke and Wheeler (1982) support Balduf's (1957) belief that the spread of the plant has been essentially along railroad rights of way. This is probably so and it suggests that both plant and insect may have been present in Connecticut for some time. The collecting site is some distance from any commercial center, several miles from a railroad and is in the interior hill country of the eastern part of Connecticut. Dowhan (1979) lists *Mirabilis nyctaginea* from Connecticut. Meyerhoff (pers. comm.) informs me that it is not uncommon in suitable habitats in western Connecticut but that he has not observed it east of the Connecticut River.

The presence of *Catorhintha mendica* in New England in a sense completes its sweep eastward to the Atlantic coast. Hoebeke and Wheeler (1982) were the first to provide an east coast record when they reported it from eastern Long Island (Yaphank). They also listed several Pennsylvania records. Balduf (1957) had also reported it from western Pennsylvania and Hoffman (1975) from inland Virginia.

It gives me particular pleasure to be able to add this insect to the New England Hemiptera fauna as the species was the subject of my first scientific paper which was published just forty years ago (Slater, 1943).—*James A. Slater, Section of Systematic and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06268.*

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BOOK REVIEW

The North American Grasshoppers. Volume I. Acrididae: Gomphocerinae and Acridinae.—Daniel Otte. 1981. Harvard University Press, Cambridge, Massachusetts. 275 pp. $45.00.

This book is the first volume of a projected three-volume work, the principal purpose of which, according to its author, is "to aid in identifying all described grasshopper species north of the Gulf of Panama, as well as those in the West Indies". It deals with two subfamilies of the family Acrididae, the Gomphocerinae and Acridinae, which together comprise those grasshoppers best fitted to bear the name by virtue of the grassy habitats frequented by most of the species. Throughout, the term "grasshopper" is taken to mean the "short-horned" grasshoppers of the orthopteran suborder Caelifera.

Taxonomic monographs tend to take one of two forms: the monographic revision and the handbook. The first aims to be a comprehensive, archival documentation, to be used by, and written in the language of, the specialist researcher who may wish to carry investigation further in the particular field. The second is intended as an identification manual and source of interesting information for a variety of non-specialist readers. Daniel Otte has written a book which falls between these two extremes, or rather displays some of the characteristics of both. By employing a variety of novel and ingenious devices, he has succeeded in meeting many of the requirements of both groups of readers in a very pleasing format.

He starts with a general introduction in which mating behaviour, sound production, and problems of identification of grasshoppers in general are emphasised and structural details illustrated by clear and well labelled drawings. Then follow an illustrated key to the families of North American grasshoppers, an itemised diagnostic characterisation of the North American acridid subfamilies that lack a prosternal spine, i.e., the Gomphocerinae, Acridinae, and Oedipodinae, a general discussion of the Gomphocerinae and Acridinae, and an illustrated key to their component genera.

The greater part of the book is then devoted to a systematic account of the 42 genera and 124 species of Gomphocerinae and two genera and three species of Acridinae recognised by Otte. The gomphocerine genera are arranged in 16 "genus groups", which in two instances receive also tribal names. The criteria used for distinguishing the categories genus group and tribe, and their ranking relationship, are not stated. Under each genus group containing more than one genus an itemised diagnosis of the component genera is given, headed "Identification of Genera". Each genus is then taken up in turn, with sections on "Recognition", "Identification of Species" (itemised diagnosis), and sometimes a key to the species. There follows individual treatment of each species, typically under the headings Distribution, Recognition, Habitat, Life Cycle, and References, often with text figures, and including an excellent distribution map on a base of state boundaries, omitting confusing topographic detail.

A major feature of the book is the 16 plates illustrating each species in colour, often including both sexes and sometimes, in variable species, more than one presentation to show the more distinctive of the alternative patterns. This takes care of a rather general objection to coloured illustrations—that they lead the reader to expect close conformity to the published figure, whereas there may be wide divergence from it amongst individuals. However, it has been represented to me that the colours in many cases are too weak. Another interesting feature of both the plates and some of the line drawings in the text is the presentation in dorsolateral view. This has the advantage of giving an impression of both the dorsal and lateral characteristics in a single drawing, although for precise comparisons it cannot replace separate dorsal and lateral views, especially since it is hardly possible to maintain exactly the same orientation from drawing to drawing. The technique is feasible only in the hands of a skilled illustrator, such as Otte obviously is, and is most appropriate for the less specialised reader.

Four valuable appendices enable the author to separate from the systematic treatment in the main part of the book those formal but essential details concerning synonymy and type species of genera, and synonymy, generic assignment, and type-specimen identity and location in species, which concern principally the research specialist. They list also taxonomic changes made for the first time in the book and the divergent subfamily assignments of certain genera by the principal world monographers of recent years. The justification for a number of new synonymies is not argued. Appendix 5, on the pronunciation of generic names is, as the author admits, more controversial, but may assist students. The book is completed by a glossary, a list of references, and a taxonomic index.

I have some difficulty in interpreting the information given at the generic level. The genus *Ligurotettix* will serve as an example chosen at random. On p. 146 under "Identification of Genera" of the *Cibolacris* genus group, four attributes of *Ligurotettix* are given. On p. 156, under "Recognition" of the genus, several more are listed, but only one of the earlier four is represented. Presumably some difference is seen between "identification" and "recognition", but what is it? We are not told. There is now virtually no disagreement that *species* should be treated as concrete populations whose members are determined by relations of reproductive compatibility and incompatibility. In the case of *genera* there are no such biological criteria, although some would claim that "evolutionary" criteria are operational. Important though the type species is in a nomenclatural context, it tells us what species must not be excluded from the genus, not which species should be included. The latter is approached nowadays with the aid of some form of clustering procedure. Having obtained a more or less discrete cluster, we search for attributes, common to all the species but not to related genera, which would be jointly or severally diagnostic, and our success in this enterprise may determine how far we adhere to the clustering pattern in building up a practical classification. But not every feature in common need be regarded as "necessary" to membership of the genus and is unlikely to be "sufficient." This situation has given rise to the distinction between diagnosis and description of a genus. The diagnosis is a listing of those attributes which, in the view of the taxonomist, would need to be possessed by any species being considered for membership, and which at the same time differentiate the genus from its near relatives. The description is a statement of the attributes common to all the species and, if desired, of the range of interspecific variation in other characters. The diagnosis is a characterisation of the pigeon-hole, the description a characterisation of the present contents. The distinction becomes of special importance in monotypic genera, where the generic diagnosis must be carefully worked out so as not to incorporate specific attributes that would be unlikely to be considered necessary in some newly discovered candidate for membership of the genus. I do not believe that this distinction corresponds to Otte's "identification" and "recognition", both of which seem to combine elements of both diagnosis and description, though leaning more towards the second.

Similar uncertainties are encountered at the subfamily level. Nearly all the genera are endemic to the region, but this is not true of the subfamilies. It must be understood, and was certainly in the mind of the author, that the characterisations and keys will not necessarily work on a world basis. Otte's comments on problems of subfamily classification in the Gomphocerinae and Acridinae, while familiar outside the subject area, are well supported by his discussion on p. 17. However, the problem is not simply where to place individual genera: it extends to the question of whether the two taxa merit separation at subfamily level. Moreover, the same question arises with respect to the subfamily distinctness of the Acridinae and Oedipodinae concerning which, along with the *ad hoc* Truxalinae (extralimital), controversy and vacillation involving Dirsh and Uvarov continued for years. The case of *Stethophyma,* discussed on p. 208 (see also pp. 17 and 34) illustrates the situation very well. This genus not only lacks the principal diagnostic feature of the Gomphocerinae (the femoral pegs), but it possesses the principal feature of the Oedipodinae (the intercalary vein); yet Otte tentatively places it in the Gomphocerinae because of its "behaviour and appearance".

It is a tribute to the publishers that my (admittedly not completely exhaustive) reading of this book has not brought to light a single printing error.

However, attention may be directed to a few minor departures from accepted terminology and to a few minor factual errors. In Figure 5, on p. 7, the scape of the antenna and the flagellum are shown and labelled, but not the pedicel, and in the glossary, p. 253, it is incorrectly stated that the flagellum is the "main portion of the antennae excluding the basal segment or scape". In Figure 8, p. 9, the terminology of the areas and carinae of the hind femur is unconventional and will not be readily understandable to the specialist; the conventional terminology can be found in many readily available works, including those of Rehn, Dirsh, and Uvarov. In Figure 6, p. 8, the structure labelled "preocular ridge" is conventionally termed the "lateral facial carina"; the "lateral foveolae" are the "temporal foveolae" (see also p. 253). On p. 254, the definitions of "sternum" and "sternite" are misleading. A sternum is the *ventral part* of a body segment; a sternite is a sclerotised plate occupying the whole or part of a sternum; since in Acrididae the whole of each sternum is sclerotised, the two terms are interchangeable (the same applies to "tergum", "tergite"). Also on p. 254, under "Subgenital plate": The term is applied in both sexes. In the female it is the eighth sternum (or sternite), in the male the "ninth sternal lobe", which articulates on the main part of the sternum. In the "Key to North American Orthopteroid Insects", the Acridoidea are shown as having a tympanum, whereas on p. 9 it is correctly stated that the tympanum may be absent. On p. 253, under "Paratype": According to the Glossary of the International Code of Zoological Nomenclature, a paratype is "every specimen in a type-series other than the holotype"; according to Article 72(b) of the Code, a type-series of a species "consists of *all* the specimens on which its author bases the species, *except* any that he refers to as variants, or doubtfully associates with the nominal species, or expressly excludes from it"—i.e., the author does not have to specifically "designate" a paratype. On p. 215, under (1), for "tibiae" read "femora"—a *lapsus calami.* On p. 208 the question of the type species of *Stethophyma* and *Mecostethus* is presented as though it were open to Otte to make his own decisions, whereas the valid type species must be determinable under the provisions of the International Code or by ruling of the International Commission on Zoological Nomenclature.

In summary, Dr. Otte has produced a useful, attractive, and very readable account of the two subfamilies he deals with. The few minor blemishes should be avoidable in the second and third volumes and in any new edition.—*K. H. L. Key, Division of Entomology, C.S.I.R.O., Canberra, Australia.*

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The *Journal of the New York Entomological Society* is devoted to the advancement and dissemination of knowledge of insects and related taxa. The Journal will consider for publication all manuscripts dealing with original research in entomology. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

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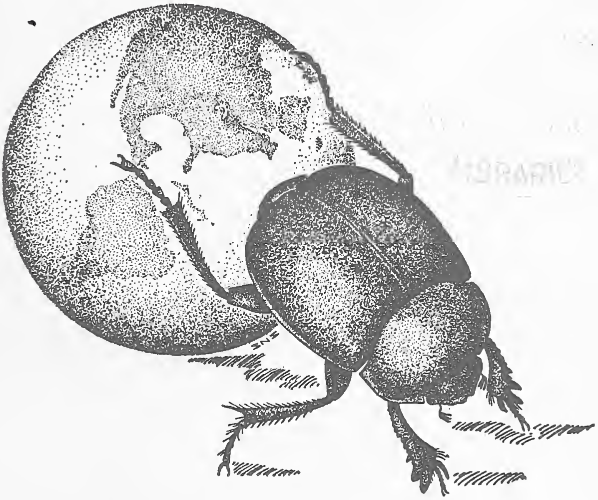

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A REVISION OF THE GENUS *ACROSTERNUM* FIEBER, SUBGENUS *CHINAVIA* ORIAN, IN THE WESTERN HEMISPHERE (HEMIPTERA: PENTATOMIDAE)

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Abstract.—The American species of *Acrosternum* Fieber, 1860, are placed in the subgenus *Chinavia* Orian, 1965, the latter taxon being elevated from synonymy. *Chinavia* is redefined, a key provided for the 51 nominal species of the Western Hemisphere and a description or diagnosis provided for each species. One nominal species is removed from *Acrosternum.* The species cataloged by Kirkaldy as *Nezara* (*Acrosternum*) *hebes* Bergroth, 1891, is a junior synonym of *Piezodorus guildinii* (Westwood, 1837). Additional new synonymy recognized is: *Nezara nigritarsis* Stål, 1872, as a junior synonym of *Acrosternum* (*Chinavia*) *grave* (Walker, 1867). Species described in the genus *Nezara* and here given new combinations as species of *Acrosternum* subgenus *Chinavia* are: *fuscopunctatum* (Breddin, 1901), *longicorialis* (Breddin, 1901), *nigridorsatum* (Breddin, 1901), *nigropictum* (Breddin, 1906) *panamensis* (Distant, 1890) and *rogenhoferi* (Stål, 1872). The following 23 species are new: *aseadum, australe, bellum, brasicola, callosum, collis, ecuadorensis, esmeraldum, euri, froeschneri, insulani, istum, macdonaldi, monticola, occasi, occultum, pecosum, pengue, plaumanni, simplicis, teretis, ubicum* and *wygodzinskyi.*

INDEX TO SPECIES

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The status and bounds of *Acrosternum* were especially uncertain for several decades after Fieber (1860) proposed the genus. The principal difficulty lay in distinguishing between *Acrosternum* and *Nezara* Stål, and even so astute an hemipterist as Stål wavered in his concept of these genera (1865, 1872, 1876). Other eminent hemipterists of the late 19th and early 20th centuries (Berg, Breddin, Distant, Horvath, Jakovlev, Schouteden, etc.) misunderstood Fieber's genus for more than half a century after it was proposed and described over a score of *Acrosternum* species in *Nezara.*

Sharp (1890) began the process of differentiating more clearly between *Acrosternum* and *Nezara.* After studying the male genitalia of *Acrosternum acutum* (Dallas), *A. marginatum* (Palisot de Beauvois) and *Nezara viridula* (L.), he remarked on the similarity of the first two species—even though the first was African and the second American—and doubted that the three species should be in the same genus. Nevertheless, he left them all in *Nezara.* Bergroth (1914) drew on Sharp's work and the external form of the metathoracic scent glands to distinguish between these genera. He transferred to *Acrosternum* those African species of the genus that Stål (1876) had included in *Nezara* and all the American species (except *viridula*) that Kirkaldy (1909) had cataloged under the "typical subgenus" of *Nezara.*

The work of Freeman (1940) apparently disposed of any reservations about the biological validity of *Acrosternum* or its proper rank. He began his revision of *Nezara* by characterizing the genus and stressing the value of the parameres in differentiating among the genera *Nezara, Acrosternum, Pellaea* and *Banasa.*

Although the validity and status of *Acrosternum* were now established, the limits of the genus were not. Orian (1965) proposed the genus *Chinavia,* with *Rhaphigaster pallidoconspersum* Stål as type species, for nine species from Africa, Madagascar and Mauritius that had been previously included in *Nezara* or *Acrosternum,* and he reserved *Acrosternum* for *A. heegeri* Fieber, the type species, and unspecified species from the Palearctic-Mediterranean region. He relied primarily upon characters of the male genitalia to distinguish *Chinavia* from *Acrosternum.* Day (1965) supported Orian's proposal but Linnavuori (1972) did not and sank *Chinavia* in the synonymy of *Acrosternum.* Nevertheless, Linnavuori recognized two groups of species within *Acrosternum,* the *heegeri*-group and the *pallidoconspersum*-group, which correspond to Orian's concept of *Acrosternum* and *Chinavia,* respectively.

In the Eastern Hemisphere, *Acrosternum* is represented in most if not all of Africa, in the Mediterranean basin and eastward into Madagascar, the Mascarine Islands, the Seychelles Islands, Arabia, southern Russia and the Indian subcontinent. In the Western Hemisphere, representation occurs from Patagonia in Argentina to southern Canada in the Great Lakes region (Ontario and Quebec). The northern limit of distribution is about the 45th parallel in both hemispheres. There are numerous species in both hemispheres, the largest number being American.

The *heegeri*-group is confined to the Eastern Hemisphere, ranging from the Cape Verde Islands and Canary Islands in the west through the Mediterranean basin and northern Africa into Arabia, southern Russia and the Indian subcontinent. Linnavuori (1972) speculates that the *heegeri*-group of species are the products of a radiation from the Sudanese subregion. This group is apparently adapted to arid and semiarid conditions.

Most of the species studied by Linnavuori belong to the *pallidoconspersum*-group. Their distribution in the Eastern Hemisphere is primarily tropical in Africa, Madagascar, Mauritius and Seychelles. It is to this group that all American species belong.

From my examination of *heegeri, graminea* (Fabricius), and *millieri* (Mulsant and Rey) of the *heegeri*-group and *acutum* (Dallas), *pallidoconspersum* (Stål), and *punctatorugosum* (Stål) of the *pallidoconspersum*-group, as well as all American species, which also belong in the latter group, I conclude that *Chinavia* deserves a better fate than synonymy. Pending a more detailed study of the Eastern Hemisphere species than has so far been undertaken, I propose to use *Chinavia* as a subgenus of *Acrosternum,* placing therein all American species of *Acrosternum* as well as the species assigned to *Chinavia* by Orian (1965).

The subgenera *Acrosternum* and *Chinavia* differ in several respects. In the females of the 18 American and three African species of *Chinavia* that were dissected, the spermathecal bulb and pump are remarkably similar. The bulb is always spherical with two long, thin, opposed diverticula that usually bend in opposite directions (Fig. 11). The duct at the base of the proximal flange is moderately expanded. In the nominal subgenus the spermathecal bulb varies in shape. It is essentially digitiform, without elaboration in *heegeri* (Fig. 1) but with rudimentary diverticula in *millieri* and *graminea* (Figs. 2, 3, 5). The duct at the base of the proximal flange is greatly expanded in all 3 species, and proximad of this expansion it is convoluted in *heegeri* and *graminea.*

The proctiger of *Chinavia* is rather flattened dorsally with a median, longitudinal impression that becomes pronounced before ending subbasally. In the nominate subgenus the proctiger bears a pair of prominent, conical projections subapically on the dorsal surface which otherwise is transversely convex.

The parameres in *Chinavia* have a basal spur and distally project into the genital cup (Fig. 10). In the nominate subgenus the basal spur is absent and the part of the parameres within the genital cup are bent sharply and appressed to the anterior wall of the genital cup (Fig. 4).

The mesosternal carina in *Chinavia* is low, conspicuously widened anteriorly and evanescent posteriorly. In the nominate subgenus this carina runs the length of the mesosternum and is about the same width and height throughout.

In general, the species of *Chinavia* are larger and darker in color than the species of the nominate subgenus.

There is no doubt, based on the species studied, that these two groups of species differ substantially. Whether or not these differences converge when other species of the Eastern Hemisphere are examined critically remains to be seen. The classificatory significance of the observed differences is, of course, a matter of subjective interpretation.

DISPOSITION OF SPECIES REMOVED FROM *Acrosternum*

One nominal species is removed from *Acrosternum.* The species cataloged by Kirkaldy (1909) as *Nezara* (*Acrosternum*) *hebes* Bergroth, 1891, is a junior synonym of *Piezodorus guildinii* (Westwood, 1837). The type of *N. hebes,* which is in the Museum National d'Histoire Naturelle, Paris, was examined.

PARATYPE DEPOSITORIES

Paratype depositories are indicated by the following abbreviations:

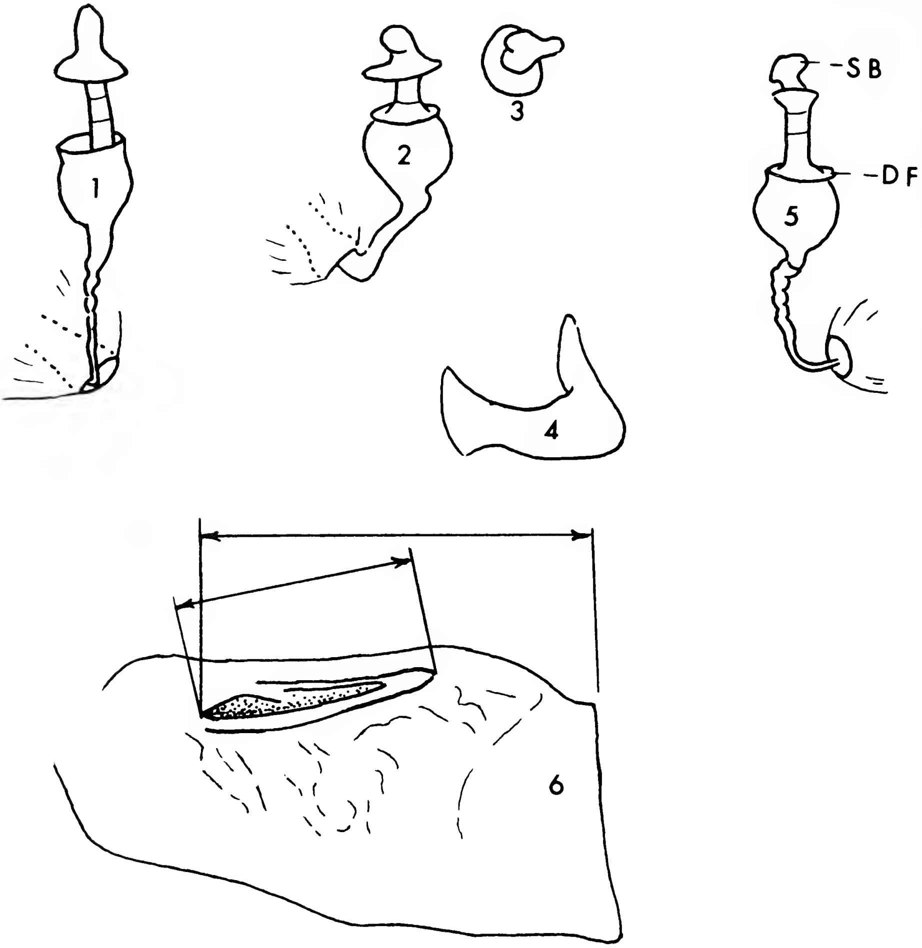
AMNH	American Museum of Natural History
CAS	California Academy of Sciences
DBT	Donald B. Thomas collection
FSCA	Florida State Collection of Arthropods
HDE	H. Dodge Engleman collection
INHS	Illinois Natural History Survey
JG	Jocélia Grazia collection
LHR	author's collection
MAI	M. A. Ivie collection
OSU	Ohio State University
RNH	Rijksmuseum van Natuurlijke Historie
TAMU	Texas A&M University
UCD	University of California at Davis
USNM	U.S. National Museum

Acrosternum Fieber, 1860

Acrosternum Fieber, 1860, p. 79; Stål, 1876, p. 90; Bergroth, 1914, p. 25 (diagnosis); Freeman, 1940, pp. 351–352 (cf. *Nezara*); Cachan, 1952, pp. 445–446 (Madagascan spp. keyed); Wagner, 1959, pp. 413–415, 417 (Palearctic spp. keyed); Linnavuori, 1972, pp. 416–420 (synonymy, African spp. keyed).

Nezara: Stål, 1865, pp. 196–198 (African spp. keyed section bb); Stål, 1876, pp. 91–92 (African spp. keyed section aa); Sharp, 1890, pp. 406–408, pl. 13, figs. 11a, 11b, 12, 17 (♂ genitalia).

Nezara (*Acrosternum*): Stål, 1872, pp. 41–43 (American spp. keyed).



Figs. 1–6. Fig. 1. *A. heegeri.* Distal part of spermatheca. Figs. 2–4. *A. millieri.* 2. Distal part of spermatheca. 3. Spermathecal bulb and distal flange, end view. 4. Paramere. Fig. 5. *A. graminea.* Distal part of spermatheca; spermathecal bulb (SB); distal flange (DF). Fig. 6. *A. montivagum.* Length of ostiolar ruga relative to distance from mesial margin of ostiole to lateral margin of thorax.

Acrosternum subgenus *Chinavia* Orian, 1965

Chinavia Orian, 1965, p. 25; Day, 1965, pp. 559, 565 (Madagascan spp. keyed).
Acrosternum pallidoconspersum-group: Linnavuori, 1972, pp. 416–418.

Diagnosis. Median projection on sternite 3 (2nd visible) ranging in length from tubercle not quite attaining metacoxae to spine surpassing mesocoxae but not reaching procoxae, usually compressed unless rudimentary, rarely circular in cross-section. First antennal segment not reaching apex of head. Bucculae percurrent caudad of obtuse anterior tooth, evanescent at base of head. Rostrum usually terminating between metacoxae, rarely at mesocoxae or on sternite bearing median projection. Mesosternal carina low, broadened anteriorly, evanescent posteriorly. Metasternum flat or slightly convex, without marginal rim, not produced ventrad. Femora unarmed. Ostiole on each side on plane of metasternum; attending sulcus and ruga elongated, latter reaching about one-half to three-fourths of distance from mesial margin of ostiole to lateral thoracic margin (Fig. 6), shorter only in *A. abnorme.*

Spermathecal bulb with two long slender diverticula (Fig. 11); expansion of spermathecal duct at proximal flange with much smaller diameter than bulb. Spiracles present on 8th paratergite (Fig. 22). Genital cup lacking tubercles on lateral walls, rarely with carina; posterior wall prominent, emarginated mesially, occasionally reduced to stout projection (Fig. 37); dorsal rim of posterior wall oriented diagonally or curved, usually denticulate and/or toothed (Figs. 9, 19), rarely covering genital cup except above proctiger (Fig. 60).

Large species about 10–18.5 mm long excluding membranes of hemelytra. Color predominantly green, sometimes blended with yellow; outer margins of body usually bordered in yellow to crimson; minor black markings usually present.

CHARACTERS OF INTERSPECIFIC VALUE

The pygophore is one of the taxonomically most useful characters, especially the structure which here is termed the posterior wall of the genital cup and which may be homologous with the inferior ridge. The posterior wall is deeply emarginated or divided mesially and the part on each side variously oriented when viewed dorsally. Usually the dorsal rim is diagonal, running anteromesad from near the posterolateral angle of the pygophore (Fig. 19) but sometimes slightly curved (Fig. 9) or reduced to a stout projection (Fig. 37). The dorsal rim of this structure is variously shaped and armed and usually constant intraspecifically, although notable variation occurs in *A. ubicum* (Figs. 95–97). In *A. longicorialis* the dorsal wall is reflexed cephalad and covers the genital cup except above the proctiger (Fig. 60). The parameres follow one general plan, and the slight differences among species are not often diagnostic.

As usual among pentatomids, the female genital plates are not always taxonomically useful, and those differences that do occur among species are usually more subtle than in the male genitalia. However, the outline of the posterior margin of the basal plates may differ appreciably from the caudoventral view, i.e., with the anterior and posterior margins of the plates approximately on the same focal plane. From a caudal view the dorsal edge of the plates may also differ in form among species. For example, *A. marginatum* and *A. hilare* females are easily separated by the basal plates (Figs. 157, 158, 164, 165). The spermathecae of all species in which this structure has been examined are similar. Insufficient specimens have been examined to determine whether or not the differences observed among species are constant.

The humeri are usually rounded from the dorsal view and little or not at all produced laterad. However, a few species have the humeri produced laterad in a right angular to spinose projection. Such species do not form a phylogenetic group, but the humeral character is nonetheless useful in recognizing species.

The length of the median projection at the base of the abdominal venter seems to vary little intraspecifically. Length ranges from a rudimentary tubercle to a spine reaching to or a little past the anterior limit of the mesocoxae. The spine is usually compressed but in *A. froeschneri* it is nearly round in cross-section.

The rather inconspicuous black markings on the cicatrices, basal angles of the scutellum and connexiva are usually constant intraspecifically, particularly those on the connexiva. *A. laetum* is exceptional in the amount of variation in the connexival markings. Interspecifically the connexiva may be immaculate, or the black mark confined to the edge of the sternite at the posterolateral angle (Fig. 34), or spill onto the laterotergite (Fig. 33), or cover the posterolateral angle of one segment and the anterolateral angle of the following segment (Fig. 40), or border most or all of the posterior margin of each segment (Fig. 26) or border the connexival segments on both sides of the transverse sutures.

The color markings that occur on the femora or both femora and tibiae of a few species are diagnostically useful.

Many species have each spiracle located on a small, differentially colored callus. In *A. australe* the spiracle is contiguous with but not on the callus. Usually the callus is ivory colored, but in *A. collis* it is black. Occasionally the area around each spiracle is more or less ivory colored but not calloused. The color of the peritreme is diagnostically helpful but unfortunately variable in some species.

Generally the costal angle of each corium lies over the penultimate connexival segment, terminating intraspecifically from the middle of the segment to the posterior margin. A few species, however, have longer coria and the costal angle lies over the last connexival segment. Usually the extremity of the coria is at or very near the costal angle (Fig. 57), but *A. longicorialis* is exceptional in that the corium of each hemelytron intrudes into the membrane and leaves an appreciable amount of membrane along the costal margin cephalad of the extremity of the corium (Fig. 58).

The rostrum generally terminates between the metacoxae, but in *A. montivagum* and *A. pennsylvanicum* it does not reach the metacoxae and in *A. viridans* it extends onto the second visible sternite. This character seems intraspecifically constant but is, of course, altered in specimens with the head abnormally positioned.

KEY TO SPECIES OF *Acrosternum*

1. Humeri produced laterad of each corium by more than half the width of an eye, right angular or spinose 4
– Humeri not or less produced, not spinose, usually rounded 2
2(1). Abdominal spine projecting past anterior limit of metacoxae 6
– Abdominal spine or tubercle not surpassing metacoxae 3
3(2). Lateral half or more of transverse connexival sutures (entire suture, not just exposed part if partially covered) bordered on one or both sides in black (Fig. 26) 47
– Connexiva immaculate or with black spot or macule at posterolateral angles of segments (Figs. 33, 34, 40) 18
4(1). Abdominal spine projecting slightly past anterior limit of mesocoxae; transverse connexival sutures bordered on both sides with black .... *insulani,* new species
– Abdominal spine not surpassing metacoxae; connexiva with black dot at posterolateral angles of segments 5
5(4). Lateral margins of head anterior to eyes tapering abruptly to narrow apex of head (Fig. 12); pygophore moderately emarginate from caudal aspect (Fig. 14) .... *bellum,* new species
– Head less tapered, apex moderately rounded (Fig. 7); pygophore deeply emarginate from caudal view (Fig. 8) .... *armigerum* Stål
6(2). Ostiolar ruga not much longer than ostiole .... *abnorme* (Berg)
– Ostiolar ruga reaching about halfway or more from mesial margin of ostiole to lateral margin of thorax 7
7(6). Posterior margin of connexival segments bordered in black 8
– Connexiva with large black macules, each divided by transverse suture, or with small black mark in posterolateral angle of each segment, or immaculate 10
8(7). Abdominal spine reaching just past metacoxae .... *herbidum* (Stål)
– Abdominal spine reaching to or beyond posterior margin mesocoxae 9
9(8). Sternites slightly calloused on both sides of transverse sutures and pseudosutures .... *callosum,* new species
– Abdominal sternites lacking calli .... *occultum,* new species
10(7). Abdominal spine projecting past mesocoxae 11
– Abdominal spine reaching no farther that anterior margin of mesocoxae 12
11(10). Lateral margins of juga black, submarginally yellow banded .... *sparnium* (Dallas)
– Lateral margins of juga not or thinly edged in black; submarginally green or weakly suffused with yellow .... *obstinatum* (Stål)
12(10). Connexival spots large, each divided by transverse sutures .... *scutellatum* (Dallas)
– No more than posterolateral angles of connexival segments black 13
13(12). Abdominal spine conical, round in cross-section .... *froeschneri,* new species
– Abdominal spine compressed 14
14(13). Distal margin of each corium parabolic, intruding into membrane (Fig. 58); abdominal spine reaching anterior limit of mesocoxae .... *longicorialis* (Breddin)
– Little or none of membrane laterad of coriaceous part of hemelytra (Fig. 57); abdominal spine terminating near posterior limit of mesocoxae 15

15(14). Lateral jugal margins barely concave before eyes (Fig. 43) 16

– Lateral jugal margins clearly concave before eyes (Figs. 50, 52) 17

16(15). Black on connexiva confined to edge of sternite at posterolateral angle of segments; outer margins of dorsum weakly and incompletely bordered in yellow .... *esmeraldum,* new species

– Black spot in posterolateral angle of connexival segments including part of laterotergite; outer margins of dorsum clearly bordered in reddish orange .... *istum,* new species

17(15). Broad submarginal depression present dorsally along anterolateral margins of pronotum .... *napaeum* (Stål)

– Transverse curvature of pronotal disk continuing smoothly to anterolateral margins .... *difficile* (Stål)

18(3). Distal end or more of femora black at least on superior surface; antennae entirely black 19

– Distal end of femora green, yellow or red; much or all of antennae usually green 22

19(18). Large black macule on dorsum comprised of distal part of each corium and hemelytral membranes .... *panamensis* (Distant)

– Dorsum not so marked, macules absent or on pronotum and scutellar base 20

20(19). Anterolateral margins of pronotum and lateral margins at base of coria widely bordered in yellow; often with yellow median stripe on pronotum and/or scutellum, and often lateral margins and/or apex of scutellum yellow .... *grave* (Walker)

– Anterolateral margins of pronotum with incomplete and diffuse yellow border or with none; scutellum and pronotal disk immaculate or marked with black 21

21(20). Cicatrices and large subquadrate patch at scutellar base on each side black .... *nigropictum* (Breddin)

– Pronotal disk and scutellum immaculate .... *geniculatum* (Dallas)

22(18). Dorsal punctation sparse, most punctures separated from nearest puncture by distance equal to or greater than diameter of second antennal segment .... *viridans* (Stål)

– Dorsal punctation much denser 23

23(22). Connexiva immaculate or black mark at posterolateral angles of segments confined to edge of sternite (Fig. 34) 24

– Connexival spots at least on basal segments expanding onto laterotergite (Figs. 33, 40) 37

24(23). Rostrum terminating at mesocoxae; anterolateral margins of pronotum strongly convex (Fig. 75) .... *pennsylvanicum* (P.B.)

– Rostrum extending to or beyond metacoxae; anterolateral margins of pronotum straight or weakly convex 25

25(24). Spiracles black 26

– Spiracles green, yellow, brown, or red 30

26(25). Most of dorsal punctation fuscous; callus around each spiracle weak, not differentiated by color .... *pecosum,* new species

– Dorsal punctures concolorous with surrounding area; callus surrounding each spiracle usually yellowish 27

27(26). Posterolateral angles of sternites with conspicuous black spot 29

– Not more than minute spine at posterolateral angles of sternites dark or black 28

28(27). Basal 3 segments of antennae without black markings; large tooth present at anteromesial corner of dorsal rim on each side of posterior wall of pygophore (Fig. 84) .... *aseadum,* new species

– All antennal segments partially black; denticle at anteromesial corner of dorsal rim little larger than other denticles on rim .... *ecuadorensis,* new species

29(27). Humeri forming obtuse angle (Fig. 87); anterolateral margin of pronotum straight .... *nigridorsatum* (Breddin)

– Humeri broadly rounded; anterolateral margin of pronotum slightly convex .... *ubicum,* new species

30(25). Black dot present at mesial limit of each cicatrice, sometimes also at lateral limit .... *laetum* (Stål)

– Cicatrices immaculate 31

31(30). Ostiolar ruga extending only halfway from mesial margin of ostiole to lateral margin of thorax 32

– Ostiolar ruga extending about ¾ distance from mesial margin of ostiole to lateral margin of thorax 33

32(31). Each spiracle on small ivory callus .... *simplicis,* new species

– Spiracles not accompanied by callus .... *euri,* new species

33(31). Each spiracle on ivory callus 35

– Spiracles not accompanied by differentially colored callus 34

34(33). Costal margin of coria basally and margin of scutellum at apex orange to yellow .... *macdonaldi,* new species

– Costal margin of coria and apex of scutellum green .... *wygodzinskyi,* new species

35(33). Abdominal spine projecting between metacoxae .... *monticola,* new species

– Abdominal tubercle not or barely attaining metacoxae 36

36(35). Posterior margin of basal plates sloping toward meson; antennal segments 4 and 5 black or green distally .... *ubicum,* new species

– Posterior margin of basal plates nearly transverse mesad of rounded lateral angle; distal parts of antennal segments 4 and 5 castaneous .... *occasi,* new species

37(23). Tibiae crimson proximally 38

– Proximal end of tibiae green or yellow 39

38(37). Costal angle of coria above last connexival segment .... *collis,* new species

– Costal angle of coria above penultimate connexival segment .... *montivagum* (Distant)

39(37). Spiracles black 44

– Spiracles pale 40

40(39). Each spiracle on or beside yellow callus 41

– Spiracles unattended by callus but sometimes in yellow spot 42

41(40). Each spiracle in edge of callus 60

– Each spiracle contiguous with but not surrounded by callus .... *australe,* new species

42(40). Costal angle of coria subacute, lying above sixth visible sternite (Fig. 153) .... *fuscopunctatum* (Breddin)

– Costal angle of coria rounded, lying above fifth visible sternite 43

43(42). Females: basal plates with posterolateral projection at base of 9th paratergite (Fig. 157); males: posterior margin of pygophore with broad V-shaped emargination from ventral view (Fig. 159) .... *marginatum* (P.B.)

– Females: posterior margin of basal plates evenly convex (Fig. 164); males: pygophoral emargination shallow with small median notch from ventral view (Fig. 166) .... *hilare* (Say)

44(39). Black spot present in basal angles of scutellum .... *brasicola,* new species

– Basal angles of scutellum immaculate 45

45(44). Abdominal tubercle nearly reaching anterior limit of metacoxae .... *teretis,* new species

– Abdominal tubercle barely reaching posterior limit of metacoxae 46

46(45). Humeral margin obtusely angular; anterolateral margin of pronotum straight .... *nigridorsatum* (Breddin)

– Humeral margin rounded; anterolateral margin of pronotum weakly convex .... *ubicum,* new species

47(3). Connexival segments bordered both anteriorly and posteriorly with black 48

– Connexival segments bordered posteriorly only with black ... 52

48(47). Some or all femora with preapical black band ... *musivum* (Berg)

– Black femoral markings apical or absent ... 49

49(48). Anterolateral margins of pronotum broadly bordered with black near humeri and yellow anteriorly ... *rogenhoferi* (Stål)

– Border of anterolateral margins of pronotum entirely red or yellow ... 50

50(49). Sutures and pseudosutures on abdominal venter black ... *erythrocnemis* (Berg)

– Sutures and pseudosutures of abdominal venter not contrasting strongly in color with remainder of abdominal venter ... 51

51(50). Each spiracle in yellowish callus ... *montivagum* (Distant)

– Spiracles unaccompanied by callus ... *runaspis* (Dallas)

52(47). Base of tibiae with reddish band ... 53

– Tibiae without basal band ... 54

53(52). Basal angles of scutellum with small black macule; spiracles and spiracular calli black ... *collis,* new species

– Basal angles of scutellum immaculate, spiracles reddish, spiracular calli yellow ... *montivagum* (Distant)

54(52). Spiracles black ... 55

– Spiracles pale, only peritreme sometimes thinly ringed in black ... 57

55(54). Abdominal tubercle pronounced; black spot usually present in basal angles of scutellum and at mesial limit of cicatrices ... 56

– Abdominal tubercle rudimentary; pronotum and scutellum without black markings ... *plaumanni,* new species

56(55). Anterior pronotal disk transversely depressed, forming shallow basin; anterolateral margins of pronotum slightly convex ... *dallasi* (Distant)

– Pronotal disk weakly convex anteriorly, any depressed area submarginal; anterolateral margins of pronotum nearly straight ... *bipunctulum* (Stål)

57(54). Each spiracle on distinct yellow callus; yellowish macules present along base of scutellum ... *laetum* (Stål)

– Callus around each spiracle weakly or not differentiated by color; yellow macules rarely present at base of scutellum ... 58

58(57). Black spot present in basal angles of scutellum ... *impicticorne* (Stål)

– Basal angles of scutellum without black spot ... 59

59(58). Dorsal borders of body not differentially colored or inconspicuous light yellow; abdominal spine reaching anterior limit of hind trochanters ... *herbidum* (Stål)

– Dorsal borders conspicuous, narrow, red; abdominal spine shorter, reaching posterior limit of metacoxae ... *pengue,* new species

60(41). Black spot present at mesial limit and sometimes also at lateral limit of cicatrices ... *laetum* (Stål)

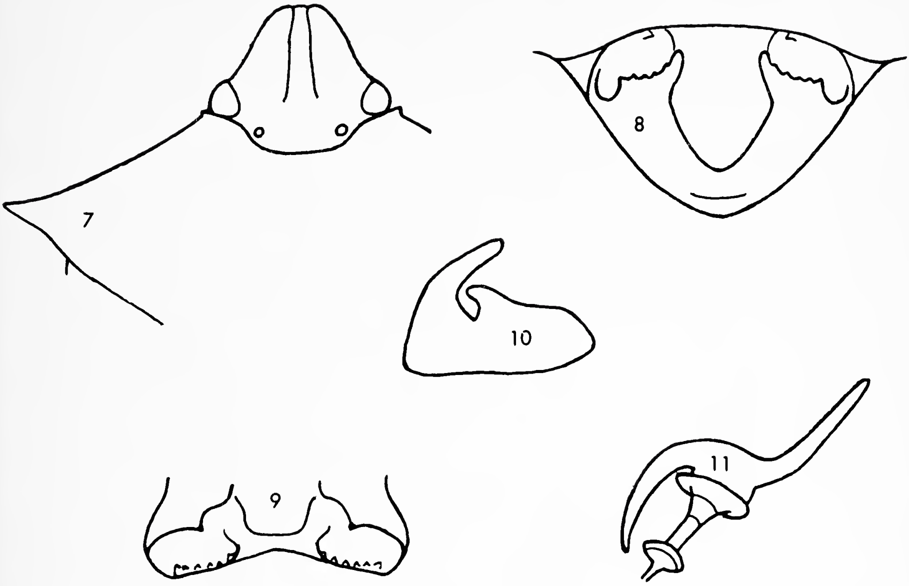
– Cicatrices immaculate ... *apicicorne* (Spinola)

Acrosternum (*Chinavia*) *armigerum* (Stål, 1859)

(Figs. 7–11)

Rhaphigaster armiger Stål, 1859, pp. 229–230.

Nezara (*Acrosternum*) *armigera:* Stål, 1872, p. 43 (keyed).



Figs. 7–11. *A. armigerum.* 7. Humeral angle and head. 8. Pygophore, caudal view. 9. Genital cup, dorsal view. 10. Paramere. 11. Spermathecal bulb and pump.

Nezara armigera: Berg, 1878, p. 28 (descriptive note; reprinted 1879, p. 58); Berg, 1883, pp. 213–214 (description; reprinted 1884, pp. 29–30).
Acrosternum armigera: Pirán, 1948, p. 9 (records); Grazia-Vieira and Casini, 1973, p. 57 (record).

Diagnosis. Humeral angles spinose. Abdominal spine terminating between metacoxae. Small black spot present at posterolateral angles of connexiva and sternites; laterotergites immaculate. Spiracles usually black, each in posterolateral edge of weak small and usually yellow callus. Ostiolar ruga on each side extending 0.6–0.7 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum reaching metacoxae. Femora green. Head moderately rounded apically (Fig. 7). Cicatrices immaculate. Basal angles of scutellum lacking black spot. Punctation on dorsum dense, punctures concolorous with surrounding area. Posterior wall of genital cup subvertical, deeply emarginate mesially, expanded mesodorsad on each side; this expansion acute apically, bearing several small black denticles on dorsal rim (Figs. 8, 9). Parameres and spermatheca as in Figures 10 and 11. Length about 10–13 mm.

Distribution. Northern Argentina, southern Brazil, Paraguay, Uruguay.

Types. Lectotype, here designated, ♂, labeled (a) "Buenos Ayres" (b) "Type" (c) "Typus" (d) "109/79" (e) "Riksmuseum Stockholm". Paralectotype: ♀ labeled (a) "Buenos Ayres" (b) "Westerman" (c) "Allotypus" (d) "110/79" (e) "Riksmuseum Stockholm".

Acrosternum (Chinavia) bellum, new species
(Figs. 12–16)

Description. Light dull green, becoming yellowish to yellowish green mesially below, with narrow yellow to red lateral borders on head, pronotum, coria basally, connexiva and abdominal venter. A black dot present at posterolateral angles of connexival segments (excluding laterotergites) and sternites. Antennae green. Legs green with base of femora, trochanters and coxae yellowish. Punctation on dorsum dense, fine; punctures concolorous with surrounding area; thoracic venter more sparsely and irregularly punctate than dorsum.

Head 2.4–2.6 mm wide across eyes, 1.9–2.0 mm long, proportionately as in *armigerum* but more narrowly rounded at apex (Fig. 12). Antennal segments 0.4–0.5, 0.9–1.0, 1.0–1.2, 1.2–1.4, 1.5 mm long. Rostral segments 2 through 4 about 1.2–1.4, 0.9–1.0, 0.7–0.9 mm long; apex reaching metacoxae.

Pronotum 7.0–8.3 mm wide at humeri, 2.4–2.8 mm long at meson. Anterolateral margins nearly straight. Humeral angles right angular to spinose. Cicatrices immaculate.

Scutellum 4.0–4.5 mm wide at base, 4.3–4.8 mm long. Four or 5 small yellow spots spaced along scutellar base.

Abdominal spine reaching only to posterior limit of metacoxae, its anterior margin subvertical. Each spiracle located in posterolateral edge of small ivory callus; peritremes black. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax.

Female unknown.

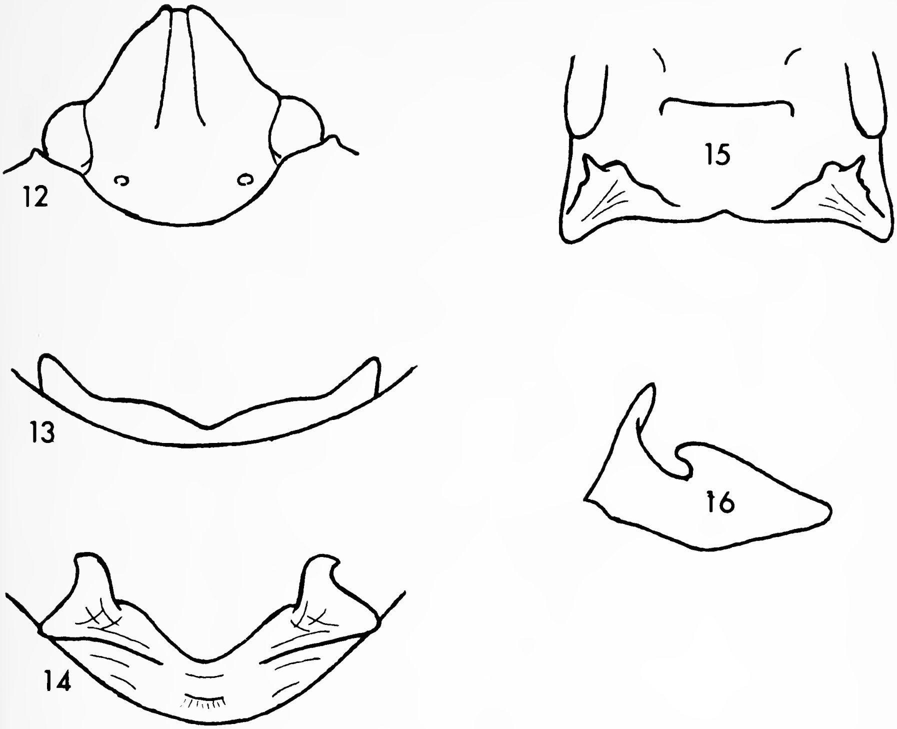
Posterior margin of pygophore from ventral view with broad shallow sinuous concavity (Fig. 13). Posterior wall of genital cup diagonal at dorsal margin on each side, there bearing a large denticle anteriorly (bent anterolaterad at apex) and elsewhere weak denticles (Figs. 14, 15). Paramere as in Figure 16.

Length about 11.0–11.5 mm.

Distribution. Northern Argentina, southern Brazil, Paraguay.

Holotype. ♂, labeled "Brazil, Embrapa, 28-IX-1976, Coll. Ev. Vogel". Deposited in U.S. National Museum, type no. 75560.

Paratypes. ♂, labeled "Museum Leiden. Argentina. Pronuntiamente, Prov. Entre Rios. I, 1965. F. H. Walz." (RHN); ♂, labeled "Museum Leiden. Dr.



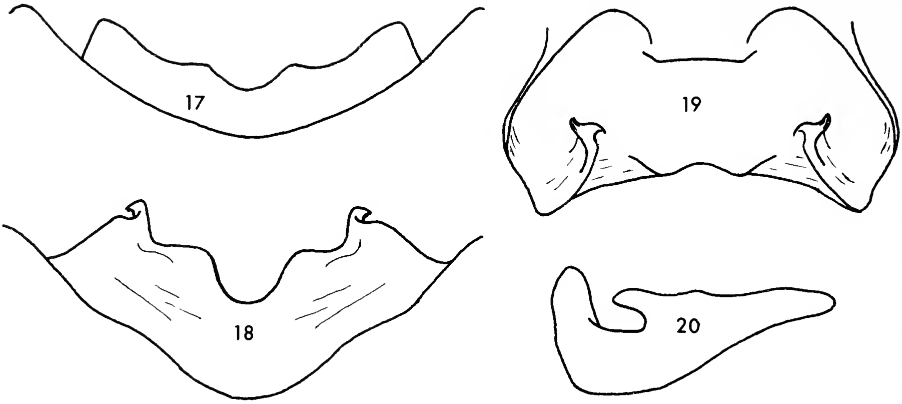
Figs. 12–16. *A. bellum.* 12. Head. 13. Pygophore, ventral view. 14. Pygophore, caudal view. 15. Genital cup. 16. Paramere.

B. Podtiaguine. Assomption; Omgev. Paraguay. 22 Feb.–25 Apr. 1936" (RNH).

Comments. Superficially resembling *A. armigerum,* the two species differ especially in the shape of the head, abdominal tubercle and pygophore.

Acrosternum (Chinavia) insulani, new species
(Figs. 17–20)

Description. Light green above, paler green below, with lateral margins of head, pronotum, coria basally, abdominal venter as well as apex of scutellum and connexiva reddish-yellow. Transverse sutures of connexiva broadly bordered on both sides with black, these bands continuing onto abdominal venter and evanescing before reaching spiracular line. Spot on superior surface of antennifers and antennae excepting base of first segment black. Legs excepting somewhat darker tarsi concolorous with venter. Punctation on



Figs. 17–20. *A. insulani.* 17. Pygophore, ventral view. 18. Pygophore, caudal view. 19. Genital cup. 20. Paramere.

dorsum moderately dense, fine; punctures concolorous with surrounding area; abdominal venter sparsely punctate and aciculate.

Head 2.85 mm wide across eyes, 2.3 mm long. Antennal segments 0.5, 1.1, 1.5, 1.8, 1.9 mm long. Rostral segments 2 through 4 about 1.5, 1.4, 1.1 mm long; apex reaching metacoxae.

Pronotum 8.0 mm wide at humeri, 5.3 mm long at meson. Humeri produced laterad, forming right angle. Cicatrices immaculate.

Scutellum 4.6 mm wide at base, 5.3 mm long, without markings other than pale apex.

Abdominal spine projecting slightly past anterior limit of mesocoxae. Spiracles yellowish, unattended by callus. Ostiolar ruga on each side extending 0.7 distance from mesial margin of ostiole to lateral margin of thorax.

Female unknown.

Posterior pygophoral margin shallowly concave from ventral view with slight protrusion on each side of mesial emargination (Fig. 17), this emargination from caudal aspect deep, U-shaped (Fig. 18). Posterior wall of genital cup diagonal dorsally on each side with large tubercle at anteromesial corner of dorsal rim; this tubercle directed anterolaterad, acute apically (Fig. 19). Parameres elongate (Fig. 20).

Length about 14 mm.

Distribution. Hispaniola.

Holotype. ♂, labeled "Constanza to Jarabacoa. Aug. '38. Dom. Rep. 2–4000 ft. Darl." Deposited in the American Museum of Natural History.

No paratypes.

Acrosternum (*Chinavia*) *abnorme* (Berg, 1892)
(Figs. 21, 22)

Nezara abnormis Berg, 1892, pp. 7–8; Pirán, 1966, p. 86, fig. 1 (record, ♀ genitalia).
Acrosternum abnorme: Pirán, 1968, p. 17 (record).

Diagnosis. Ruga from metathoracic scent gland about as long as ostiole. Humeri not produced, rounded. Abdominal spine terminating between meta- and mesocoxae. Each spiracle located in lateral part of large yellowish callus; peritreme little darker than callus. Rostrum reaching metacoxae. Femora without black markings. Cicatrices immaculate. Subcalloused orange-yellow spot present in basal angles of scutellum. Dorsal punctation dense, fine, concolorous with light green dorsum, in irregular transverse rows with pale to orange-yellow interstices forming subtle mesial stripe on pronotum and on scutellum except basally. Pygophore from caudal aspect deeply emarginated mesially, appearing bilobed laterally (Fig. 21). Genital plates as in Figure 22. Length about 10.5 mm.

Distribution. Northern Argentina, southern Brazil, Uruguay.

Type. Described from a single male preserved in the Universidad Nacional de La Plata.

Comment. The holotype was examined.

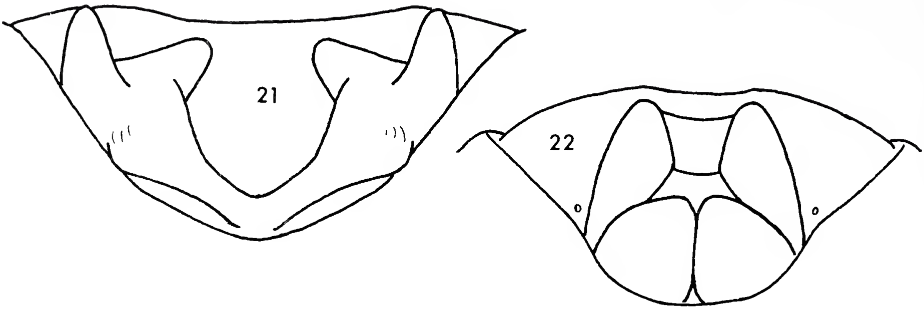
Acrosternum (Chinavia) callosum, new species
(Figs. 23–25)

Description. Light green above with lateral submargins of head and many interstices between punctures yellow. Venter yellowish green laterally, blending to yellow mesially. Antennae green with last 2 segments brownish. Coxae and trochanters yellow, remainder of legs green. Border along posterior margin of connexival segments, posterolateral angles of sternites, elongated macule on antennifers and edge of head before eyes, all black. Dorsal punctation moderately dense, fine, in irregular transverse rows on most of pronotum, green; abdominal venter lightly and densely aciculate.

Head 2.6–2.8 mm wide across eyes, 2.1–2.2 mm long. Antennal segments 0.4–0.5, 1.0–1.1, 1.2–1.4, 1.6–1.7, 1.5–1.6 mm long. Last 3 rostral segments about 1.3–1.4, 1.0–1.1, 0.8–0.9 mm long; rostrum reaching metacoxae.

Pronotum 6.6–7.1 mm wide at humeri, 2.4–2.8 mm long at meson. Humeri not produced laterad, rounded. Anterolateral margins straight. Cicatrices immaculate.

Scutellum, 4.2–4.6 mm wide at base, 4.5–4.9 mm long; basal angles immaculate.



Figs. 21, 22. *A. abnorme*. 21. Pygophore, caudal view. 22. Genital plates, caudoventral view.

Abdominal spine compressed, projecting slightly beyond mesocoxae. Spiracles not on callus, concolorous with surrounding area of sternites. Sternites slightly calloused on both sides of transverse sutures, latter green except mesially and at lateral margins. Pseudosuture between spiracle and trichobothria similarly calloused and colored. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax.

Genital plates similar to those of following species (Fig. 27).

Posterior margin of pygophore from ventral view sinuously emarginate, notched mesially and protruding slightly on each side of notch (Fig. 23); from caudal view posterior margin sinuously emarginate with denticles visible on dorsal rim of posterior wall of genital cup (Fig. 24). Posterior wall of genital cup diagonal dorsally on each side, bearing small black denticles posteriorly on dorsal rim and large anterolaterally directed curved denticle anteriorly (Fig. 25).

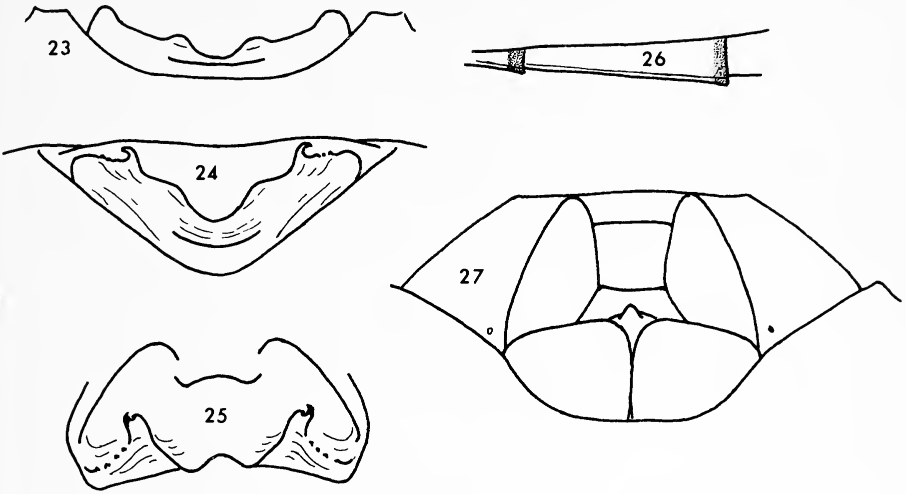
Length about 11.5 mm.

Distribution. Paraguay, Bolivia.

Holotype. ♂, labeled (a) "Village #17. Fern. Col. Chaco. Paraguay. III-1-56." (b) "cotton" (c) "J. L. Nichel, Collector." (d) "He-21." Deposited in U.S. National Museum, type no. 75561.

Paratypes. ♂, ♀, labeled "Bolivia, S. C., 1 mi. W. Pto. Pailas. Apr. 21, 1978. C. W. O'Brien & Marshall" (♂ HDE; ♀ LHR).

Comment. This species is especially distinguished from the following species by the longer abdominal spine, black margins of the head, and calli along the transverse sutures and pseudosutures of the abdominal venter. These two species, among the *Acrosternum* of the Western Hemisphere whose abdominal spine projects past the metacoxae, are the only ones having the posterior margin of the connexival segments completely bordered in black.



Figs. 23–27. Figs. 23–25. *A. callosum.* 23. Pygophore, ventral view. 24. Pygophore, caudal view. 25. Genital cup. Figs. 26, 27. *A. occultum.* 26. Connexival segment. 27. Genital plates, caudoventral view.

Acrosternum (Chinavia) occultum, new species
(Figs. 26, 27)

Description. Light green above and below including appendages. Venter blending to yellowish brown mesially; abdominal margins yellow. Posterior border of connexival segments, posterolateral angles of abdominal sternites and elongated mark on antennifers black (Fig. 26). Dorsal punctation dense, fine; punctures concolorous with surrounding area; transverse interstices on pronotum somewhat rugose.

Head 2.8 mm wide across eyes, 2.2 mm long. Antennal segments 0.5, 1.0, 1.2, 1.5–1.7, 1.7 mm in length. Last 3 rostral segments about 1.5, 1.1, 0.9–1.0 mm long; rostrum reaching metacoxae.

Pronotum 7.0 mm wide at humeri, 2.7 mm long. Humeri not produced laterad, rounded; anterolateral margins slightly convex. Cicatrices immaculate.

Scutellum 4.6–4.7 mm wide at base, 4.9 mm long. Obscure dark dot sometimes present in basal angles.

Abdominal spine compressed, reaching to or between mesocoxae. Spiracles not on callus, more or less concolorous with surrounding area of sternites. Ostiolar ruga on each side extending 0.7 distance from mesial margin of osiole to lateral margin of thorax.

Genital plates as in Figure 27.

Male unknown.

Length about 12 mm.

Distribution. Bolivia (Beni).

Holotype. ♀, labeled (a) "Bolivia: Dept. Beni, Rio Itenez at mouth of Rio Baures. X-10-1964". (b) "J. K. Bouseman, Collector". Deposited in the American Museum of Natural History.

Paratype. ♀, with same data as holotype except date "IX–X-1964" and (b) "J. K. Bouseman, J. Lugenhop, Collectors" (LHR).

Comment. Excepting the longer abdominal spine, this species appears indistinguishable from *A. herbidum.* While some intraspecific variation occurs in the length of the abdominal spine, it seems improbable that so much variability is contained in one species.

Acrosternum (*Chinavia*) *obstinatum* (Stål, 1860)
(Figs. 28–33)

Rhaphigaster obstinatus Stål, 1860, p. 23.

Nezara (*Acrosternum*) *obstinatus:* Stål, 1872, p. 42 (keyed, *A. difficile* compared).

Diagnosis. Humeri obtusely rounded, not produced. Abdominal spine compressed, reaching anterior limit of mesocoxae. Posterior angles of connexival segments (sometimes including posterolateral angles of laterotergite) and of sternites with small black spot (Fig. 33). Lateral jugal margins thinly or not edged in black; distinct submarginal band absent. Each spiracle at posterolateral edge of weak callus; peritremes brown to narrowly black. Ostiolar ruga on each side extending 0.6–0.8 distance from mesial margin of ostiole to lateral margin of thorax. Femora green. Cicatrices immaculate. Diffuse yellow spot often present at basal angles of scutellum. Dorsal punctation dense, fine. Pygophore from ventral view with mesial notch in broad shallow emargination (Fig. 28). Posterior wall of genital cup dorsally diagonal on each side; dorsal rim with small denticles posteriorly and large denticle anteriorly, latter bending first anterolaterad then cephalad at acute apex (Fig. 30). Parameres and spermatheca as in Figures 31 and 32.

Length about 11–15 mm.

Distribution. Southern Brazil.

Types. Lectotype, here designated, ♂, labeled (a) "Brasil" (b) "F. Sahlb" (c) "Type" (d) "Typus" (e) "122/79" (f) "Riksmuseum Stockholm"; paralectotype, ♂, labeled (a) "Rio Jan" (b) "Stal" (c) "Type" (d) "Paratypus" (e) "123/79" (f) "Riksmuseum Stockholm".

Acrosternum (*Chinavia*) *sparnium* (Dallas, 1851)
(Fig. 34)

Rhaphigaster sparnius Dallas, 1851, p. 280.

Nezara sparnius: Stål, 1872, p. 43 (listed).

Acrosternum sparnium: Rolston, 1976, p. 4 (generic placement).

Diagnosis. Lateral margins of head black with well-defined yellow band submarginally. Humeral angles rounded, not produced laterad. Abdominal spine compressed, projecting beyond mesocoxae, ending about midway between meso- and procoxae. Posterolateral angles of sternites and of connexiva where protruding, black; this mark on connexiva often elongated anteriorly (Fig. 34). Spiracles unattended by callus; peritremes brown to rufous. Ostiolar ruga on each side extending 0.7–0.8 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum reaching metacoxae. Femora green to yellowish green. Cicatrices immaculate. A yellowish spot present at basal angles of scutellum. Dorsal punctation dense, shallow.

Length about 10.5 mm.

Distribution. Jamaica, Cayman Is.

Comment. The female holotype was examined. No male was seen.

Acrosternum (Chinavia) scutellatum (Distant, 1890)
(Figs. 35–40)

Nezara scutellata Distant, 1890, pp. 339–440, pl. 31, fig. 21.
Acrosternum scutellatum: Rolston, 1976, p. 4 (generic placement).

Diagnosis. Connexiva with large black macules, each bisected by transverse connexival suture, continuing onto margin of venter (Fig. 40). Distal end of femora and proximal end of tibiae usually reddish. Humeri rounded, not produced laterally. Abdominal spine compressed, ending beyond metacoxae, sometimes reaching mesocoxae. Spiracles yellowish, unattended by callus. Ostiolar ruga on each side extending 0.6–0.8 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum extending to metacoxae. Cicatrices and basal angles of scutellum immaculate. Dorsal punctation dense, fine. Pygophore broadly emarginate from ventral view; emargination shallow, somewhat sinuous (Fig. 35). Posterior wall of genital cup represented on each side by large tubercle projecting anterodorsad and appearing capitate from caudal view (Figs. 36, 37). Paramere and spermatheca as in Figures 38 and 39.

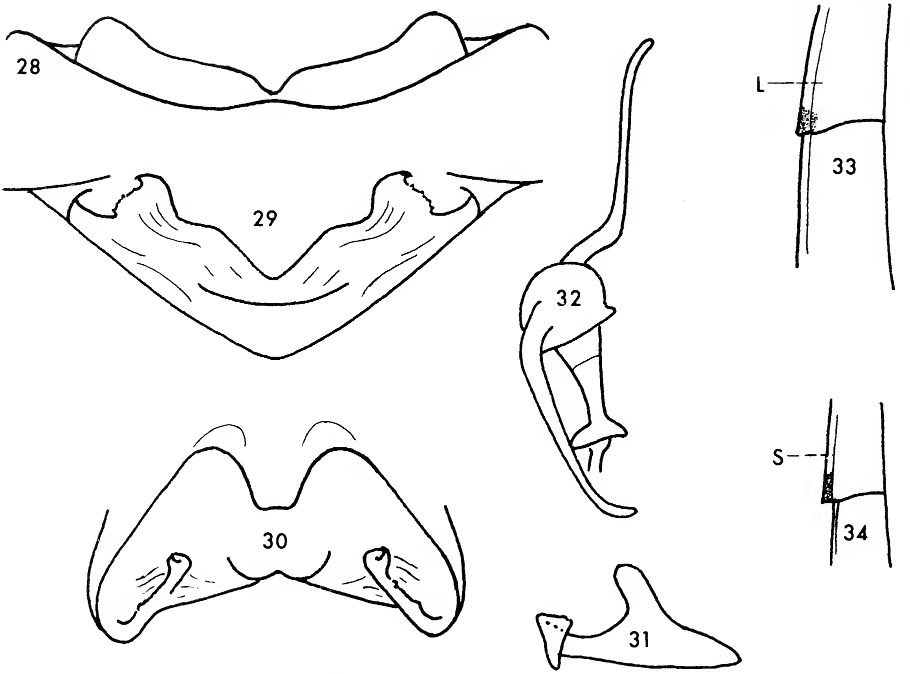
Length about 14–18 mm.

Distribution. From Mexico (Veracruz) into Panama.

Comment. The female holotype was examined.

Acrosternum (Chinavia) froeschneri, new species
(Figs. 41, 42)

Description. Yellowish green above and below including appendages, tinted reddish orange along lateral margins of head, anterolateral angles of pronotum and labial groove. Punctation mostly of moderate strength and density, somewhat rugose on pronotal disk, less dense on scutellum, fine



Figs. 28–34. Figs. 28–33. *A. obstinatum.* 28. Pygophore, ventral view. 29. Pygophore, caudal view. 30. Genital cup. 31. Paramere. 32. Spermathecal bulb and pump. 33. Connexival marking; laterotergite (L). Fig. 34. *A. sparnium.* Connexival marking; edge of sternite (S).

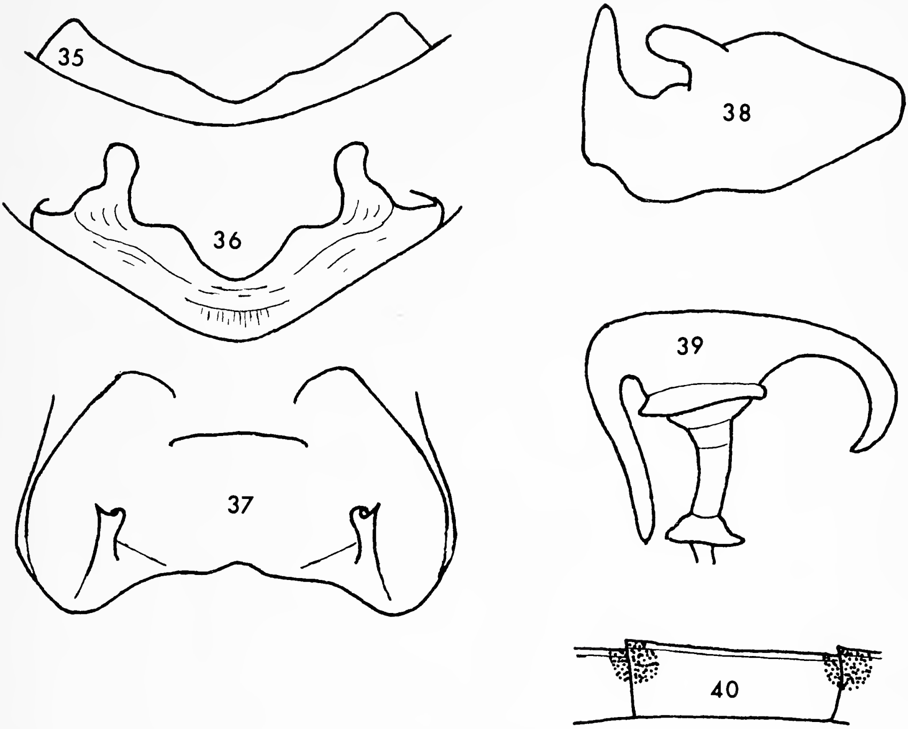
and sparse on abdominal venter; punctures concolorous with surrounding area.

Head 3.0–3.1 mm wide across eyes, 2.5–2.6 mm long. Lateral margin of juga scarcely concave before eyes, tapering to rather broadly rounded apex of head (Fig. 42). Length of antennal segments 0.5–0.6, 1.0–1.1, 1.3–1.4, 1.4, 1.4 mm; last 3 segments subequal in length. Rostral segments 2 through 4 about 1.5, 1.1–1.2, 0.9–1.0 mm long; rostrum reaching anterior limit of metacoxae.

Pronotum 8.2–8.8 mm wide at humeri, 3.1–3.5 mm long at meson. Humeri broadly rounded, slightly produced laterad. Cicatrices immaculate.

Scutellum 5.1–5.5 mm wide at base, 5.9–6.5 mm long, without markings. Posterolateral angles of connexival segments bearing small black mark.

Abdominal spine conical, projecting beneath mesocoxae and there terminating. Spiracles not accompanied by callus; peritremes nearly concolorous with surrounding areas of venter. Posterolateral angles of sternites minutely marked with black. Ostiolar ruga on each side extending 0.7–0.8 distance from inner margin of ostiole to lateral margin of thorax.

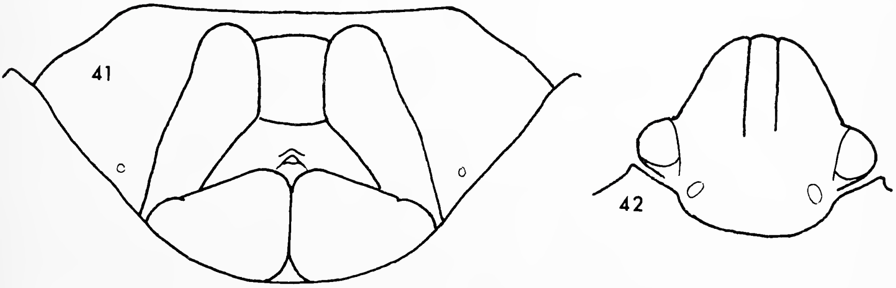


Figs. 35–40. *A. scutellatum.* 35. Pygophore, ventral view. 36. Pygophore, caudal view. 37. Genital cup. 38. Paramere. 39. Spermathecal bulb and pump. 40. Connexival markings.

Posterior edge of basal plates produced as small ridge at base of 9th paratergites (Fig. 41).

Male unknown.

Length about 14.4–15.4 mm.



Figs. 41, 42. *A. froeschneri.* 41. Genital plates, caudoventral view. 42. Head.

Distribution. Mexico (Sinaloa).

Holotype. ♀, labeled (a) "4 mi. N. San Blas, Sinaloa, Mexico. VIII-17-65. H. R. Burke & J. Meyer" (b) "taken at light". Deposited in U.S. National Museum, type no. 75559.

Paratype. ♀, labeled as holotype (TAMU).

Comment. This species is dedicated in gratitude to Dr. Richard C. Froeschner of the U.S. National Museum.

Among the species of *Acrosternum* in the Western Hemisphere whose abdominal spine projects beyond the metacoxae, only *A. scutellatum, A. istum* and this species are found in Middle America.

Acrosternum (Chinavia) esmeraldum, new species
(Figs. 43–48)

Description. Dark green dorsally, lighter below and blending irregularly to yellow mesially; lateral margins of head, pronotum, coria basally and abdomen very narrowly yellow; antennae and legs dark green, latter often discolored brown on inferior surface. Punctation on dorsum dense, fine, with many punctures on pronotum and scutellum forming irregular transverse lines; punctures dark green.

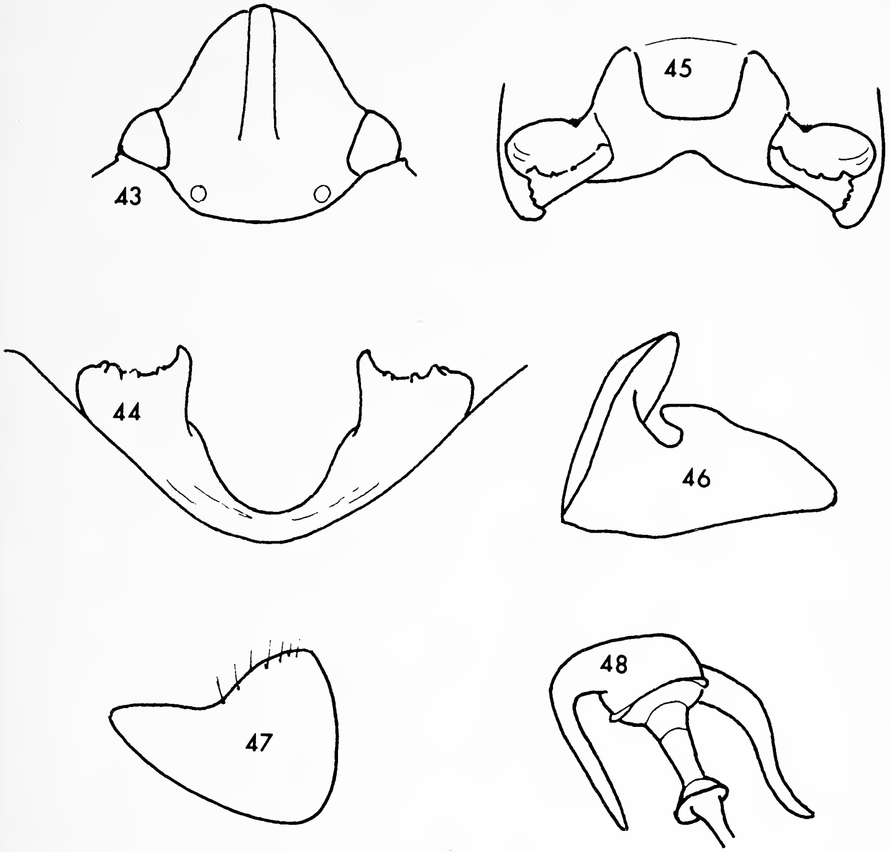
Head width across eyes 3.2–3.3 mm ♀♀, 2.9 mm ♂♂; length 2.4–2.5 mm ♀♀, 2.0–2.2 mm ♂♂. Antennal segments 0.6–0.7, 1.3, 1.5, 2.0, 2.1 mm long ♀♀, 0.6, 0.9–1.1, 1.3–1.6, 1.8, 2.0 mm long ♂♂. Length of rostral segments 2 through 4 about 1.9–2.0, 1.5, 1.1–1.2 ♀♀, 1.4–1.5, 1.2–1.3, 1.0 ♂♂; rostrum reaching metacoxae. Lateral margins of head rather strongly tapered toward apex (Fig. 43).

Pronotal width at humeri 7.7–7.9 mm ♀♀, 6.6–6.9 mm ♂♂; mesial length 3.2–3.3 mm ♀♀, 2.7–2.9 ♂♂. Humeri rounded, not produced laterad. Disk evenly convex transversely between anterolateral margins. Cicatrices without black markings.

Scutellar width at base 5.1 mm ♀♀, 4.3–4.6 mm ♂♂; length 5.9 mm ♀♀, 4.6–5.2 mm ♂♂. A small ivory callus present at each basal angle.

Abdominal spine compressed, reaching mesocoxae. Each spiracle in posterolateral margin of small ivory callus; peritremes black. Minute spine at posterolateral angles of connexival segments black, connexiva otherwise immaculate. Ostiolar ruga on each side reaching 0.6–0.8 distance from mesial margin of ostiole to lateral margin of thorax.

Pygophore deeply emarginate from caudal view (Fig. 44). On each side posterior wall of genital cup expanded mesodorsad; dorsal rim concave, denticulate, curved from dorsal view; dorsally serrated ridge projecting posteriorly from lateral limit of dorsal rim. Dorsal margin of genital cup bearing black denticle at angle formed by lateral and anterior concavities, this angle a little laterad of and cephalad from mesial limit of dorsal rim of posterior wall (Fig. 45). Ventral surface of pygophore narrowly sulcate submarginally.



Figs. 43–48. *A. esmeraldum.* 43. Head. 44. Pygophore, caudal view. 45. Genital cup. 46. Paramere. 47. Right basal plate. 48. Spermathecal bulb and pump.

Posterior surfaces densely setose. Parameres as in Figure 46. Basal plates and spermatheca as in Figures 47 and 48.

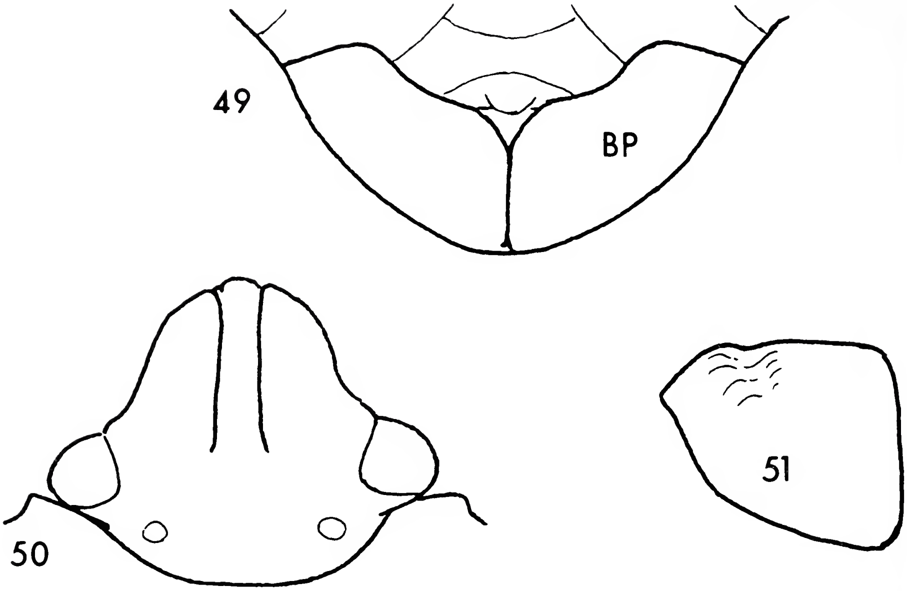
Distribution. Brazil (Minas Gerais).

Holotype. ♂, labeled (a) "Brazil. Minas Gerais: Santa Barbara, Sierra do Caraca" (b) "1450 m. Jan. 1970. F. M. Oliveira." Deposited in American Museum of Natural History.

Paratypes. 2♂♂, 2♀♀, labeled as holotype (♂ LHR; ♂, 2♀♀ AMNH).

Acrosternum (Chinavia) istum, new species
(Fig. 49)

Description. Light green above and below with yellowish orange border along outer margins. Black markings confined to posterolateral angles of sternites, connexival spots that include posterolateral angles of laterotergites,



Figs. 49–51. Fig. 49. *A. istum.* Basal plates, caudal view (BP). Figs. 50, 51. *A. napaeum.* 50. Head. 51. Right basal plate.

apex of rostrum, distal one-third of antennal segment 3 and distal one-fourth of segment 4. Dorsal punctation moderately dense, dark green.

Head 3.0 mm wide across eyes, 2.7 mm long; lateral jugal margins slightly concave. Antennal segments 0.5, 1.4, 1.5, 2.0, 2.0 mm long. Rostral segments 2–4 about 1.8, 1.4, 1.1 mm long; rostrum reaching posterior limit of metacoxae.

Pronotum 7.8 mm wide at humeri, 3.2 mm long at meson. Humeri narrowly rounded, little produced laterad; anterior pronotal margin straight.

Scutellum 5.0 mm wide at base, 5.9 mm long. Costal angle of coria rounded, reaching posterior half of penultimate connexival segment.

Abdominal tubercle compressed, attaining posterior limit of mesocoxae. Spiracles brown, each in posterolateral margin of bright green subcalloused spot. Ostiolar ruga on each side extending about three-fourths distance of mesial margin of ostiole to lateral thoracic margin.

Posterior margin of basal plates protruding beneath 9th paratergite; dorsal edge of combined plates mesially emarginate from caudal view (Fig. 49).

Male unknown.

Length about 13.7 mm.

Distribution. Panama.

Holotype. ♀, labeled "Panama. Pan. Prov. Altos de Maje, Chepo. 14–15

May 1976, at lights. Col: D. Engleman." Deposited in U.S. National Museum, type no. 75565. No paratypes.

Comments. This species is similar in appearance to *A. marginatum,* which also occurs in Panama, but differs especially in the longer abdominal spine and less dense dorsal punctation.

Acrosternum (*Chinavia*) *napaeum* (Stål, 1872)
(Figs. 50, 51)

Nezara (*Acrosternum*) *napaea* Stål, 1872, p. 42.

Diagnosis. Pronotum broadly depressed submarginally along cephalic half of anterolateral margins. Abdominal spine compressed, terminating between mesocoxae. Humeral angles rounded, not produced laterad. Connexiva immaculate excepting black spine at posterolateral angles of each segment. Spiracles unattended by callus; peritremes brown. Ostiolar ruga on each side extending about 0.8 distance from inner margin of ostiole to lateral margin of thorax. Rostrum reaching metacoxae. Dorsum light green, femora concolorous, cicatrices and scutellum immaculate; antennae black excepting green first segment. Lateral margins of head sigmoid (Fig. 50). Punctation on dorsum moderate in density and strength, less dense and weaker on scutellum. Basal plates longitudinally sulcate below 9th paratergite (Fig. 51).

Length about 13.5 mm.

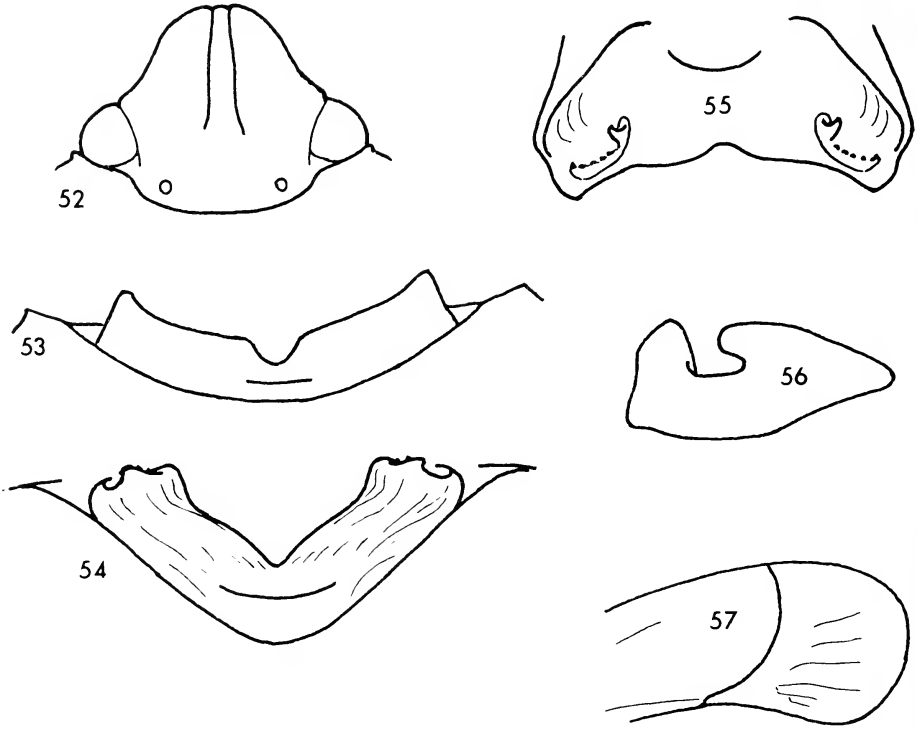
Distribution. Brazil.

Comment. Of this species I have seen only the holotype.

Acrosternum (*Chinavia*) *difficile* (Stål, 1860)
(Figs. 52–57)

Rhaphigaster difficilis Stål, 1860, p. 23.
Nezara (*Acrosternum*) *difficilis:* Stål, 1872, p. 42 (keyed, descriptive note).

Diagnosis. Humeri broadly rounded, not produced laterad. Abdominal spine compressed, terminating between mesocoxae. Posterolateral connexival angles minutely marked with black. Lateral jugal margins sigmoid (Fig. 52). Weak callus bearing spiracles not strongly differentiated by color; peritremes thinly black. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax. Anterior disk of pronotum weakly convex without submarginal depression along anterolateral margins. Dorsum dark green; neither cicatrices nor basal angles of scutellum with black spots; femora green. Punctation on dorsum moderately strong, dense; less dense and weaker on scutellum. Junction between corium and membrane rounded (Fig. 57). Rostrum reaching metacoxae. Pygophore from ventral view notched at bottom of broad shallow emargination of



Figs. 52–57. *A. difficile.* 52. Head. 53. Pygophore, ventral view. 54. Pygophore, caudal view. 55. Genital cup. 56. Paramere. 57. Hemelytron.

posterior margin (Fig. 53); deeply emarginate from caudal view (Fig. 54). Posterior walls on each side of genital cup curving anteromesad, with large anterior denticle curving anterolaterad and several small black denticles posteriorly on dorsal rim (Fig. 55). Paramere as in Figure 56.

Length about 11–15 mm.

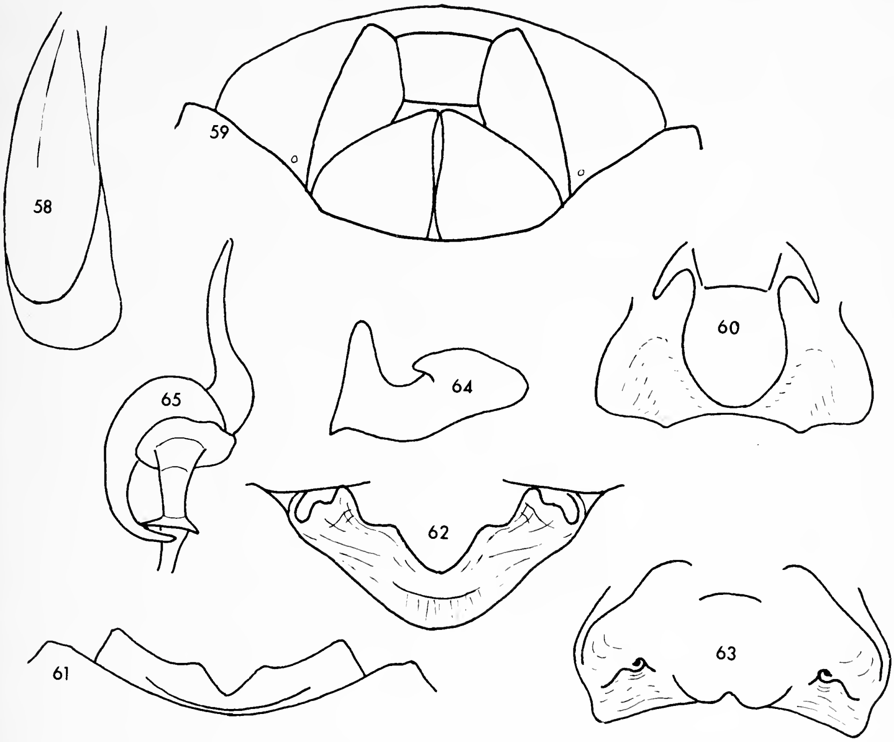
Distribution. Southern Brazil.

Comment. The female type was examined.

Acrosternum (*Chinavia*) *longicorialis* (Breddin, 1901), **New Combination**
(Figs. 58–60)

Nezara longicorialis Breddin, 1901, p. 123; Gaedike, 1971, p. 91 (lectotype designated).

Diagnosis. Posterior margin of corium parabolic, intruding into and reducing membrane of hemelytra (Fig. 58). Humeral angles rounded; anterolateral margin of pronotum slightly convex. Abdominal spine compressed,



Figs. 58–65. Figs. 58–60. *A. longicorialis.* 58. Hemelytron. 59. Genital plates, caudoventral view. 60. Genital cup. Figs. 61–65. *A. grave.* 61. Pygophore, ventral view. 62. Pygophore, caudal view. 63. Genital cup. 64. Paramere. 65. Spermathecal bulb and pump.

reaching anterior limit of mesocoxae. Connexiva immaculate. Spiracles reddish, each located laterally in edge of yellow oval spot. Ostiolar ruga on each side reaching about halfway from inner margin of ostiole to lateral margin of thorax. Rostrum reddish, terminating between metacoxae. Femora uniformly green. Cicatrices and basal angles of scutellum immaculate. Punctation of dorsum fine, dense. Narrow yellowish mesial stripe running length of pronotum and scutellum. Apex of scutellum subacute. Posterior walls of genital cup strongly reflexed with low elevation along posterior half of mesial margin, terminating in projection directed anteromesad which reaches superior ridge of genital cup; only proctiger visible in genital cup, remainder covered by posterior walls (Fig. 60). Basal plates subtriangular (Fig. 59). Length about 12 mm.

Distribution. Uruguay (Montevideo) and Argentina (Buenos Aires).

Comment. The lectotype, designated by Gaedike (1971), was examined.

The male genitalia of this species are distinctive in that the entire genital cup excepting the proctiger is entirely closed. The shape of the corium, intruding far into and reducing the membraneous area of the hemelytra, is also diagnostic.

Acrosternum (*Chinavia*) *panamensis* (Distant), **New Combination**

Nezara panamensis Distant, 1890, p. 339, pl. 32 fig. 1.
Nezara (*Pellaea*) *panamensis:* Kirkaldy, 1909, p. 121 (listed).
Pellaea panamensis: Rolston, 1976, p. 7 (systematic position queried).

Description. Large black macule on dorsum comprised of distal part of each corium and tergites beneath hemelytral membranes; also black: antennae, rostrum excepting parts of first and base of second segments, tarsi, tibiae, femora distally and on front legs femora proximally and trochanters. Remainder of insect excepting eyes and ocelli brownish yellow, perhaps green in life. Dorsal punctation fine, rather dense.

Head 2.9 mm across eyes, 2.4 mm long. Antennae 0.5, 1.0, 1.8, —, —, mm long. Rostral segments 2–4 about 1.8, 1.5, 1.2 mm long; apex of rostrum lying between metacoxae. Juga not convergent apically.

Pronotum 7.8 mm wide at humeri, 3.1 mm long mesially. Humeri broadly rounded, not produced laterad. Anterolateral margins slightly convex, without submarginal depression.

Scutellum 5.0 mm wide at base, 5.4 mm long. Coria ending distally near middle of penultimate connexival segment; boundary between each corium and membrane slightly convex; membranes heavily fumose excepting narrow hyaline border.

Abdominal tubercle reaching a little beyond posterior limits of metacoxae, compressed apically. Ostiolar ruga on each side reaching about 0.75 distance from inner margin of ostiole to lateral margin of thorax.

Posterior margins of basal plates forming nearly transverse line between lateral angles.

Length about 13 mm.

Distribution. Panama. Known only from the female holotype collected at Bugaba.

Comment. This species meets all of the morphological criteria for the genus *Acrosternum* subgenus *Chinavia* insofar as can be determined from the single known specimen. Only its coloration seems especially remarkable.

Acrosternum (*Chinavia*) *grave* (Walker, 1867)
(Figs. 61–65)

Strachia gravis Walker, 1867, p. 322.
Nezara nigritarsis Stål, 1872, p. 40. **New Synonymy.**

Nezara gravis: Distant, 1900, p. 393.
Nezara gentilis Breddin, 1903, p. 368; Gaedike, 1971, p. 86 (lectotype designated). **New Synonymy.**
Acrosternum grave: Rolston, 1976, p. 4 (generic placement).

Diagnosis. Anterolateral margins of pronotum and coria basally bordered broadly in yellow; often all or margins of head, median stripe on pronotum and/or scutellum also yellow. Antennae, most of rostrum and at least apex of femora black. Humeri rounded, not produced. Abdominal spine just reaching between metacoxae, sometimes reduced to obtuse tubercle. Connexiva immaculate excepting tiny spine at posterolateral angles of segments darkened. Membrane of hemelytra dark. Spiracles not accompanied by callus; peritremes pale. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum terminating between metacoxae. Cicatrices immaculate. Basal angles of scutellum usually immaculate, rarely with small dark dot. Dorsal punctation moderately dense, dark. Posterior wall on each side of genital cup dorsally diagonal, with short obtuse projection anteriorly (Figs. 62, 63). Parameres as in Figure 64. Spermatheca as in Figure 65.

Length about 12.5–13.5 mm.

Distribution. Amazon region.

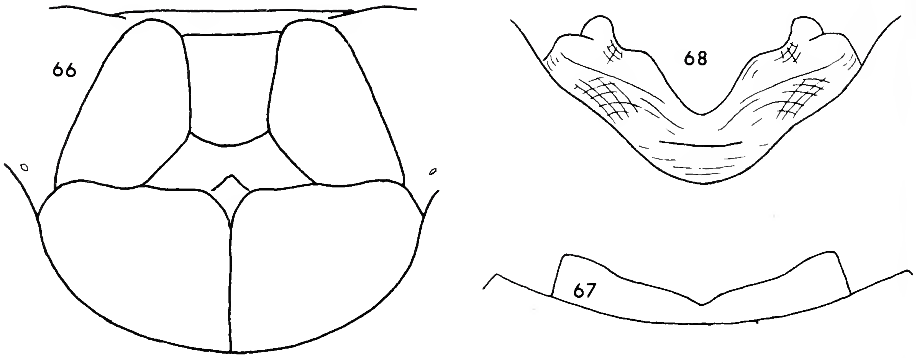
Types. Lectotype of *Nezara nigritarsis* Stål, here designated, ♂ with wings spread, labeled (a) "Amazon" (b) "Stevens" (c) "Type" (d) "Paratype" (e) "120/79" (f) "Riksmuseum Stockholm". Paralectotypes, ♂, labeled as lectotype except (d) "Type" (e) "119/79"; ♂, labeled as lectotype except (e) "121/79".

Comment. The holotype of *Strachia gravis* and of *Nezara gentilis,* both females, as well as the syntypes of *Nezara nigritarsis,* were examined.

Acrosternum (*Chinavia*) *geniculatum* (Dallas, 1851)
(Figs. 66–68)

Rhaphigaster geniculatus Dallas, 1851, p. 279.
Rhaphigaster obscuricornis Stål, 1860, p. 22 (synonymized by Stål, 1872).
Nezara geniculata: Stål, 1872, p. 40 (keyed, synonymy).
Acrosternum geniculatum: Rolston, 1976, p. 3 (generic placement).

Diagnosis. Distal end of femora narrowly banded in black excepting inferior surface. Cicatrices and scutellum unicolorous, green. Humeri rounded, not produced. Abdominal tubercle compressed, terminating between metacoxae. Connexiva immaculate excepting spine on posterolateral angles of segments dark. Spiracles unaccompanied by conspicuous yellow callus; peritremes brown to green. Ostiolar ruga on each side extending about 0.8 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum



Figs. 66–68. *A. geniculatum*. 66. Genital plates, caudoventral view. 67. Pygophore, ventral view. 68. Pygophore, caudal view.

terminating between or slightly caudad of metacoxae. Basal angles of scutellum immaculate. Posterior margin of basal plates nearly transverse except at convex angles (Fig. 66). Pygophore as in Figures 67 and 68. Length about 14.5–17 mm.

Distribution. Southern Brazil, Bolivia.

Type. Described from one ♂ and one ♀, the latter mislabeled with France as locality. This specimen was not located. Lectotype, here designated, ♂ bearing labels (a) "Type" (b) "720a" (c) "a" (d) "*Rhaphigaster geniculatus*".

Acrosternum (*Chinavia*) *nigropictum* (Breddin, 1906), **New Combination**

Nezara nigropicta Breddin, 1906, pp. 193–194; Gaedike, 1971, p. 93 (lectotype designated).

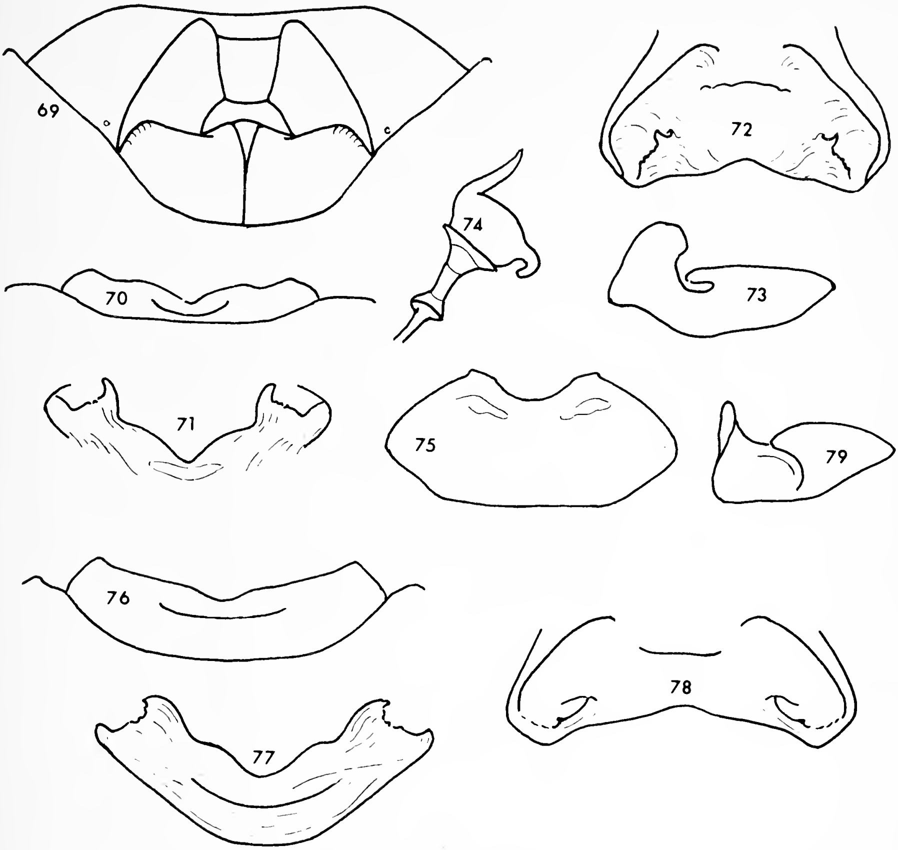
Diagnosis. Apparently differing from *A. geniculatum* only in color. Tylus excepting narrow mesial wedge at base, cicatrices, large subquadrate patch on each side of scutellum at base (confluent basally), sutures of abdominal venter except mesially and at lateral ends, all black. Length about 19 mm.

Distribution. Brazil (Manaus). Known only from lectotype.

Comment. This form may be a color variation of *A. geniculatum* Dallas. The lectotype, a ♀ designated by Gaedike (1971), was examined.

Acrosternum (*Chinavia*) *viridans* (Stål, 1859)
(Figs. 69–74)

Rhaphigaster viridans Stål, 1859, p. 228.
Nezara (*Acrosternum*) *viridans:* Stål, 1872, p. 41 (keyed).
Nezara viridans: Distant, 1880, p. 79 (synonymy).
Acrosternum viridans: Froeschner, 1981, p. 68 (catalog).



Figs. 69–79. Figs. 69–74. *A. viridans.* 69. Genital plates, caudoventral view. 70. Pygophore, ventral view. 71. Pygophore, caudal view. 72. Genital cup. 73. Paramere. 74. Spermathecal bulb and pump. Figs. 75–79. *A pennsylvanicum.* 75. Pronotum. 76. Pygophore, ventral view. 77. Pygophore, caudal view. 78. Genital cup. 79. Paramere.

Diagnosis. Dorsum sparsely punctate, most punctures separated from nearest puncture by distance equal to or greater than diameter of second antennal segment. Humeri rounded, slightly produced laterad. Abdominal tubercle reaching posterior limit of metacoxae. Connexiva and sternites with small black spot at posterolateral angles of each segment, connexival spot extending onto laterotergite. Spiracles pale, unaccompanied by callus. Ostiolar ruga on each side reaching about halfway from mesial margin of ostiole to lateral margin of thorax. Rostrum extending past metacoxae onto sternite bearing tubercle. Legs green. Pronotum and scutellum without black markings. Posterior margin of basal plates at lateral angles bent up against 9th paratergite (Fig. 69). Posterior wall on each side of genital cup dorsally diagonal; dorsal rim straight, denticulate, with large denticle anteriorly (Figs. 71, 72). Spermatheca as in Figure 74. Parameres as in Figure 73. Length about 10–12.5 mm.

Distribution. Panama, Peru, Galapagos Islands.

Types. Lectotype, here designated, ♂, labeled (a) "Callao" (b) "Kinb" (c) "Typus" (d) "124/79" (e) "Riksmuseum Stockholm". Paralectotypes: ♂, labeled (a) "Panama" (b) "Kinb" (c) "Paratypus" (d) "125/79" (e) "Riksmuseum Stockholm"; ♀, labeled (a) "Panama" (b) "Paratypus" (c) "127/79" (d) "Riksmuseum Stockholm"; ♀, labeled (a) "Ins. Gallop" (b) "Allotypus" (c) "126/79" (d) "Riksmuseum Stockholm".

Comments. No other species of the genus is so sparsely punctate dorsally.

Acrosternum (*Chinavia*) *pennsylvanicum* (Palisot de Beauvois, 1805)
(Figs. 75–79)

Cimex viridis pennsylvanica DeGeer, 1773, p. 330, pl. 34, fig. 5; Gmelin in Linnaeus, 1788, p. 2148 (unavailable trinomen).

Pentatoma pennsylvanica Palisot de Beauvois, 1805, p. 186, Hem. pl. 11, fig. 5.

Pentatoma abrupta Say, 1831, p. 6; Say, 1859, p. 317 (synonymized by Uhler, 1871).

Rhaphigaster parnisus Dallas, 1851, p. 279 (synonymized by Uhler, 1886).

Rhaphigaster pennsylvanicus: Uhler, 1871, p. 98 (synonymy, records excluding Panama); Uhler, 1878, p. 380 (identity verified).

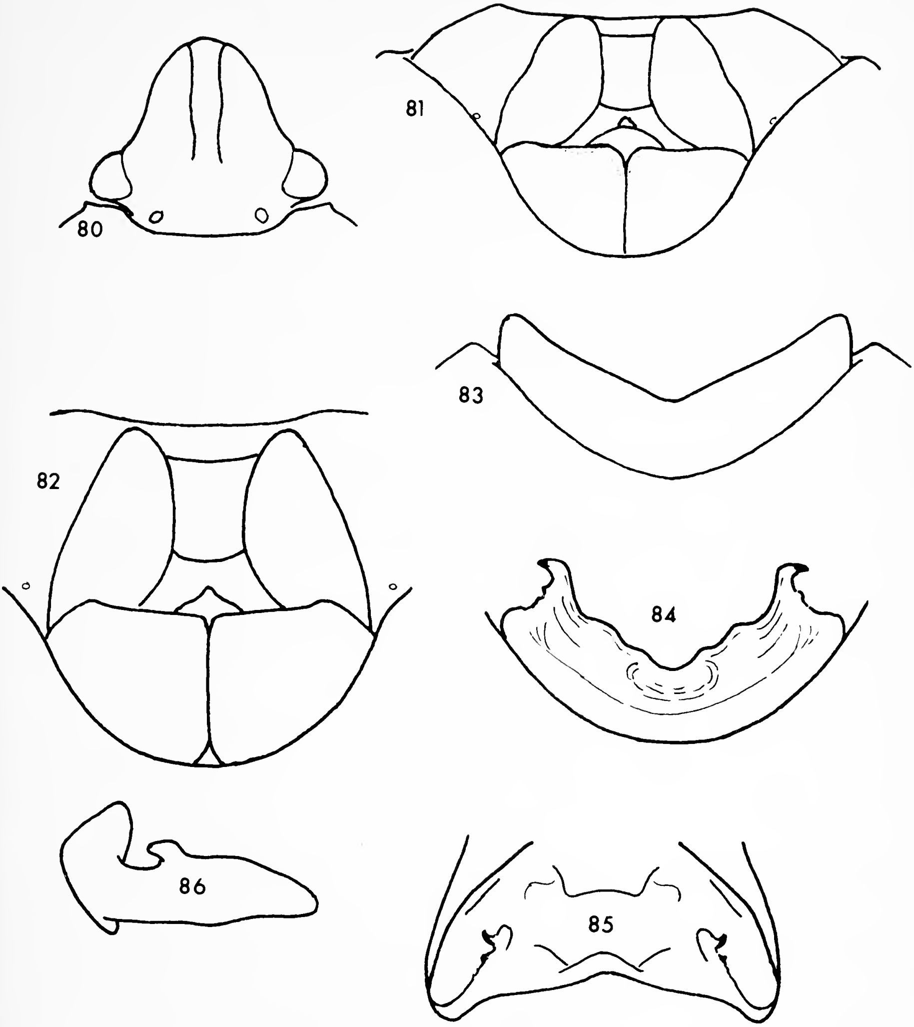
Nezara (*Acrosternum*) *pennsylvanica:* Stål, 1872, p. 42 (keyed).

Nezara pennsylvanica: Uhler, 1886, p. 8 (synonymy); Osborn, 1892, p. 122 (records); Van Duzee, 1904, pp. 57, 58 (keyed, records); Van Duzee, 1909, p. 157 (records); Olsen, 1912, p. 55 (records, host); Barber, 1914, p. 523 (records).

Nezara parnisus: Distant, 1900, p. 392 (listed).

Acrosternum pennsylvanicum: Parshley, 1915, p. 175 (keyed); Van Duzee, 1916, p. 7 (listed); Van Duzee, 1917, pp. 59–60 (cataloged); Parshley, 1917, p. 24 (records); Hart, 1919, p. 181 (record); Stoner, 1920, pp. 107–108, pl. 7, fig. 1 (keyed, description); Hussey, 1922, p. 15 (record); Parshley, 1923, p. 767 (record); Blatchley, 1926, pp. 160–161 (keyed, description); Brimley, 1938, p. 63 (record); Torre Bueno, 1939, p. 236 (keyed); Froeschner, 1941, p. 130 (keyed); McPherson, 1970, pp. 54–55, fig. 52 (records); Hoffman, 1971, p. 48 (records); Furth, 1974, p. 40, pl. 2, fig. 22, pl. 3, fig. 37 (records).

Diagnosis. Rostrum reaching only to mesocoxae. Anterolateral margins of pronotum usually strongly convex. Humeri rounded, not produced. Abdominal tubercle compressed, reaching posterior limits of metacoxae. Con-



Figs. 80–86. Figs. 80, 81. *A. pecosum.* 80. Head. 81. Genital plates, caudoventral view. Figs. 82–86. *A. aseadum.* 82. Genital plates, caudoventral view. 83. Pygophore, ventral view. 84. Pygophore, caudal view. 85. Genital cup. 86. Paramere.

nexiva and sternites with small black spot at posterolateral angles, spot not extending onto laterotergite. Spiracles usually black, each on yellow callus. Ostiolar ruga on each side extending about 0.6 distance from mesial margin of ostiole to lateral margin of thorax. Femora green. Pronotum and scutellum without black markings. Genitalia as in Figures 76 and 77. Length about 10.5–14.5 mm.

Distribution. Eastern United States and southeastern Canada.

Acrosternum (Chinavia) pecosum, new species
(Figs. 80, 81)

Description. Emerald green above, paler green below blended with yellow mesially; lateral margins of head, pronotum and basal part of coria narrowly bordered in yellow. Connexiva and lateral margins of abdominal venter yellow excepting spine at posterolateral angles of segments dark. Spiracles black, surrounding area weakly calloused and not differentially colored. Antennae green with apex of segment 2, distal half of segments 3 and 5, distal three-fourths of segment 4 black; spot on superior surface of antennifers black. Dorsal punctation on head green, elsewhere distinctly black, moderately dense.

Head 2.7 mm wide across eyes, 2.2 mm long, narrowly parabolic apically (Fig. 80). Antennal segments 0.5, 1.0, 1.4, 1.8, 1.9 mm long. Rostral segments 2–4 about 1.6, 1.0, 1.0 mm long; rostrum terminating between metacoxae.

Pronotum 6.4 mm wide at humeri, 2.4 mm long at meson. Humeri rounded, not produced. Anterolateral margins slightly convex. Cicatrices without black marking.

Scutellum 4.1 mm wide at base, 4.2 mm long; basal angles immaculate; very apex yellowish.

Abdominal tubercle compressed, barely attaining metacoxae. Ostiolar ruga on each side extending 0.6–0.7 distance from mesial margin of ostiole to lateral margin of thorax.

Posterior margin of basal plates nearly transverse, thin and hyaline around mesial angle (Fig. 81).

Male unknown.

Length about 10.9 mm.

Distribution. Peru.

Holotype. ♀, labeled "Manu, Peru. X-21-63. Pena, Coll." Deposited in the American Museum of Natural History. No paratypes.

Comment. The black dorsal punctation together with the immaculate connexiva distinguish this species.

Acrosternum (Chinavia) aseadum, new species
(Figs. 82–86)

Description. Light green above and below, becoming yellow mesially on venter; margins of head, pronotum, coria basally and connexiva usually bordered thinly in yellow or orange; lateral margins of venter with somewhat wider border, without black markings on lateral margins of abdomen. Spiracles black, each located on ivory callus. Antennae green with last 2 segments sometimes mostly ferrugineous to fuscous; spot on superior surface of antennifers black. Dorsal punctation dense; punctures concolorous with surrounding surface.

Head 2.5–2.9 mm wide across eyes, 2.1–2.3 mm long; jugal margins sinuous. Antennal segments 0.5–0.6, 1.1–1.4, 1.2–1.5, 1.6–1.8, 1.6–1.7 mm long. Rostral segments 2–4 about 1.6–1.9, 1.0–1.2, 0.9–1.1 mm long; rostrum terminating between metacoxae.

Pronotum 6.8–8.1 mm wide across humeri, 2.5–3.1 mm long at meson. Humeri not or little produced laterad, rounded. Cicatrices immaculate.

Scutellum 4.3–5.1 mm wide at base, 4.7–5.8 mm long, without markings.

Abdominal tubercle rudimentary, not projecting past anterior margin of second visible sternite. Ostiolar ruga on each side extending about 0.8 distance from mesial margin of ostiole to lateral margin of thorax.

Posterior margin of basal plates sigmoid from caudoventral view, slightly concave between 9th paratergite and mesial angle, convex laterally (Fig. 82).

Posterior wall on each side of genital cup dorsally diagonal with anterior projection ending in laterally curved black tooth; basad of this tooth a small denticle present on dorsal rim of posterior wall (Figs. 84, 85). Parameres as in Figure 86.

Length about 11.5–14.3 mm.

Distribution. Southern Brazil and northern Argentina.

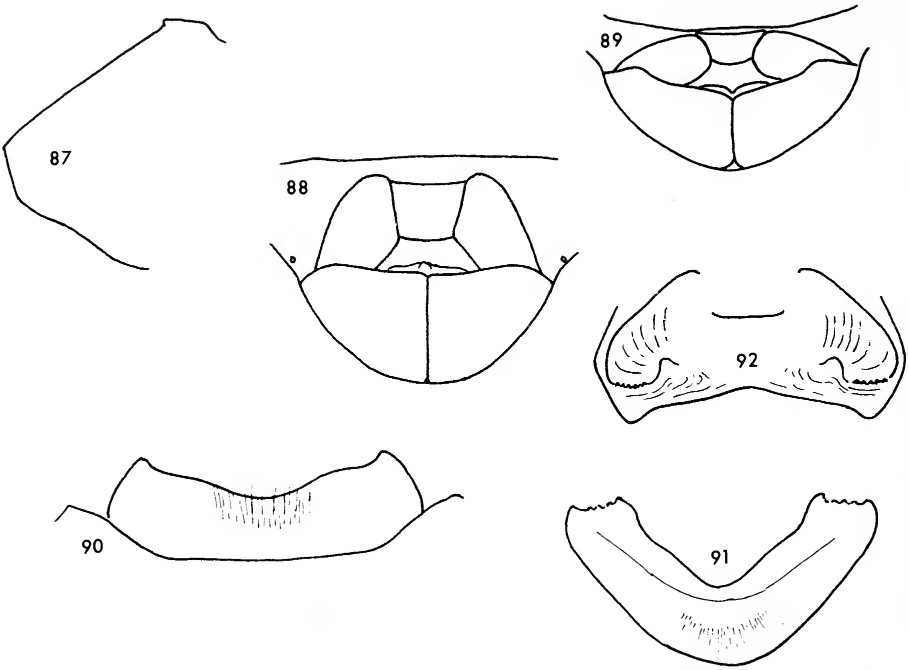
Holotype. ♂, labeled (a) "Passo Fundo, I-14-74, RS, E. Heinrichs" (b) "224". Deposited in U.S. National Museum, type no. 75562.

Paratypes. 3♀♀, 2♂♂, "Museum Leiden, Argentina, Cordoba, Almafuerte, Calamucrita La Cascada, I. 1965, F. H. Walz" (♀ RNH); "Museum Leiden, Argentina, Cordoba, El Quebracho, Calamucrita, I. 1965. F. H. Walz" (♀ RNH); (a) as holotype except date "I-15-74" (b) "218" (♀ INHS); (a) "E. E. Gualba, I-10-74 RS, E. Heinrichs" (b) "223" (♂ LHR); (a) "Carazinho, I-1-74, E. Heinrichs" (b) "220" (♂ INHS).

Acrosternum (*Chinavia*) *nigridorsatum* (Breddin, 1901), **New Combination**
(Figs. 87–89)

Nezara nigridorsata Breddin, 1901, p. 123; Gaedike, 1971, p. 93 (lectotype designated).

Diagnosis. Humeral angles obtusely angulate (Fig. 87). Abdominal tubercle compressed, anterior and ventral margins forming slightly acute angle, reaching posterior limit of metacoxae. Black mark at posterolateral angles of connexival segments confined to edge of sternite, continuing as black spot in posterolateral angles of sternites; connexiva narrowly red margined. Spiracles black, each located on ivory callus. Ostiolar ruga on each side extending about 0.8 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum terminating between metacoxae. Femora light green. Cicatrices and basal angles of scutellum immaculate. Punctation of dorsum dense, green. Posterior margin of basal plates projecting into concavity of 9th paratergite (Figs. 88, 89). Length about 12.5 mm.



Figs. 87–92. Figs. 87–89. *A. nigridorsatum.* 87. Humerus. 88. Genital plates, caudoventral view. 89. Genital plates, caudal view. Figs. 90–92. *A. ecuadorensis.* 90. Pygophore, ventral view. 91. Pygophore, caudal view. 92. Genital cup.

Distribution. Southern Brazil (Curitiba). Known only from lectotype.

Comment. Similar to *A. aseadum* but differing in having angulate humeri, a black spot in posterolateral angles of the sternites and connexival segments, shape of the abdominal tubercle and in the form of the basal plates. The lectotype, a ♀ designated by Gaedike (1971), was examined.

Acrosternum (Chinavia) ecuadorensis, new species
(Figs. 90–92)

Description. Light green above and below with narrow yellowish orange outer margins. Cicatrices and scutellum immaculate. All antennal segments banded distally with black or fuscous; these bands broadest on last 3 segments, covering about three-, five-, and five-tenths of last 3 segments, respectively. Black spot present on superior surface of antennifers. Spine at posterolateral angles of abdominal segments black. Spiracles black, unattended by callus. Legs green. Dorsal punctation moderately dense, fine, green.

Head 2.8 mm wide across eyes, 2.1 mm long. Outer jugal margins sigmoid, moderately concave before eyes. Antennal segments 0.5, 1.1, 1.3, 1.9, 1.9

mm long. Rostral segments 2–4 about 1.7, 1.0, 0.9 mm long; apex lying between metacoxae.

Pronotum 6.7 mm wide at humeri, 2.8 mm long at meson. Humeri scarcely produced laterad, rounded; anterolateral pronotal margins nearly straight.

Scutellum 4.3 mm wide at base, 4.8 mm long. Coria ending near posterior margin of penultimate connexival segment, costal angle rounded.

Abdominal spine compressed, reaching posterior limit of metacoxae. Ostiolar ruga on each side extending about three-fourths distance from mesial margin of ostiole to lateral thoracic margin.

Pygophore with somewhat sinuous V-shaped emargination from both ventral and caudal views (Figs. 90, 91). Semicircular mesial projection on ventral surface of pygophore densely setose. Dorsal rim of posterior wall of genital cup curved on each side from dorsal view, with several black denticles of which largest located at mesial corner of rim (Fig. 92).

Female unknown.

Length about 9.5 mm.

Distribution. Ecuador.

Holotype. ♂, labeled "Ecuador, 25 km. W. Puyo. April 27, 1978. CW & LB O'Brien & Marshall". Deposited in U.S. National Museum, type no. 72131. No paratypes.

Acrosternum (Chinavia) ubicum, new species
(Figs. 93–99)

Description. Light green, below often blending to yellow mesially, with narrow dorsal border of red to yellow along lateral margins of head, pronotum, coria basally and abdomen. Connexiva usually with small black spot at posterolateral angles of segments, this spot sometimes reduced and confined to protruding angle. Antennae green, usually with apex of segment 3 and distal half of segments 4 and 5 dark. Legs green. Spiracles usually black, each located on conspicuous yellow callus. Dorsal punctation fine, dense, green.

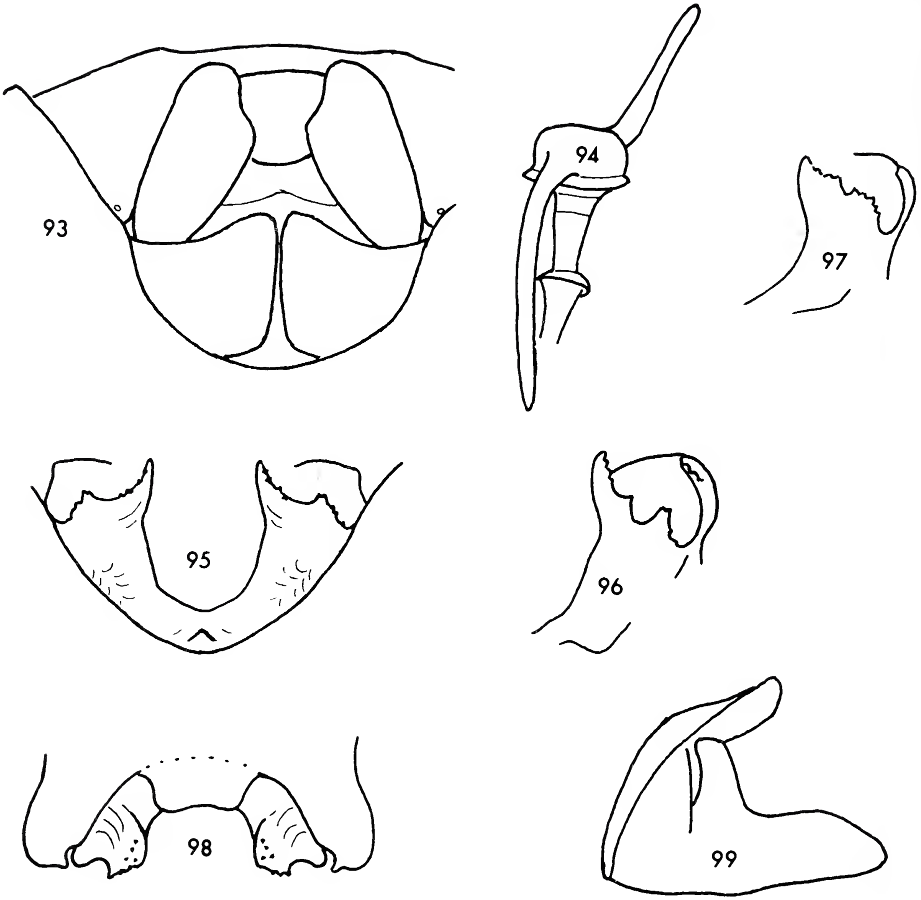
Head 2.5–3.0 mm wide across eyes, 2.0–3.5 mm long. Antennal segments 0.5, 1.1–1.4, 1.2–1.6, 1.5–1.7, 1.5–1.7 mm long. Rostral segments 2–4 about 1.4–1.8, 1.0–1.2, 0.9–1.1 mm long; rostrum terminating between metacoxae.

Pronotum 6.5–8.2 mm wide at humeri, 2.4–3.3 mm long at meson. Humeri rounded, not produced. Cicatrices usually immaculate, rarely with small dark dot at mesial limits.

Scutellum 4.0–5.3 mm wide at base, 4.4–5.6 mm long, without markings.

Abdominal tubercle compressed, not or barely reaching metacoxae; anterior margin subvertical. Ostiolar ruga on each side extending about 0.7–0.8 distance from inner margin of ostiole to lateral margin of thorax.

Most posterior portion of basal plates at mesial angles (Fig. 93); posterior



Figs. 93–99. *A. ubicum.* 93. Genital plates, caudoventral view. 94. Spermathecal bulb and pump. 95. Pygophore, caudal view. 96. Posterior wall, right side, variation in dorsal rim. 97. Same, 98. Genital cup. 99. Paramere.

edge from caudal view flattened above 9th paratergite. Spermatheca as in Figure 94.

Posterior wall of genital cup approximately transverse, expanded dorsad, mesially curved cephalad on each side of deep mesial emargination (Fig. 95); posterior surface prominently armed with short curved carina on each side; posteroventral surface with stout median tooth. Dorsal rim of posterior wall bearing several black denticles; cephalic surface on this wall with several smaller denticles (Fig. 98); usually one large tooth present on dorsal rim (Fig. 95), sometimes 2 large teeth separated by notch (Fig. 96), or notch without adjacent large tooth or teeth (Fig. 97). Parameres as in Figure 99.

Length about 10.6–13.7 mm.

Distribution. Hispaniola, Colombia, Guyana, Surinam, Ecuador, Bolivia, Brazil, Galapagos Islands. Presumably present in other West Indian islands besides Hispaniola.

Holotype. ♂, labeled (a) "Bolivia: Dept. Beni, Rio Itez, Pampa de Meio. IX-11–13-1964" (b) "J. K. Bouseman, J. Lussenhop, Collectors". Deposited in American Museum of Natural History.

Paratypes. 6♀♀, 10♂♂, (a) "Colombia, Buenaventura XI-6-1950" (b) "Michelbacher and Ross" (♀, ♂ LHR); "Brazil: Ceara State, Barbalha. V-1969. M. Alvarenga" (2♀♀, 2♂♂ AMNH); (a) "British Guiana" (b) "Babcock Coll'n" (♀ RNH); "Suriname, Paramaribo, 16–18 VII-75. Coll: D. Engleman" (♀ HDE); "Brazil: Est. Rio Muriqui Mangaratiba. July, 1969. M. Alvarenga" (♀ LHR); (a) "27-III-1925" (b) "Galapagos" (c) "Gift of New York Zoo. Soc. Dept. Tropical Research, William Beebe, Dir." (2♂♂ AMNH), "Guaruja Is. Sao Paulo, Brazil IV-17-1966" (b) "Collr. C. A. Triplehorn" (♂ OSU); "Ecuador, Guayas, Boliche. Oct. 13, 1976 M. E. Irwin, soybean breeding line trial seed maturation. 1298" (♂ INHS); "Mallares. 23·3·66. J. Alva N." (b) "Meunprg. No. 1160-68" (♂ JG); (a) "La Vega Prov., Rep. Dominicana, 11-X-1967" (b) "L. H. Rolston, Collector" (2♂♂ LHR).

Acrosternum (*Chinavia*) *laetum* (Stål, 1859)

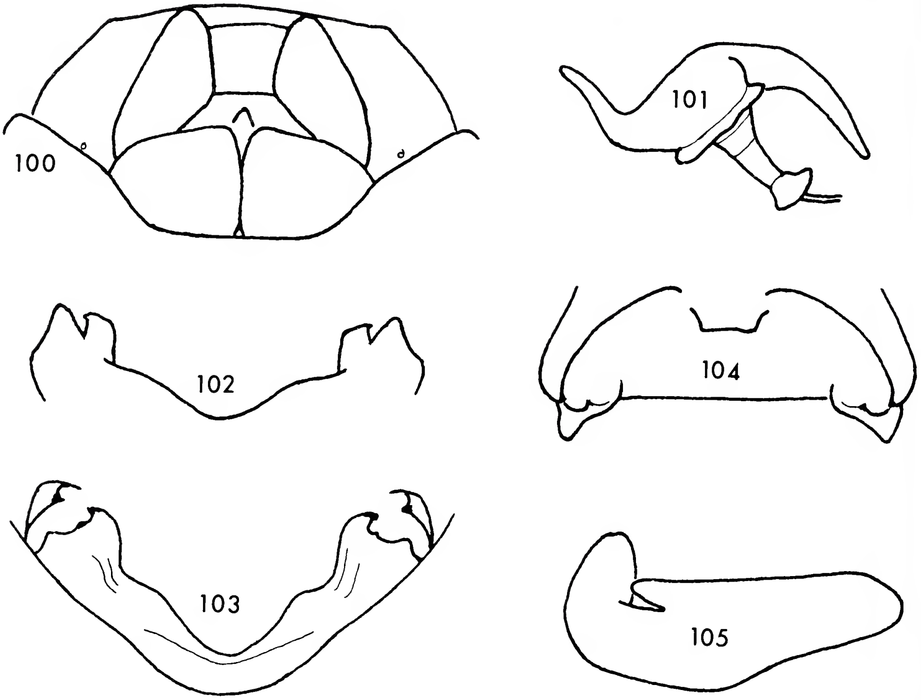
(Figs. 100–105)

Rhaphigaster laetus Stål, 1859, pp. 228–229.
Nezara (*Acrosternum*) *laeta:* Stål, 1872, p. 42 (keyed, descriptive note).
Acrosternum laetum: Froeschner, 1981, p. 67.

Diagnosis. Humeri rounded, not produced. Abdominal tubercle compressed, reaching posterior margin of metacoxae. Connexiva immaculate or variously marked with black: minute dot at posterolateral angles of segments, or narrow border along posterior margin of segments, or macule lying across transverse sutures. Each spiracle located in posterolateral edge of small yellow callus; peritremes red to yellow. Ostiolar ruga on each side extending 0.6–0.8 distance from mesial margin of ostiole to lateral margin of thorax. Rostrum ending between or slightly caudad of metacoxae. Femora green. Small black dot present at mesial limit of cicatrices, another usually present at lateral limit. Posterior margin of basal plates slanting, most posterior part at mesial angle (Fig. 100). Spermatheca as in Figure 101. Male genitalia as in Figures 102–105. Posterior wall on each side of genital cup dorsally diagonal; large denticle on dorsal rim apposed by acute dorsolateral angle of pygophore; posterolateral wall of pygophore deeply emarginated (Fig. 103).

Distribution. Northern Chile, Peru, Ecuador.

Types. Lectotype, here designated ♂ labeled (a) "Puna" (b) "Kinb" (c)



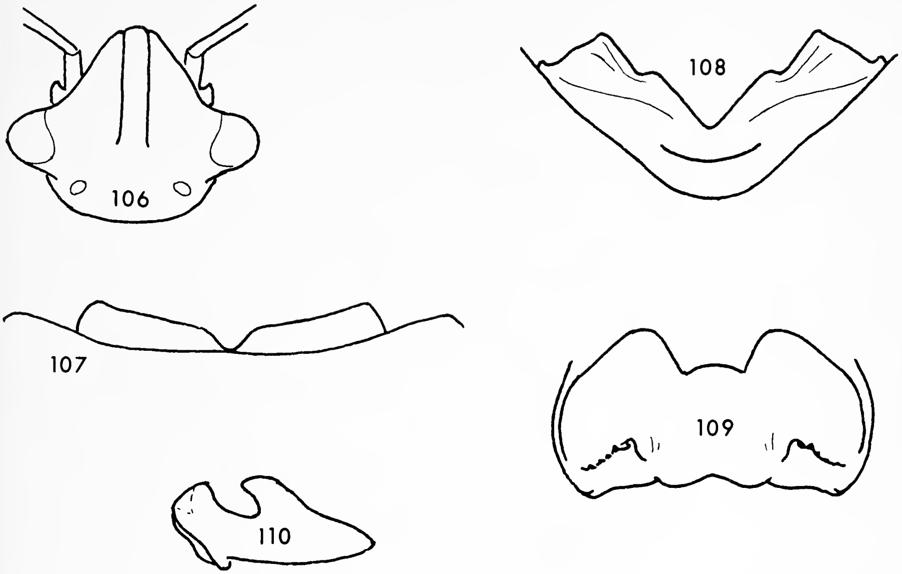
Figs. 100–105. *A. laetum.* 100. Genital plates, caudoventral view. 101. Spermathecal bulb and pump. 102. Posterior margin of exserted pygophore, ventral view. 103. Pygophore, caudal view. 104. Genital cup. 105. Paramere.

"Type" (d) "Typus" (e) "305/73" (f) "Riksmuseum Stockholm". Paralectotype, ♀ labeled as lectotype except (d) "Allotypus" and (e) "304/73".

Comment. The degree of variability of connexival markings in this species seems unique within the genus in the hemisphere.

Acrosternum (Chinavia) simplicis, new species
(Figs. 106–110)

Description. Green above with lateral margins of head, pronotum, coria basally and connexiva narrowly bordered in yellow or red, when red with very edges of body yellowish in lateral view. Scutellum with 4 small yellowish spots or transverse macules along base; apex usually bordered narrowly with yellow. Connexiva with small black mark on edge of sternites at posterolateral angles of each segment, this mark sometimes continuing vaguely onto first laterotergite. Venter paler green than dorsum, becoming yellowish mesially. Only peritreme of spiracles dark; each spiracle located in lateral edge of ivory callus. Black mark at posterolateral angles of sternites small. Femora



Figs. 106–110. *A. simplicis.* 106. Head. 107. Pygophore, ventral view. 108. Pygophore, caudal view. 109. Genital cup. 110. Paramere.

green. Small black line or macule on superior surface of antennifer. Antennae green, sometimes variously blended with fuscous on distal 2 segments. Dorsal punctation dense; punctures concolorous with surrounding area.

Apex of head narrowly rounded; lateral jugal margins weakly concave before eyes (Fig. 106). Width of head across eyes 2.6 mm, length 2.0–2.1 mm. Antennal segments 0.5, 1.0–1.1, 1.2, 1.5–1.6, 1.4–1.6 mm long. Rostral segments 2–4 about 1.4–1.6, 1.2–1.3, 0.9 mm long; rostrum terminating between metacoxae.

Pronotum 6.6–8.0 mm wide at humeri, 2.6–2.8 mm long at meson. Cicatrices immaculate. Humeri slightly produced laterad, rounded.

Scutellum 4.2–4.5 mm wide at base, 4.4–4.7 mm long. Basal angles immaculate.

Abdominal tubercle barely reaching posterior margin of metacoxae. Ostiolar ruga on each side reaching halfway from mesial margin of ostiole to lateral margin of thorax.

Female unknown.

Posterior wall of genital cup on each side of deep mesial emargination diagonal dorsally; weakly concave dorsal rim bearing several tiny black denticles (Figs. 108, 109). Parameres as in Figure 110.

Length about 10.0–11.3 mm.

Distribution. Paraguay.

Holotype. ♂, labeled "Museum Leiden, Dr. B. Podtiaguine, Assomption Omgev., Paraguay, 22 Feb.–25 Apr. 1936". Deposited in Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

Paratypes. 3♂♂, labeled as holotype with second label "Cat. No. 9" (♂ RNH); labeled as holotype (♂ RNH; ♂ LHR).

Acrosternum (Chinavia) euri, new species
(Figs. 111–119)

Description. Green above with a liberal amount of yellow on interstices between punctures except on head; lighter green below blending to yellow mesially at least on thorax. Lateral dorsal and ventral margins of head, pronotum, coria basally and connexiva crimson; protruding angles of abdominal segments black. Antennae green; black spot present at base of antennifers on superior surface. Very apex of femora, base or all of tibiae, tarsi, and often rostrum crimson or suffused with crimson. Spiracles narrowly ringed with black and suffusion of crimson or crimson alone. Neither cicatrices nor basal angles of scutellum marked with black. Dorsal punctation dark green, dense on pronotum and head, less so on scutellum and thorax.

Apex of head moderately rounded; lateral margins of juga weakly concave. Width of head across eyes 2.7–2.9 mm, length 2.2–2.3 mm. Antennal segments 0.5, 1.0–1.2, 1.2–1.4, 1.6–1.7, 1.5–1.6 mm long. Rostral segments 2–4 about 1.4–1.6, 1.2–1.3, 0.9–1.0 mm long; apex terminating between metacoxae.

Pronotum 6.6–7.3 mm wide at humeri, 2.6–2.9 mm long. Humeral angles somewhat produced laterad (0.3 mm or less beyond base of coria), narrowly rounded. Anterolateral margins of pronotum nearly straight.

Scutellum 4.2–4.7 mm wide at base, 4.7–5.5 mm long.

Abdominal tubercle compressed, reaching between metacoxae. Ostiolar ruga on each side extending about halfway from mesial margin of ostiole to lateral margin of thorax.

Posterior margin of basal plates projecting strongly caudad at rounded mesial angle (Fig. 111), from caudal view curving ventrad at lateral portion of 2nd gonacoxae (Fig. 112). Spermatheca as in Figure 113.

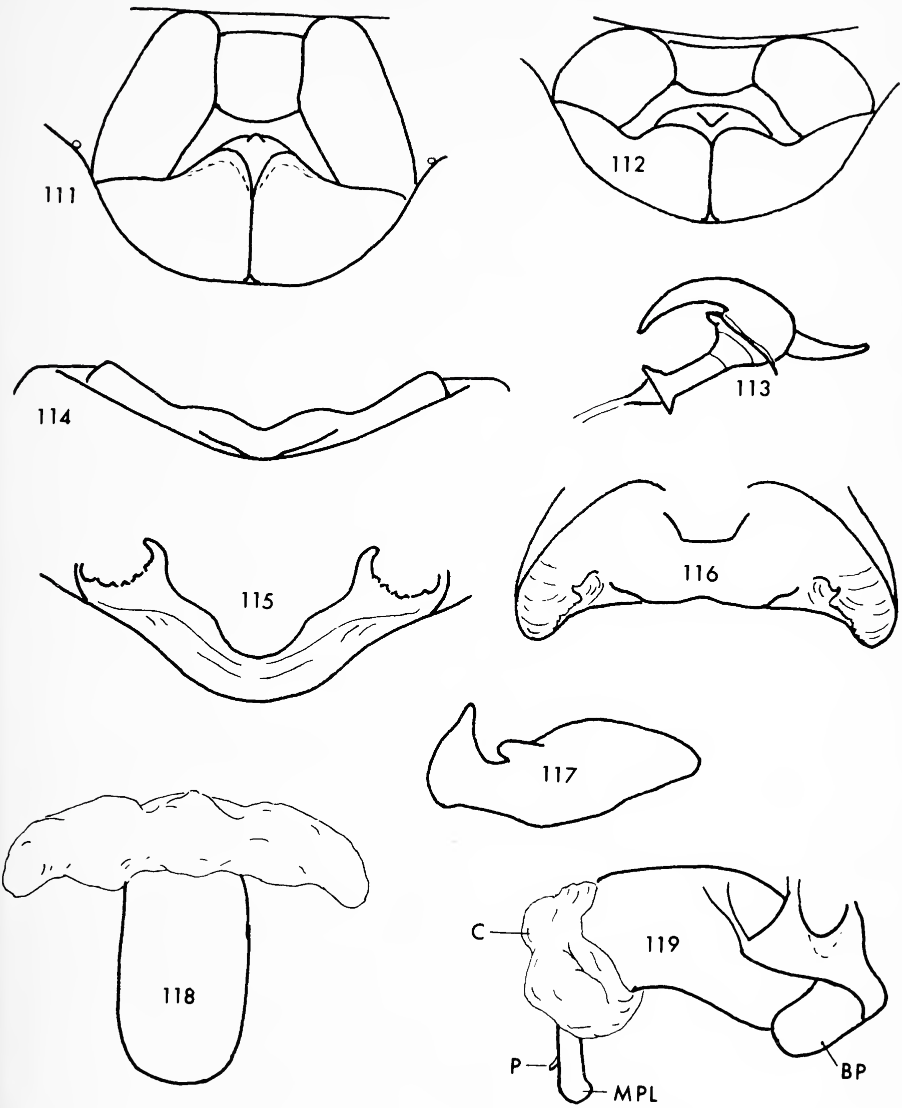
Male genitalia as in Figures 114–119. Posterior wall on each side of genital cup with stout hook at anteromesial corner of dorsal rim, hook curving laterad at apex (Figs. 115, 116).

Length about 11.1–12.8 mm.

Distribution. Bahama Islands (Mayaguana, Grand Bahama?).

Holotype. ♂, labeled "Bahama, VII-28-1926". Deposited in American Museum of Natural History.

Paratypes. 1♂, 3♀♀, labeled as holotype (♂, ♀ LHR; ♀ AMNH); "Bahamas: Mayaguana Is. 30-VIII-63, C. Murvosh, black light trap" (♀ FSCA).



Figs. 111–119. *A. euri.* 111. Genital plates, caudoventral view. 112. Same, caudal view. 113. Spermathecal bulb and pump. 114. Pygophore, ventral view. 115. Pygophore, caudal view. 116. Genital cup. 117. Paramere. 118. Aedeagus, dorsal view. 119. Aedeagus, lateral view; conjunctiva (C); median penial lobes (MPL); penisfilum (P); basal plate (BP).

Acrosternum (Chinavia) macdonaldi, new species
(Figs. 120–123)

Description. Bright green above, paler below, yellowish on thoracic sterna and sometimes on abdominal disk. Lateral dorsal and ventral borders of head, pronotum, coria basally, connexiva and apical borders of scutellum orange-yellow; connexival borders sometimes suffused over much of laterotergites. Cicatrices and basal angles of scutellum immaculate. Antennae green with apical end of segment 3 and apical half of segments 4 and 5 black; antennifers rarely with black dot on superior surface near base. Legs green. Spiracles pale without callus. Punctation dense, fine, green.

Head 2.8–3.0 mm wide across eyes, 2.3–2.4 mm long. Antennal segments 0.5–0.6, 1.1, 1.3–1.5, 1.9–2.1, 2.1–2.2 mm long. Rostral segments 2–4 about 1.6–1.7, 1.3–1.4, 1.0–1.1 mm long; rostrum extending a little past metacoxae.

Pronotum 7.1–7.3 mm wide at humeri, 2.8–2.9 mm long. Humeri slightly produced laterad, rounded.

Scutellum 4.5–4.6 mm wide at base, 4.8–5.0 mm long.

Abdominal tubercle compressed, reaching between metacoxae. Ostiolar ruga on each side extending about three-fourths of distance from mesial margin of ostiole to lateral margin of thorax.

Male genitalia as in Figures 120–123. Posterior wall on each side of genital cup dorsally diagonal, dorsal rim concave; denticulate low ridge running from obtuse mesial corner of dorsal rim onto concave anterolateral surface of posterior wall (Fig. 122).

Basal plates from caudoventral view with posterior margin nearly straight between convex lateral angles; dorsal edge of each slightly sinuous from caudal view, the two together bowed a little ventrad.

Length about 11.8–12.3 mm.

Distribution. Panama.

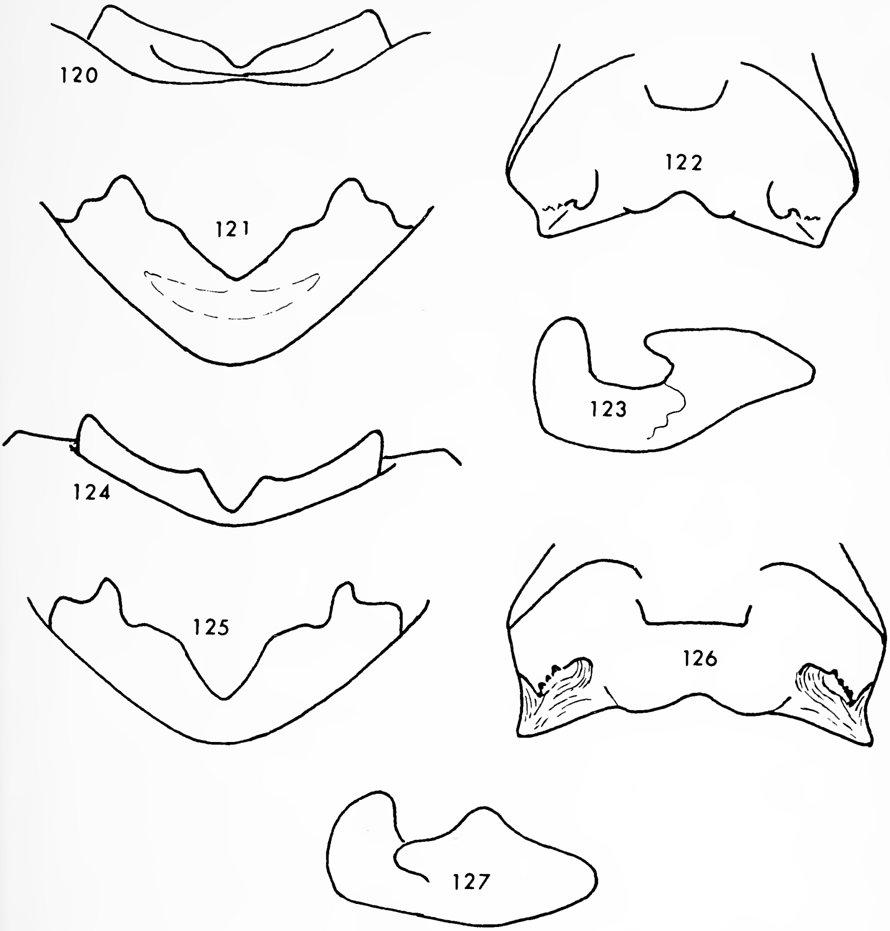
Holotype. ♂, labeled (a) "Canal Zone: Barro Colorado, 3 IV" (b) "W. M. Wheeler" (c) "light". Deposited in American Museum of Natural History.

Paratypes. 3♂♂, 1♀, "Panama" (♂ LHR); "Coco Solo Hospital, Canal Zone, 27 Apr. 72 L. T. Col: D. Engleman" (♂ HDE). "Panama, dist. Chepo, Altos de Maje. 17 May 75 at lights Stockwell-Engleman" (♂ HDE); "Coco Solo Hosp. C. Z. Panama. Light Trap. 20-V-75. Col: D. Engleman" (♀ LHR).

Comment. This species is dedicated to my friend and colleague F. J. D. McDonald. He has contributed much to our knowledge of pentatomoids.

Acrosternum (Chinavia) wygodzinskyi, new species
(Figs. 124–127)

Description. Dark green above, paler below. Lateral margins of head and usually anterolateral margins of pronotum thinly bordered in red or yellow.



Figs. 120–127. Figs. 120–123. *A. macdonaldi.* 120. Pygophore, ventral view. 121. Pygophore, caudal view. 122. Genital cup. 123. Paramere. Figs. 124–127. *A. wygodzinskyi.* 124. Pygophore, ventral view. 125. Pygophore, caudal view. 126. Genital cup. 127. Paramere.

Posterolateral angles of connexiva with black mark on edge of sternites; corresponding angles of sternites more generously blackened ventrally. Cicatrices and basal angles of scutellum immaculate. Antennae and legs green or greenish yellow; black macule present at base of antennifers on superior surface. Peritremes of spiracles brown, surrounded by yellowish uncalloused ring. Dorsal punctation dense, green.

Head 2.9–3.5 mm wide across eyes, 2.4–2.9 mm long; lateral jugal margins weakly concave. Antennal segments 0.5–0.6, 1.2–1.5, 1.5–2.0, 2.0–2.3, 1.8–

2.1 mm long. Rostral segments 2–4 about 1.6–2.0, 1.3–1.6, 1.0–1.2 mm long; rostrum terminating between metacoxae.

Pronotum 7.6–9.6 mm wide at humeri, 3.0–3.8 mm long at meson. Humeri produced laterad 0.2–0.3 mm beyond costal margin of coria; humeral angle at least slightly obtuse, narrowly rounded; anterolateral margin of pronotum nearly straight.

Scutellum 4.7–6.0 mm wide at base, 5.3–6.7 mm long.

Abdominal tubercle compressed, projecting between metacoxae. Ostiolar ruga on each side reaching 0.7–0.8 distance from mesial margin of ostiole to lateral margin of thorax.

Posterior margin of basal plates sinuous from caudoventral view, each slightly concave below second gonocoxae, broadly rounded at lateral angles.

Male genitalia as in Figures 124–127. Posterior wall on each side of genital cup dorsally diagonal, rim shallowly concave; denticulate carina on anterolateral face of posterior wall curving posterolaterad from anterior angle of posterior wall; at base of this carina another thin low carina proceeds anterolaterad to lateral margin of pygophore (Fig. 126).

Length about 12.2–17.0 mm.

Distribution. St. Thomas and St. John Islands (Virgin Islands, West Indies).

Holotype. ♂, labeled "St. Thomas V.I., Est. Lilliendahls El. 1000′, 15-X-78, M. A. Ivies, Coll." Deposited in U.S. National Museum, type no. 75563.

Paratypes. 8♂♂, 9♀♀, same data as holotype (♂ AMNH); same data as holotype except date "25-X-78" (2♂♂ DBT); same data as holotype except date "24-VIII-78" (♂ LHR); (a) "Virgin Is: St. Thomas. Est. Lilliendahl. 08 Aug. 1980. At Light" (b) "M. A. Ivie, Colr." (♂ MAI); (a) "Virgin Is.: St. John V.I.E.R.S. 15 Aug. 1980. At UV Light" (b) "M. A. Ivie, Colr." (♂, 4♀♀ UCD); (a) "Virgin Is. French. Bay Estate. El. 360 ft. St. Thomas. 30 Sep. 1978" (b) "C. Petrovic, colr." (♂ OSU); same data except date "03 Oct. 1978" (♂, ♀ LHR; ♀ UCD); "Virgin Is.: St. Thomas. Estate Lilliendahl. 1000 ft. Oct. 1978, M. A. Ivie, Colr." (♀ MAI); "Virgin Is.: St. Thomas. Frenchman Bay Estate. 09 July 1978. 750 ft. M. A. Ivie, Colr." (♀ OSU); (a) "Virgin Is. St. Thomas. Red Hook 14 Oct. 1979" (b) "M. A. Ivie, Colr."

Comment. This species is similar to the preceding, differing in details of coloration and the genitalia.

The species is dedicated to Dr. P. Wygodzinsky, whose contributions to the knowledge of Hemiptera are many.

Acrosternum (Chinavia) monticola, new species
(Figs. 128–130)

Description. Pale green above and below with narrow orange-yellow border on lateral margins of head, pronotum, base of coria and connexiva. Posterolateral angles of connexiva and sternites with small black spot confined on connexiva to edge of sternites except on first two segments, there barely extending onto laterotergites. Connexiva and basal angles of scutellum immaculate. Legs and antennae green, antennifers immaculate. Spiracles pale, surrounded by pale ivory uncalloused area. Dorsal punctation dense, shallow, pale green.

Head 2.9 mm wide across eyes, 2.2 mm long. Antennal segments 0.5, 1.1, 1.5, 1.9, 1.9 mm long. Rostral segments 2–4 about 1.7, 1.1, 0.9 mm long; rostrum terminating between metacoxae.

Pronotum 7.4 mm wide at humeri, 2.9 mm long at meson. Humeri little produced, obtusely angulate. Anterolateral margins of pronotum straight.

Scutellum 4.6 mm wide at base, 5.0 mm long.

Abdominal tubercle compressed, reaching middle of metacoxae. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax.

Female unknown.

Male pygophore as in Figures 128–130. Posterior wall on each side of genital cup dorsally diagonal with laterally bent hook on anterior angle (Figs. 129, 130); concave dorsal rim of posterior walls weakly denticulate.

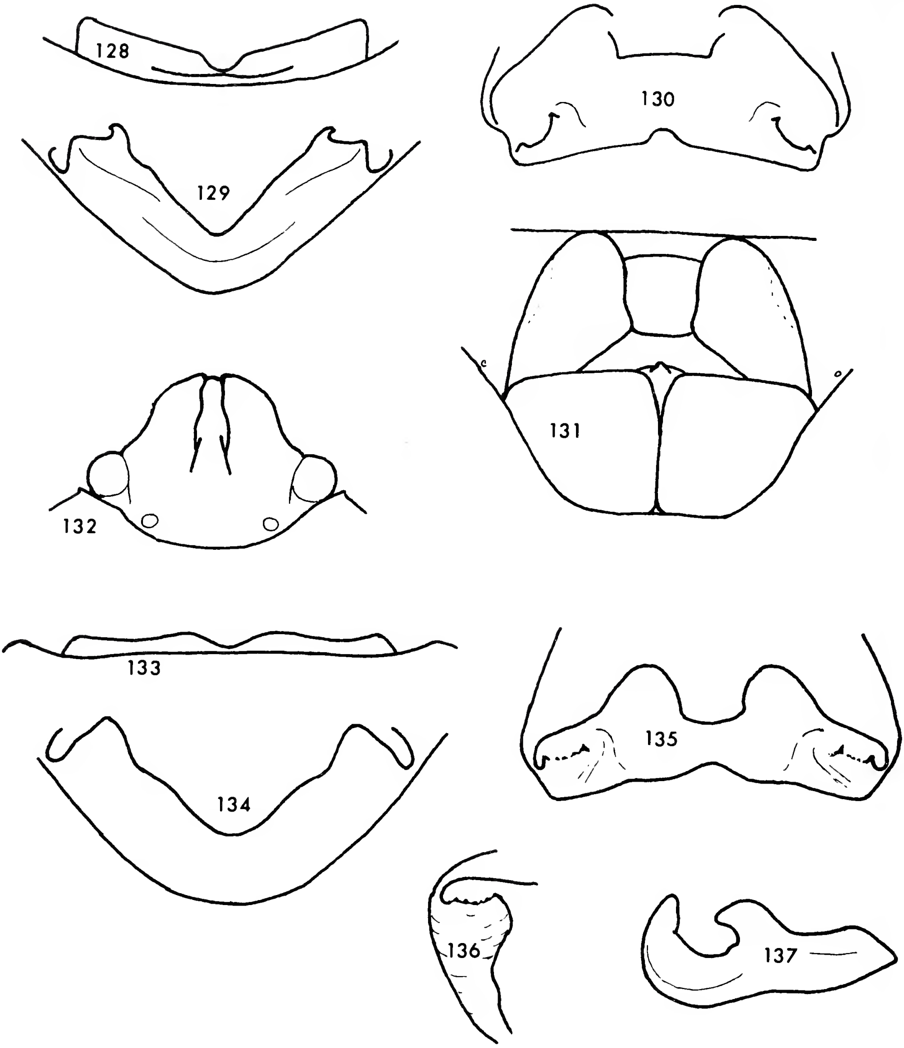
Distribution. Peru. Known only from holotype.

Holotype. ♂, labeled (a) "Peru, 10 Km. S. of Chiclayo. III-21-1961" (b) "Ross and Michelbacher, Collectors". Deposited in California Academy of Sciences. No paratypes.

Acrosternum (Chinavia) occasi, new species
(Fig. 131)

Description. Medium green above, paler below becoming yellowish mesially. Narrow yellow lateral border of body sometimes incomplete on head, entire on pronotum and base of coria, sometimes diffusing over most of connexiva. Spine at posterolateral angle of connexiva and dot at posterolateral angles of sternites black. Cicatrices and basal angles of scutellum immaculate. Spots (3 or 5) along base of scutellum and narrow apical border yellow to orange. Antennal segments 4 (except base) and 5, and sometimes apex of 3 ferrugineous to purple; remainder of antennae green; black macule present at base of antennifers on superior surface. Each spiracle located in posterolateral edge of yellow callus; peritremes green. Punctation on dorsum dense, somewhat rugose on pronotum and scutellum, green; somewhat indistinct median longitudinal band on scutellum formed by discontinuous irregular yellowish calli on interstices between punctures.

Head 2.7–2.9 mm wide across eyes, 2.4 mm long. Antennal segments 0.5–0.6, 1.0–1.2, 1.0–1.2, 1.3–1.4, 1.4 mm long. Rostral segments 2–4 about 1.5–1.6, 1.1–1.3, 0.9 mm long; rostrum terminating between metacoxae.



Figs. 128–137. Figs. 128–130. *A. monticola.* 128. Pygophore, ventral view. 129. Pygophore, caudal view. 130. Genital cup. Fig. 131. *A. occasi.* Genital plates, caudoventral view. Figs. 132–137. *A. montivagum.* 132. Head. 133. Pygophore, ventral view. 134. Pygophore, caudal view. 135. Genital cup. 136. Posterior wall, left side, dorsomesial view. 137. Paramere.

Pronotum 6.9–7.8 mm wide at humeri, 4.9–5.7 mm long at meson. Humeri little produced laterad, broadly rounded; anterolateral margins straight.

Scutellum 4.4–5.0 mm wide at base, 4.9–5.7 mm long.

Abdominal tubercle barely or not attaining metacoxae. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax.

Basal plates forming nearly straight line along posterior margin except at convex lateral angles (Fig. 131). Paratergite 9 not concave above posterior margin of basal plates.

Male unknown.

Distribution. Chile (Coquimbo Prov.).

Holotype. ♀, labeled (a) "50 Km S. of La Serena, Chile, XII-1-50" (b) "Ross and Michelbacher, Collectors". Right basal plate partially detached, last antennal segments lacking. Deposited in California Academy of Sciences.

Paratype. "Chile" and "XI", remainder illegible (♀ LHR).

Comment. The abdominal tubercle of this species is nearly as rudimentary as that of *A. aseadum.* The basal plates and some markings of the two species are dissimilar, however.

Acrosternum (*Chinavia*) *montivagum* (Distant, 1890)
(Figs. 132–137)

Chlorochroa montivaga Distant, 1890, p. 333, pl. 31, fig. 13.
Nezara majuscula Distant, 1890, p. 339, pl. 31, fig. 20 (synonymized by Rolston, 1976).
Pentatoma montivaga: Lethierry and Severin, 1893, p. 119.
Acrosternum montivagum: Rolston, 1976, p. 4 (lectotype designated).

Diagnosis. Proximal end of tibiae and broad border along outer margins of body crimson. Juga converging apically over tylus, rarely contiguous (Fig. 132). Humeri rounded, little produced laterad. Abdominal spine barely attaining posterior limit of metacoxae, its anterior margin subvertical. Posterior margins of connexival segments except last black bordered for about half their width, or black marginal macule mostly on posterolateral angle but extending onto anterolateral angle of succeeding segment; this macule continuing onto venter and forming spot at posterolateral angles of sternites. Distal end of coria ending above penultimate connexival segment. Each spiracle positioned in posterolateral edge of yellowish callus; peritremes black or reddish. Ostiolar ruga on each side reaching about 0.5–0.6 distance from mesial margin of ostiole to lateral thoracic margin. Rostrum terminating between meso- and metacoxae. Femora green. Cicatrices and basal angles of scutellum immaculate. Dorsal punctation dense; punctures concolorous with surrounding area. Posterior margin of basal plates transverse between rounded lateral angles from caudoventral view; dorsal margin of each basal plate slightly convex from caudal view. Male genitalia as in Figures 133–137. Posterior wall of genital cup diagonal dorsally on each side with shallowly concave rim and line of black denticles on anterolateral face.

Length about 13–17 mm.

Distribution. Southern Mexico into Panama, Hispaniola.

Comment. The types of *Chlorochroa montivaga* and *Nezara majuscula* were examined.

Acrosternum (Chinavia) collis, new species
(Figs. 138–142)

Description. Emerald green above, greenish yellow below with apex of tibiae and outer margins of body crimson. Posterior margin of connexival segments bordered with black along lateral half, this border continuing as black spot at posterolateral angles of sternites. Dot at mesial limit of cicatrices, basal angles of scutellum, spiracles and wide ring around spiracles, and antennae, black. Dorsal punctation moderately dense; punctures concolorous with surrounding area.

Head 2.9–3.3 mm wide across eyes, 2.2–2.7 mm long. Antennal segments 0.6–0.7, 1.1–1.4, 1.6–2.1, 1.9–2.4, 2.3–2.5 mm long. Rostral segments 2–4 about 1.6–1.9, 1.1–1.4, 0.9–1.2 mm long; apex of rostrum lying between metacoxae. Juga not convergent apically.

Pronotum 6.8–8.6 mm wide at humeri, 2.5–3.4 mm long at meson. Humeri little produced laterad, broadly rounded to obtusely angulate. Anterolateral margin more or less straight, sometimes weakly concave or sinuous.

Scutellum 4.2–5.3 mm wide at base, 4.4–6.1 mm long. Coria ending distally above anterior part of last connexival segment.

Abdominal tubercle reaching posterior margin of metacoxae. Ostiolar ruga on each side extending about 0.7–0.8 distance from mesial margin of ostiole to lateral margin of thorax.

Genital plates as in Figure 138. Paratergites 9 flat basally.

Large obtuse tooth projecting posterodorsad from posterolateral angles of pygophore. Posterior wall of genital cup dorsally diagonal on each side; posterolateral and anteromesial angles of dorsal rim with smaller tooth projecting laterad (Figs. 140, 141).

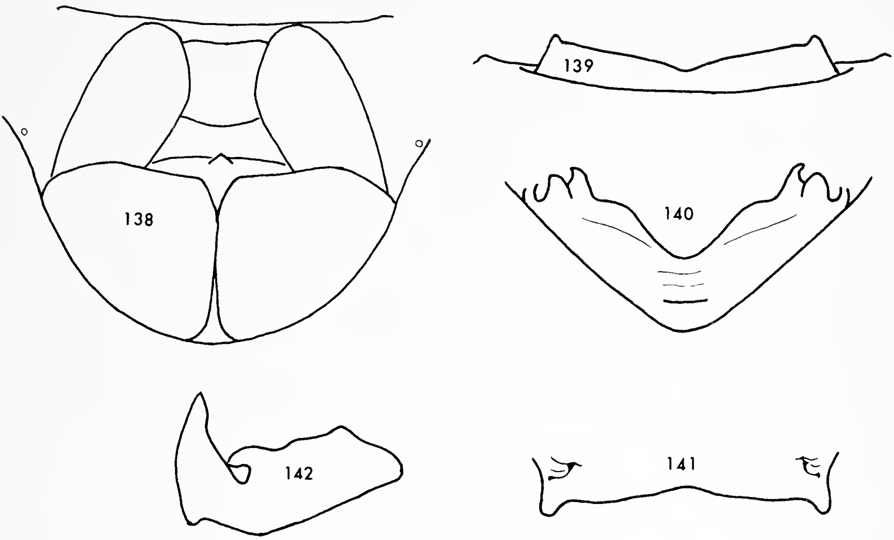
Length about 11.5–15.5 mm.

Distribution. Costa Rica.

Holotype. ♂, labeled "Costa Rica, Puntar. - Alajuela: Monteverde For. Res. 1600 m. 17/18 Aug. 1976. E. M. Fisher." Deposited in U.S. National Museum, type no. 75564.

Paratypes. 1♂, 2♀♀, labeled as holotype (♂, ♀ DBT); "Costa Rica: San Jose, 8.3 mi. N. San Isidro del General, 30 June 1972. R. R. & M. E. Murray" (♀ LHR).

Comment. This species is distinguished from *A. montivagum,* which it resembles superficially, by the black markings, rostral length and male genitalia.

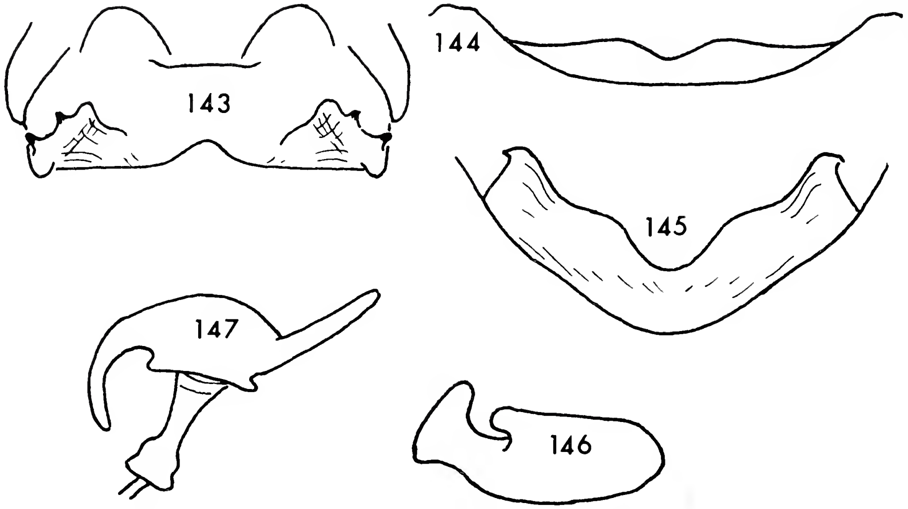


Figs. 138–142. *A. collis.* 138. Genital plates, caudoventral view. 139. Pygophore, ventral view. 140. Pygophore, caudal view. 141. Posterior margin of pygophore, dorsal view. 142. Paramere.

Acrosternum (*Chinavia*) *apicicorne* (Spinola, 1852)
(Figs. 143–147)

Pentatoma apicicorne Spinola in Gay, 1852, pp. 131–132, pl. 1, fig. 1.
Nezara apicicornis: Signoret, 1863, p. 548, pl. 1, fig. 1 (description); Reed, 1898, p. 135 (synonymy); Haglund, 1899, p. 77; Berg, 1900, p. 83 (corrects Reed's synonymy).
Rhaphigaster apicicornis: Walker, 1867, p. 360 (listed).
Acrosternum apicicornis: Pirán, 1948, p. 9 (record).

Diagnosis. Humeral angles rounded, little produced. Abdominal tubercle scarcely reaching metacoxae. Posterolateral angles of connexiva and sternites black, macule on connexiva including part of laterotergite and sometimes anterolateral angle of following connexival segment. Spiracles green to brown, each located in posterolateral edge of yellow callus. Ostiolar ruga on each side extending about 0.7–0.8 distance from mesial margin of ostiole to lateral thoracic margin. Rostrum terminating between metacoxae. Femora green. Cicatrices immaculate. Small yellow callus located adjacent to basal angles of scutellum; 3 additional yellow spots present along scutellar base. Dorsal punctation dense, concolorous with surrounding area. Posterior margin of basal plates nearly transverse between rounded lateral angles; spermatheca as in Figure 147. Male genitalia as in Figures 143–146. Posterior wall of



Figs. 143–147. *A. apicicorne.* 143. Genital cup. 144. Pygophore, ventral view. 145. Pygophore, caudal view. 146. Paramere. 147. Spermathecal bulb and pump.

genital cup diagonal dorsally on each side with small black tooth at anteromesial angle of rim curving anterolaterad; from this tooth a subvertical denticulate black carina descends anterolateral face of wall, with largest denticles subterminal. Pygophore deeply emarginated subterminally from lateral view.

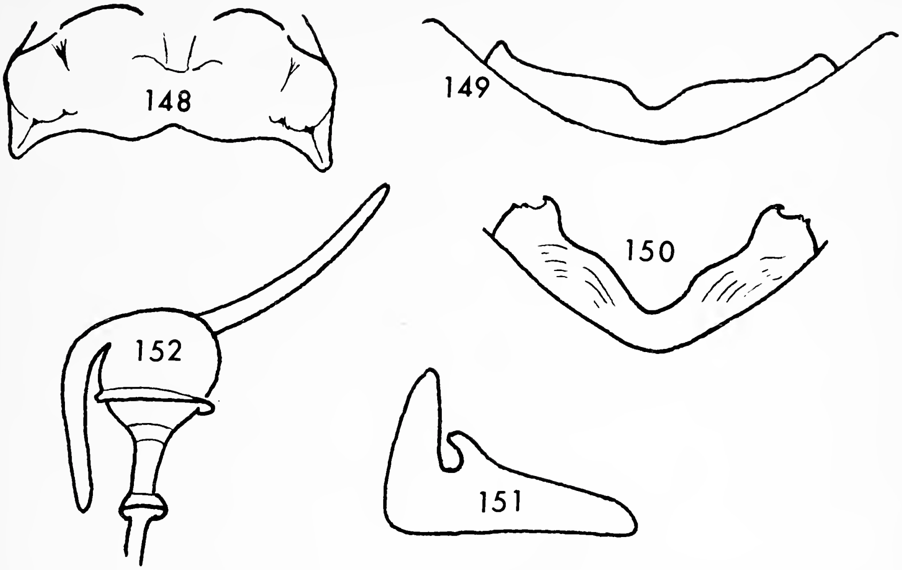
Length about 11.5–13.0 mm.

Distribution. Chile, Argentina (fide Pirán, 1948).

Acrosternum (Chinavia) australe, new species
(Figs. 148–152)

Description. Green above and below with narrow yellow to orange-yellow border along outer margins, usually excepting head apically; thoracic sterna, coxae, trochanters, femora and abdominal tubercle yellowish, often with rufous suffusion. Posterolateral angles of connexiva including corresponding corner of laterotergites and posterolateral angle of sternites black. Cicatrices and basal angles of scutellum immaculate. Spot adjacent to each basal angle, usually 2 additional spots along base, and apex of scutellum yellowish. Spiracles green, each contiguous with but not on a small yellowish callus. Dorsal punctation dense, rugose on pronotum; punctures concolorous with surrounding area.

Head 2.7–3.0 mm wide across eyes, 2.2–2.7 mm long. Antennal segments 0.5–0.6, 1.0–1.2, 1.3–1.7, 1.7–1.9, 1.3–1.6 mm long. Rostral segments 2–4



Figs. 148–152. *A. australe.* 148. Genital cup. 149. Pygophore, ventral view. 150. Pygophore, caudal view. 151. Paramere. 152. Spermathecal bulb and pump.

about 1.3–1.6, 1.2–1.6, 0.8–1.1 mm long; rostrum terminating between or projecting a little past metacoxae.

Pronotum 6.2–8.2 mm wide at humeri, 2.3–3.1 mm long at meson. Humeri rounded, little produced laterad. Anterolateral margins straight.

Scutellum 3.9–5.2 mm wide at base, 4.2–5.6 mm long.

Abdominal tubercle projecting little past posterior limit of metacoxae. Ostiolar ruga on each side extending about three-fourths distance from mesial margin of ostiole to lateral thoracic margin.

Posterior margin of basal plates slightly sinuous, their most posterior part mesial, there bent slightly dorsad toward 2nd gonocoxae. Spermatheca as in Figure 152.

Male genitalia as in Figures 148–151. Posterior wall of genital cup diagonal dorsally on each side; dorsal rim with denticle at anteromesial and posterolateral corners, concave between these corners and usually with one or more small denticles along concavity (Figs. 148, 150).

Length about 10–14 mm.

Distribution. Northern Argentina.

Holotype. ♂, labeled (a) "5 mi. N. of Dean Fumes, Cordoba, Arg. II-8-51" (b) "leg. Ross and Michelbacher". Costal area of left hemelytron swollen above posterior half of first and anterior half of second connexival segments. Deposited in American Museum of Natural History.

Paratypes. 6♀♀, 7♂♂, "Museum Leiden, Argentina, La Rioja, Mascasin, II 1964, F. H. Walz." (3♀♀, 3♂♂ RNH; ♀ LHR); "Museum Leidn., Argentina, Bs. Aires, Fandel, II 1953, F. H. Walz" (♀, 3♂♂ RNH; ♂ LHR); "Cruz del Eje. Argentina" (♀ HDE).

Comment. The contiguous callus and spiracle arrangement, rather than the spiracle on the callus, are diagnostic.

Acrosternum (*Chinavia*) *fuscopunctatum* (Breddin, 1901), **New Combination**
(Figs. 153–156)

Nezara fuscopunctata Breddin, 1901, pp. 123–124; Gaedike, 1971, p. 86 (lectotype designated).

Diagnosis. Pronotum transversely impressed caudad of cicatrices. Coria nearly reaching posterior margin of last connexival segment; costal angles of coria subacute (Fig. 153). Humeri rounded, not produced, with short black line on edge. Abdominal tubercle compressed, reaching middle of metacoxae. Posterolateral angles of connexiva with triangular black mark extending onto laterotergite; posterolateral angles of sternites bearing small black spot. Spiracles light brown, unattended by callus. Ostiolar ruga on each side extending about 0.65 distance from mesial margin of ostiole to lateral thoracic margin. Rostrum terminating between metacoxae. Femora entirely green. Lateral jugal margin moderately concave (Fig. 154). Neither pronotum nor scutellum with black markings. Dorsal punctation dense, concolorous with area surrounding punctures. Mesial angle of basal plates rounded; most posterior part of plates near this angle; posterior margin rather abruptly reflexed toward 9th paratergites (Figs. 155, 156). Length about 10.7 mm.

Distribution. Brazil (Espirito Santo). Known only from lectotype.

Comment. The lectotype, a ♀ designated by Gaedike (1971), was examined.

Acrosternum (*Chinavia*) *marginatum* (Palisot de Beauvois, 1805)
(Figs. 157–163)

Pentatoma marginata Palisot de Beauvois, p. 147, Hem. pl. 10, fig. 1.

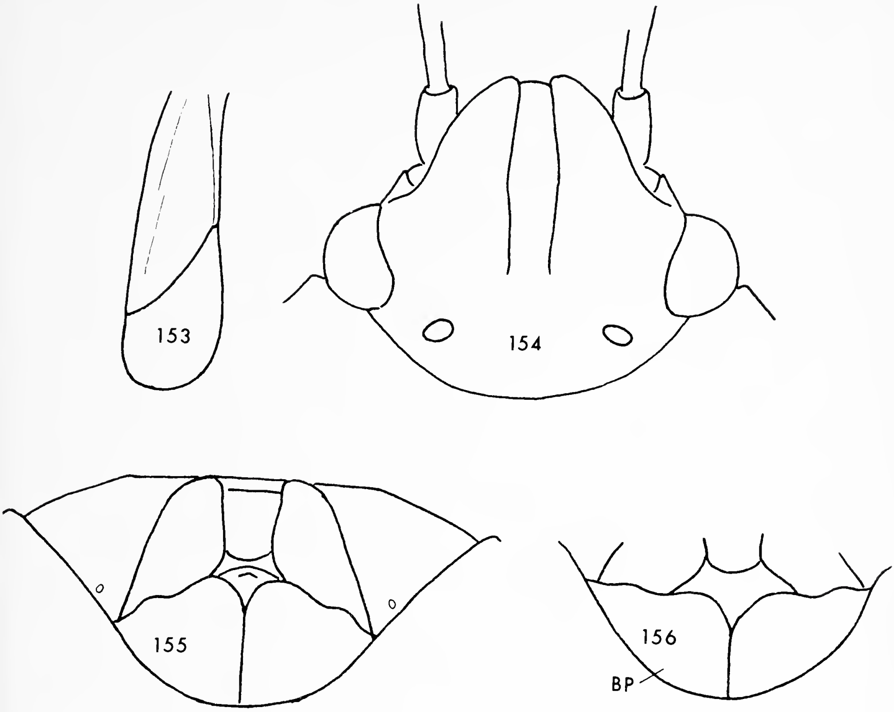
Nezara marginata: Amyot and Serville, 1843, p. 145; Distant, 1880, p. 79, pl. 7, fig. 23 (records); Distant, 1890, p. 339 (records); Sharp, 1890, p. 408, pl. 13, fig. 17 (♂ genitalia); Uhler, 1894a, pp. 175–176 (record); Uhler, 1894b, p. 232 (record); Van Duzee, 1904, p. 58 (keyed, records); Van Duzee, 1907, p. 10 (records).

Rhaphigaster spirans Dallas, 1851, p. 280 (synonymized by Stål, 1872).

Pentatoma (*Nezara*) *marginata:* Guerin in Sagra, 1857, p. 374.

Nezara juriosa Stål, 1862, p. 106 (synonymized by Stål, 1872).

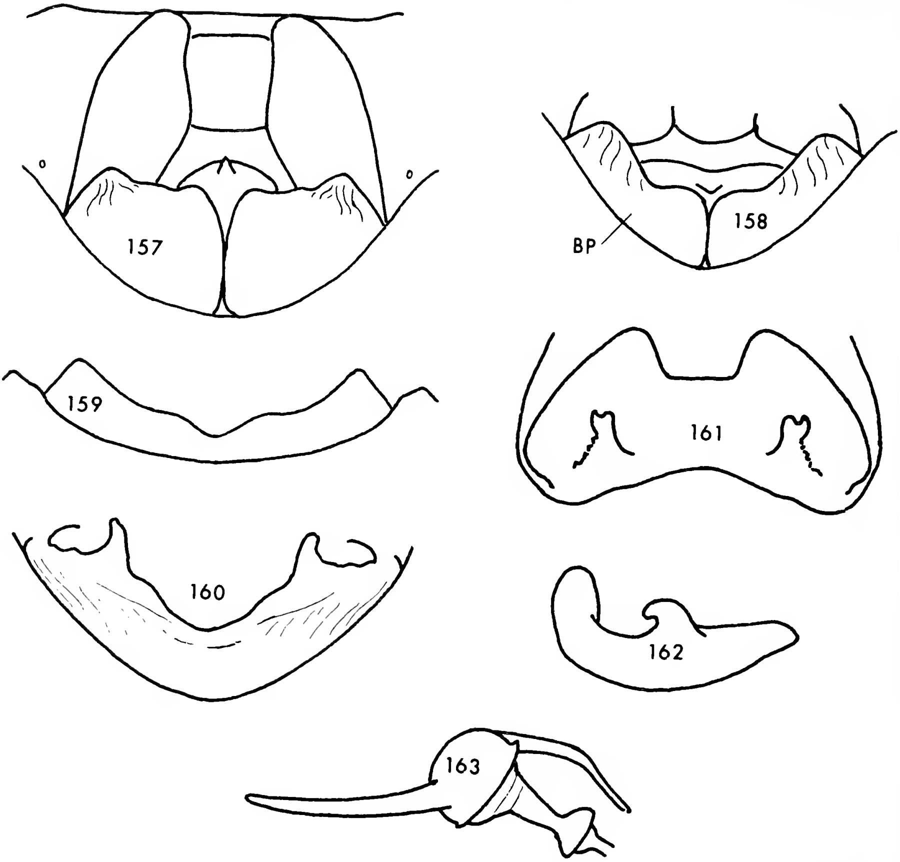
Nezara (*Acrosternum*) *marginata:* Stål, 1872, p. 42 (keyed, synonymy).



Figs. 153–156. *A. fuscopunctatum.* 153. Hemelytron. 154. Head. 155. Genital plates, caudoventral view. 156. Basal plates, caudal view (BP).

Acrosternum marginatum: Bergroth, 1914, p. 25; Van Duzee, 1917, p. 60 (catalog); Barber, 1923, p. 12 (record); Blatchley, 1926, pp. 160, 163 (keyed, description); Barber and Bruner, 1932, p. 262 (Cuban record, descriptive note); Barber, 1939, p. 296 (record); Torre Bueno, 1939, p. 237 (keyed); Wolcott, 1948, p. 194 (records); Alayo, 1967, pp. 27–28, pl. 1, fig. 3, pl. 9, fig. 5; Gaud and Martorell, 1974, p. 258 (records); Froeschner, 1981, p. 67 (catalog).

Diagnosis. Humeri little produced laterad, rounded. Abdominal tubercle compressed, reaching middle of metacoxae. Posterolateral angles of connexival segments including corner of laterotergites and sternites with black spot. Spiracles unattended by callus; peritremes narrowly and usually incompletely ringed with black. Ostiolar ruga on each side extending about three-fourths distance from mesial margin of ostiole to lateral margin of thorax. Rostrum terminating between metacoxae. Femora green. Cicatrices and basal angles of scutellum immaculate. Dorsal punctation dense, concolorous with area surrounding punctures. Basal plates with projection of

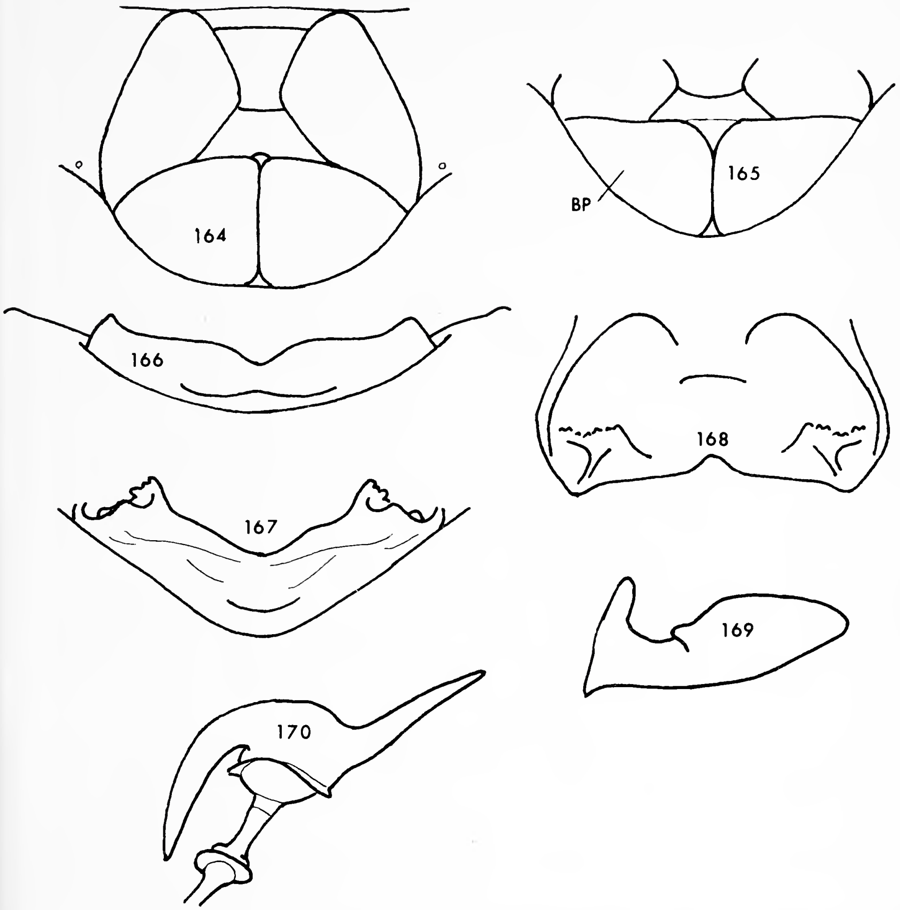


Figs. 157–163. *A. marginatum.* 157. Genital plates, caudoventral view. 158. Basal plates, caudal view (BP). 159. Pygophore, ventral view. 160. Pygophore, caudal view. 161. Genital cup. 162. Paramere. 163. Spermathecal bulb and pump.

posterior margin reflexed toward 9th paratergites; margin between lateral angles and projection diagonal, between projection and mesial angles convex (Figs. 157, 158). Spermatheca as in Figure 163. Posterior margin of pygophore broadly and sinuously emarginate from ventral view (Fig. 159); posterior wall of genital cup dorsally diagonal on each side, rim finely denticulate, concave, bearing small tooth at anteromesial angle (Figs. 160, 161). Parameres as in Figure 162. Length about 11.5–17.0 mm.

Distribution. Southwestern U.S. into Colombia, Ecuador and Venezuela; and from Florida as far south as Guadeloupe in the West Indies.

Comment. This is the common species of *Acrosternum* in Middle America. Both sexes are readily distinguished from *A. hilare,* with which it is partially sympatric and often confused.



Figs. 164–170. *A. hilare.* 164. Genital plates, caudoventral view. 165. Basal plates, caudal view (BP). 166. Pygohpore, ventral view. 167. Pygophore, caudal view. 168. Genital cup. 169. Paramere. 170. Spermathecal bulb and pump.

Acrosternum (*Chinavia*) *hilare* (Say, 1831)
(Figs. 164–170)

Pentatoma hilaris Say, 1831, p. 5; Say, 1832, pp. 9–10; Say, 1859, pp. 304–305, 316–317.
Rhaphigaster sarpinus Dallas, 1851, p. 276 (synonymized by Uhler, 1878).
Nezara (*Acrosternum*) *sarpinus:* Stål, 1872, p. 43 (keyed).
Nezara hilaris: Uhler, 1878, p. 380 (synonymy); Uhler, 1893, p. 368 (record); Van Duzee, 1894, p. 172 (record); Van Duzee, 1904, p. 58 (keyed, records); Barber, 1906, p. 261 (record); Torre Bueno, 1908, p. 225 (host, records);

Van Duzee, 1909, p. 157 (record); Olsen, 1912, p. 55 (hosts, record); Zimmer, 1912, p. 233 (records); Van Duzee, 1914, p. 5 (record); Barber, 1914, p. 523 (record); Whitmarsh, 1917, pp. 519–552 (biology).

Nezara (*Acrosternum*) *hilaris:* Kirkaldy, 1909, p. 119.

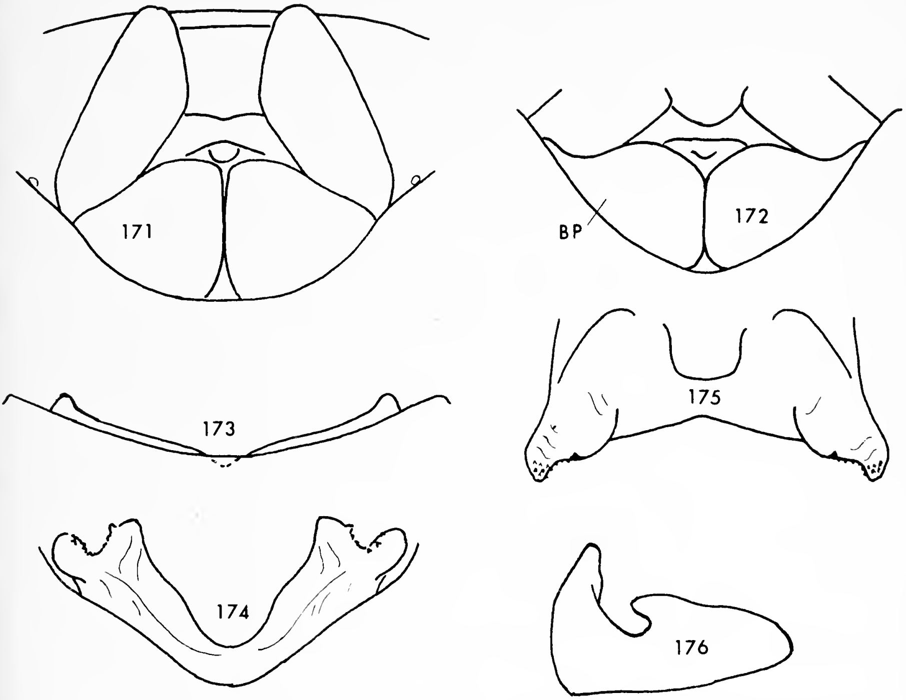
Acrosternum hilare: Parshley, 1915, p. 175 (keyed); Parshley, 1917, p. 24 (records); Hart, 1919, p. 181 (keyed, hosts); Stoner, 1920, pp. 107, 108–109, pl. 7, fig. 2 (keyed, synonymy, description, hosts); Hussey, 1922, p. 15 (records); Parshley, 1923, pp. 767–768 (keyed, records); Blatchley, 1926, pp. 160, 161–162, fig. 33 (keyed, description); Pack and Knowlton, 1930, p. 250 (host, records); Brimley, 1938, p. 63 (record); Froeschner, 1941, p. 130 (keyed); Esselbaugh, 1946, pp. 682–683 (eggs); Esselbaugh, 1948, pp. 41–44 (biology); Russell, 1952, pp. 5, 7–9 (biology); Sailer, 1953, pp. 70–71 (biology); Miner, 1966, pp. 8–17, figs. 2–5 (biology); McPherson, 1970, p. 54, fig. 51 (keyed, hosts, records); Hoffman, 1971, p. 48, fig. 12 (records); Burks, 1972, pp. 367–368 (parasite); Furth, 1974, pp. 40–41, pl. 1, fig. 3, pl. 5, figs. 64, 70 (keyed, hosts, records); McPherson and Mohlenbrock, 1976, pp. 155–156 (hosts, parasites); Nixon, 1976, p. 412 (host).

Acrosternum hilaris: Van Duzee, 1917, p. 60 (synonymy, distribution); Baker, 1931, p. 201, figs. 116, 117 (♂ genitalia); Underhill, 1934, pp. 1–26 (biology); Torre Bueno, 1939, p. 236 (keyed).

Diagnosis. Humeri little produced laterad, rounded. Abdominal tubercle compressed, reaching between metacoxae. Posterolateral angle of connexiva including corner of laterotergite and of sternites with black spot. Spiracles green to brown, in posterolateral part of subcalloused and usually yellowish spot. Ostiolar ruga on each side extending about three-fourths distance from mesial margin of ostiole to lateral margin of thorax. Rostrum ending between metacoxae. Femora green. Cicatrices and basal angles of scutellum immaculate. Punctation dense dorsally, green. Posterior margin of basal plates forming shallow convex arc from caudoventral view, nearly straight from caudal view (Figs. 164, 165). Spermatheca as in Figure 170. Emargination of pygophore from ventral view broad, shallow, sinuous (Fig. 166). Posterior wall dorsally on each side creating triangle with diagonal obtuse ridge posteriorly and transverse ridge anteriorly; rim of latter concave, armed with several black denticles (Figs. 167, 168). Parameres as in Figure 169. Length about 11–19 mm.

Distribution. Ranging from Ontario and Quebec, Canada, apparently throughout the United States. A single specimen was seen from Mexico, that from the state of Jalisco. Uhler's (1878) record from the West Indies is dubious, and those from Panama and Brazil are clearly erroneous.

Comment. A. hilare is of some economic importance and there are nu-



Figs. 171–176. *A. brasicola.* 171. Genital plates, caudoventral view. 172. Basal plates, caudal view (BP). 173. Pygophore, ventral view. 174. Pygophore, caudal view. 175. Genital cup. 176. Paramere.

merous references to the species in this connection. Some of these references have been noted in the synonymy cited, but those of a purely economic nature have not.

Acrosternum (Chinavia) brasicola, new species
(Figs. 171–176)

Description. Dark green above, paler below, with narrow bright red border along outer margins. Black spot present at mesial limits of cicatrices and black fovea in basal angles of scutellum; a small yellow spot usually mesad of and contiguous with each scutellar fovea. Small black spot in posterolateral angles of connexiva extending onto laterotergites. Elongate black mark present on superior surface at base of antennifers; antennae usually emerald green with black ring on distal end of segment 3, often much of antennae apparently discolored, black. Legs green. Spiracles black, each in posterolateral part of callus distinguished in varying degrees by yellowish color. Dorsal punctation green, fine, dense, less dense on scutellum; many yellowish small calli scattered on dorsum.

Head 2.9–3.1 mm wide across eyes, 2.2–2.6 mm long. Antennal segments 0.5–0.6, 1.0–1.4, 1.3–1.7, 1.7–2.1, 2.0–2.2 mm long. Last 3 rostral segments about 1.5–1.7, 1.2–1.4, 1.0–1.2 mm long; rostrum reaching metacoxae.

Pronotum 7.5–9.4 mm wide at base, 4.8–6.7 mm long. Humeri rounded, little or not at all produced laterad. Anterolateral margins straight or weakly convex.

Scutellum 4.5–5.9 mm wide at base, 4.8–6.7 mm long.

Abdominal tubercle compressed, projecting little beyond posterior limit of metacoxae. Ostiolar ruga on each side extending 0.6–0.8 distance from mesial margin of ostiole to lateral thoracic margin.

Basal plates subtriangular; posterior margin arched ventrad beneath 9th paratergites from caudal view (Figs. 171, 172).

Male genitalia as in Figures 173–176. Posterior wall on each side with tooth near posterior limit; pygophoral margin posterior to this tooth with field of denticles extending onto dorsal surface of posterolateral projection on each side (Figs. 174, 175).

Distribution. Southern Brazil.

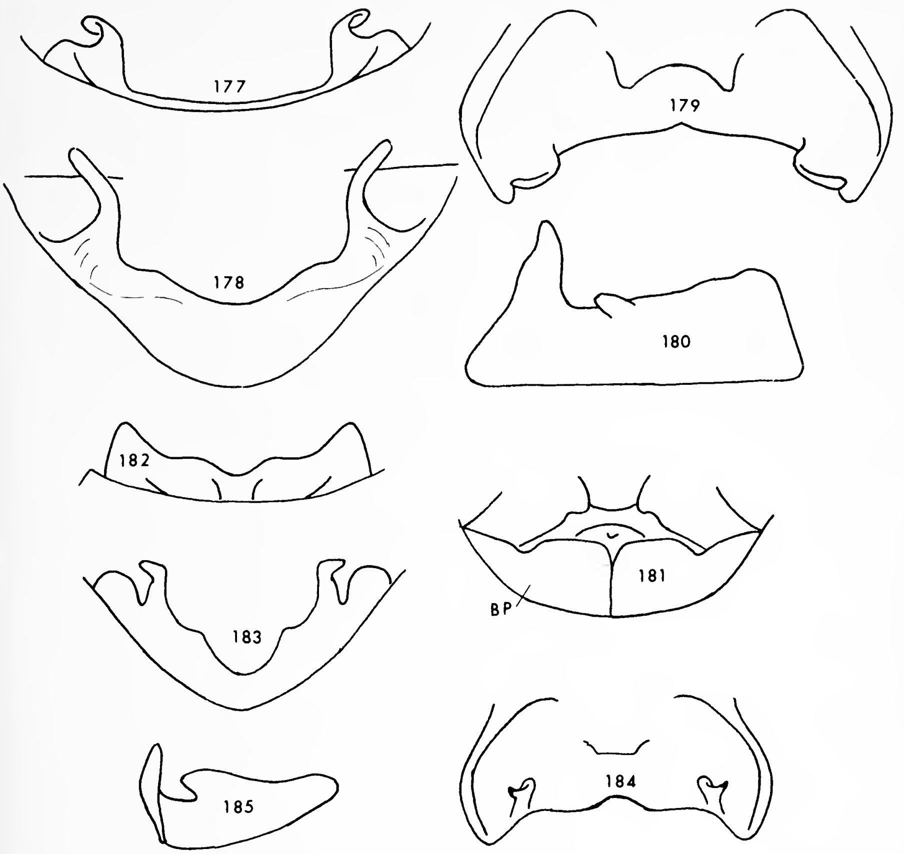
Holotype. ♂, labeled "Brasilien, Nova Teutonia, 27° 11′B 52° 23′L. Fritz Plaumann", on one edge "II 1974", on other edge "300–500 m". Deposited in U.S. National Museum, type no. 75566.

Paratypes. 5♀♀, 2♂♂, all from same locality: labeled as holotype (2♀♀ LHR); dated "X-31-1958" (b) "Ex. Coll. H. Ruckes" (♂ AMNH); labeled as preceding except date "XI-28-195" (♂ LHR); same labeling except date "I. 3. 1962" (♀ AMNH); same labeling except date "XI-12-1959" (♀ AMNH); labeled as holotype except date "III-3-1960" (♀ LHR).

Acrosternum (Chinavia) teretis, new species
(Figs. 177–180)

Description. Light green, below blending to yellow mesially, with reddish-yellow border along outer margins. Black spot present in posterolateral angles of connexiva and sternites, those on connexiva extending onto laterotergites, at mesial and sometimes lateral limits of cicatrices. Small macule on superior surface at base of antennifers also black; antennae green with black ring at distal end of segment 3 and short dense setose vestiture giving last 2 segments brownish appearance. Legs green. Spiracles black, unattended by callus. Dorsal punctation dense, fine, concolorous with area around punctures.

Head 2.8–2.9 mm wide across eyes, 2.2–2.3 mm long. Antennal segments 0.6, 1.1–1.2, 1.5, 1.9, 2.0 mm long. Rostral segments 2–4 about 1.5–1.6, 1.2–1.3, 1.1 mm long; apex of rostrum lying between metacoxae.



Figs. 177–185. Figs. 177–180. *A. teretis.* 177. Pygophore, ventral view. 178. Pygophore, caudal view. 179. Genital cup. 180. Paramere. Figs. 181–185. *A. musivum.* 181. Basal plates, caudal view (BP). 182. Pygophore, ventral view. 183. Pygophore, caudal view. 184. Genital cup. 185. Paramere.

Pronotum 7.5–7.7 mm wide at humeri, 2.7–2.9 mm long at meson. Humeri narrowly rounded, somewhat produced laterad. Anterolateral margins nearly straight or weakly convex.

Scutellum 4.3–4.6 mm wide at base, 4.8–5.1 mm long, without markings.

Abdominal tubercle somewhat compressed, terminating between metacoxae. Ostiolar ruga on each side extending 0.6–0.7 distance from mesial margin of ostiole to lateral thoracic margin.

Female unknown.

Posterior wall of genital cup extremely produced on each side as flat protuberance curving dorsolaterad, projecting above tergum; concave dorsal rim next to lateral wall denticulate (Figs. 177–179). Parameres projecting past posterior margin of pygophore, spatulate apically (Fig. 180).

Length about 12–13 mm.

Distribution. Colombia.

Holotype. ♂, labeled (a) "Colombia; Sierra Nevada de Santa Marta, San Sebastian de Rabago, 2000 m. April 1–14, 1968" (b) "Borys Malkin, Collector." Deposited in American Museum of Natural History.

Paratype. ♂, labeled as holotype (LHR).

Acrosternum (*Chinavia*) *musivum* (Berg, 1878)
(Figs. 181–185)

Nezara musiva Berg, 1878, pp. 26–27; Berg, 1879, pp. 56–57 (reprint).
Acrosternum musiva: Pirán, 1948, p. 9 (record); Pirán, 1963, p. 337 (record); Grazia-Vieira and Casini, 1973, p. 58 (record).

Diagnosis. Connexival segments bordered both anteriorly and posteriorly with black; some or all femora with preapical black band, this often incomplete or fragmented; dorsum variously marked with black macules and vermiform punctate lines. Apex of scutellum reflexed. Humeral angles rounded, little produced laterad. Abdominal tubercle not or barely reaching metacoxae. Spiracles black, each in posterolateral edge of prominent yellowish callus. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral thoracic margin. Apex of rostral segment 3 lying between metacoxae, apex of last segment on sternite 4 (3rd visible). Cicatrices at least partially black bordered. Large yellowish or green basal callus located beside each basal angle of scutellum. Many dorsal punctures clustered or in transverse vermiform lines, these areas of aggregate punctures usually black. Posterior margin of basal plates emarginated from caudal view at mesial margin of 9th paratergites (Fig. 181). Male genitalia as in Figures 182–185. Posterior wall of genital cup on each side reduced to stout hook, this bent anterolaterad at apex and denticulate along lateral margin (Figs. 183, 184). Length about 10.5–13 mm.

Distribution. Argentina, Uruguay.

Type. The holotype is preserved at Universidad de La Plata.

Comments. Black borders on both sides of the transverse connexival sutures for the entire width of the connexivum coupled with preapical black femoral bands are diagnostic. The holotype was examined.

Acrosternum (*Chinavia*) *rogenhoferi* (Stål, 1872), **New Combination**
(Figs. 186–190)

Nezara rogenhoferi Stål, 1872, pp. 40–41.

Diagnosis. Both anterior and posterior borders of connexival segments broadly black bordered; anterior margin of humeri bordered in black, remainder of outer pronotal borders orange-yellow; large yellowish macule at base of scutellum on each side located about midway between lateral angles and meson; femora black apically, otherwise green. Humeri rounded, little or not produced laterad. Abdominal tubercle barely reaching between metacoxae. Coria bearing many irregular pale green calli. Spiracles black, unattended by callus. Ostiolar ruga on each side extending from mesial ostiolar margin 0.65–0.85 distance to lateral thoracic margin. Cicatrices black bordered posteriorly. Basal angles of scutellum immaculate. Dorsal punctation dense, rather regularly distributed. Posterior margin of basal plates from caudal view forming shallow V (Fig. 186). Male genitalia as in Figures 187–190. Posterior wall of genital cup dorsally diagonal; dorsal rim slightly convex and denticulate caudad of moderate sized bent tooth at anterolateral corner (Figs. 188, 189). Length about 12.5 mm.

Distribution. Southern Brazil.

Comment. This species is easily recognized by the broad, colored border along the anterolateral pronotal margins. This border is black at the humeri and otherwise orange-yellow.

Acrosternum (*Chinavia*) *erythrocnemis* (Berg, 1878)
(Figs. 191–195)

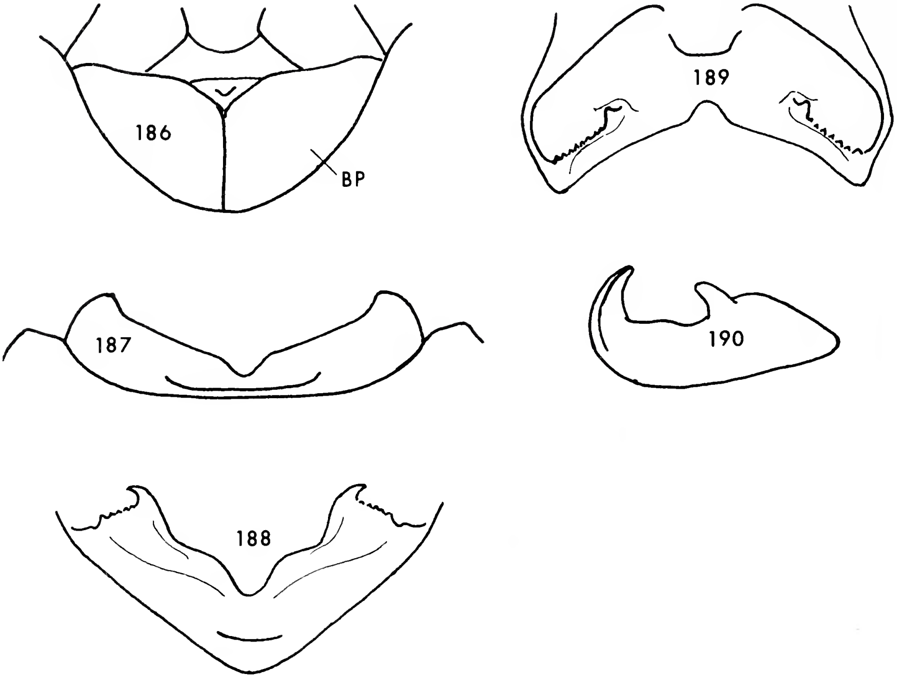
Nezara erythrocnemis Berg, 1878, pp. 27–28; Berg, 1879, pp. 57–58 (reprint).
Acrosternum erythrocnemis: Pirán, 1966, p. 87 (records).

Diagnosis. Connexival segments bordered anteriorly and posteriorly with black; distal end of femora and at least proximal end of tibiae crimson; outer border of head crimson, remaining outer border of body yellowish. Humeri rounded, not produced. Abdominal tubercle compressed, reaching between metacoxae. Spiracles pale, narrowly ringed with fuscous, not attended by callus. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral thoracic margin. Rostrum reaching or somewhat surpassing posterior limit of metacoxae. Cicatrices partially bordered in black, sometimes entirely black. Basal scutellar angles black. Dorsal punctation dense, punctures concolorous with surrounding area. Basal plates subtriangular, their posterior margin from caudoventral view forming nearly straight line between rounded lateral angles. Spermatheca as in Figure 191. Male genitalia as in Figures 192–195. Posterior wall on each side of genital cup an obtuse projection with concave anterolateral face and finely denticulate lateral rim (Figs. 193, 194). Length about 11.5–14.5 mm.

Distribution. Southern Brazil, northern Argentina, Uruguay.

Type. The holotype is conserved in the Universidad Nacional de La Plata.

Comments. Of the few species with the transverse connexival suture bordered with black on both sides for at least half the width of the connexivum, only this species has the femora and tibiae marked with crimson as indicated. The holotype was examined.

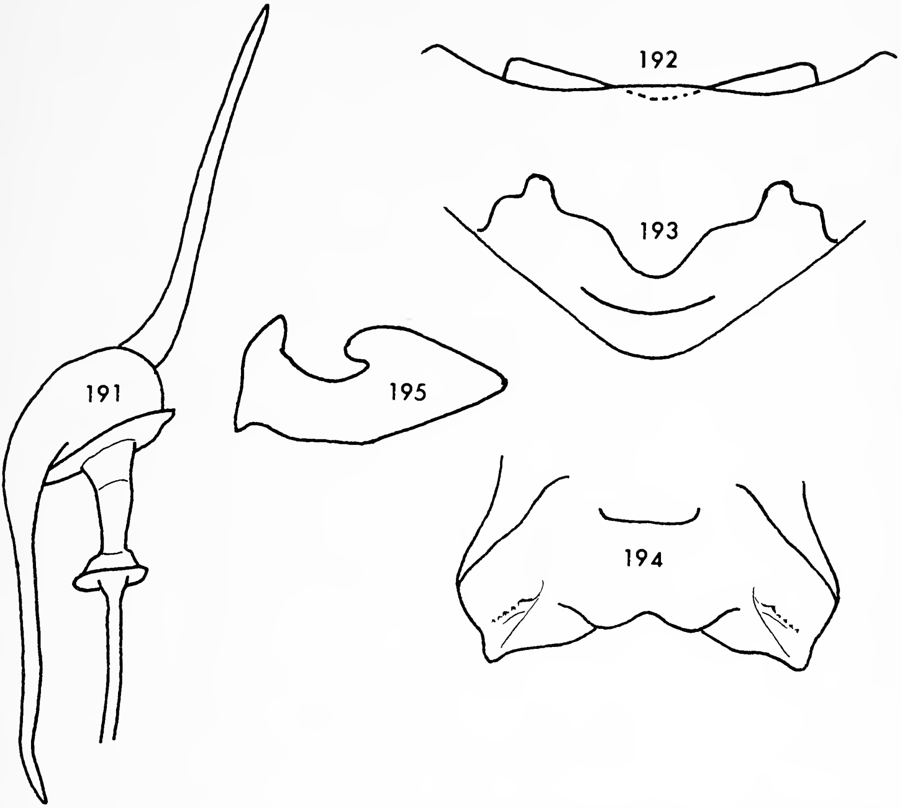


Figs. 186–190. *A. rogenhoferi.* 186. Basal plates, caudal view (BP). 187. Pygophore, ventral view. 188. Pygophore, caudal view. 189. Genital cup. 190. Paramere.

Acrosternum (*Chinavia*) *runaspis* (Dallas, 1851)
(Figs. 196–200)

Rhaphigaster runaspis Dallas, 1851, p. 280 (keyed).
Nezara runaspis: Stål, 1872, p. 43 (listed).
Acrosternum runaspis: Becker and Grazia-Vieira, 1977, pp. 54–55 (descriptive note, record); Froeschner, 1981, p. 68 (catalog).

Diagnosis. Both anterior and posterior borders of connexival segments black, dorsum otherwise devoid of black; venter (excluding appendages) with black only as small macules at base of antennifers and both anterior and posterior lateral angles of sternites. Legs green. Humeri rounded, not produced. Abdominal tubercle compressed, reaching between metacoxae. Spiracles pale, unaccompanied by callus. Ostiolar ruga reaching about 0.7 distance from mesial margin of ostiole to lateral thoracic margin. Rostral apex lying between metacoxae. Dorsal punctation dense, fine, green. Posterior margin of basal plates from caudoventral view transverse between rounded lateral angles, rounded dorsoventrally, rather thick from caudal view. Spermatheca as in Figure 196. Male genitalia as in Figures 197–200. Posterior



Figs. 191–195. *A. erythrocnemis.* 191. Spermathecal bulb and pump. 192. Pygophore, ventral view. 193. Pygophore, caudal view. 194. Genital cup. 195. Paramere.

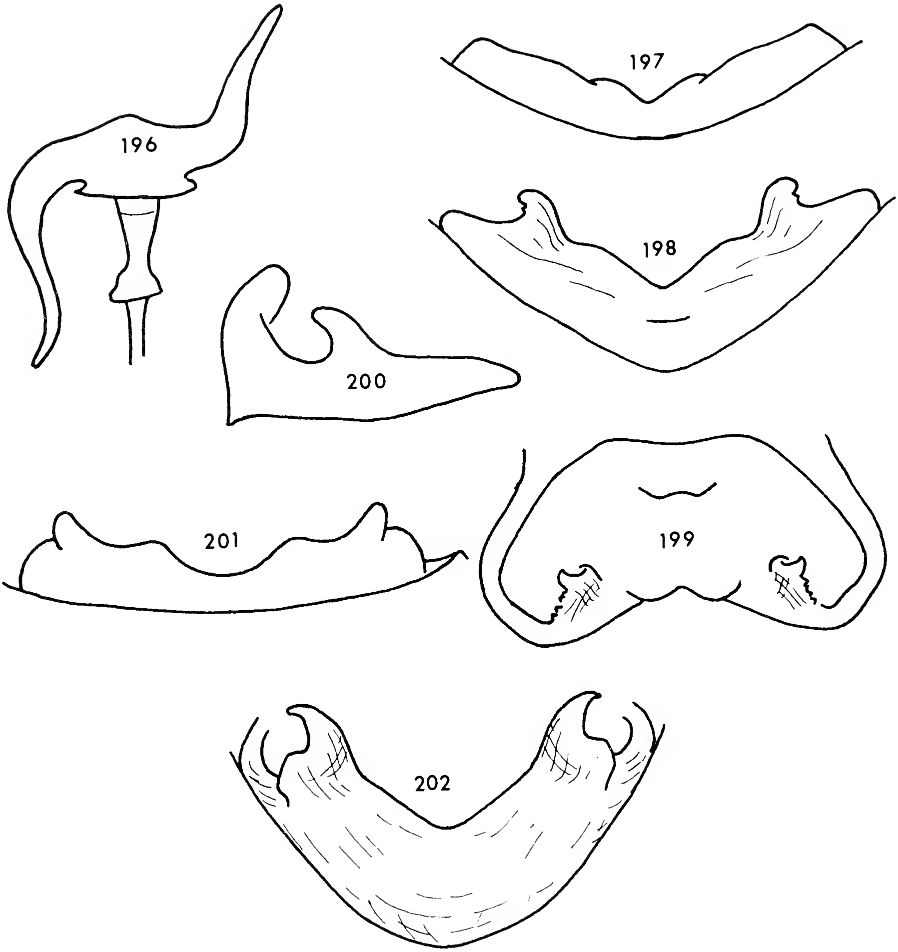
wall of genital cup dorsally diagonal on each side with tooth at anterior angle bent anterolaterad and small black denticles along concave dorsal rim (Figs. 198, 199). Length about 15–18.5 mm.

Distribution. Argentina (Misiones), Brazil (Bahia, Pará, Mato Grosso, Santa Catarina, São Paulo), Colombia, Ecuador, French Guiana, Paraguay, Peru (Loreto).

Comment. The type was examined.

Acrosternum (Chinavia) plaumanni, new species
(Figs. 201, 202)

Description. Dark green above; yellowish green below, especially on thoracic sterna and abdomen. Outer margins narrowly bordered with orange-yellow, diffusing mesad along transverse connexival sutures; apex of scutel-



Figs. 196–202. Figs. 196–200. *A. runaspis.* 196. Spermathecal bulb and pump. 197. Pygophore, ventral view. 198. Pygophore, caudal view. 199. Genital cup. 200. Paramere. Figs. 201, 202. *A. plaumanni.* 201. Pygophore, ventral view. 202. Pygophore, caudal view.

lum similarly colored. Connexival segments narrowly bordered posteriorly with black. Spot at base of antennifers on superior surface and spiracles black, latter in posterolateral edge of paler green subcalloused spot. Cicatrices, basal angles of scutellum and lateral angles of sternites immaculate. Antennae green with distal half or somewhat less of last 3 segments fuscous to black. Legs apparently green (discolored in holotype). Dorsal punctation dense, fine, green.

Head 2.7 mm wide across eyes, 2.3 mm long. Antennal segments 0.5, 1.1, 1.5, 2.1, 2.0 mm long. Rostral segments 2–4 about 1.6, 1.3, 1.0 mm long; rostrum reaching posterior limit of metacoxae.

Pronotum 6.7 mm wide at humeri, 2.5 mm long at meson. Humeri rounded, slightly produced laterad. Anterolateral margins of pronotum straight.

Scutellum 4.3 mm wide at base, 4.5 mm long.

Abdominal tubercle apically obtuse, scarcely reaching metacoxae. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral thoracic margin.

Female unknown.

Pygophore incised narrowly between posterior and lateral walls of genital cup (Figs. 201, 202). Posterior wall of genital cup on each side with diagonal orientation dorsally; anteromesial corner developed as large tooth bent laterad; dorsal rim concave, roughened but without apparent denticles.

Length about 11.6 mm.

Distribution. Ecuador (Pastaza). Known only from holotype.

Holotype. ♂, labeled "Ecuador, Pastaza, Ashuara Village on Rio Macuma, 10 km from Rio Morona, 300 m. July 5–16, 1971. B. Malkin." Deposited in the American Museum of Natural History.

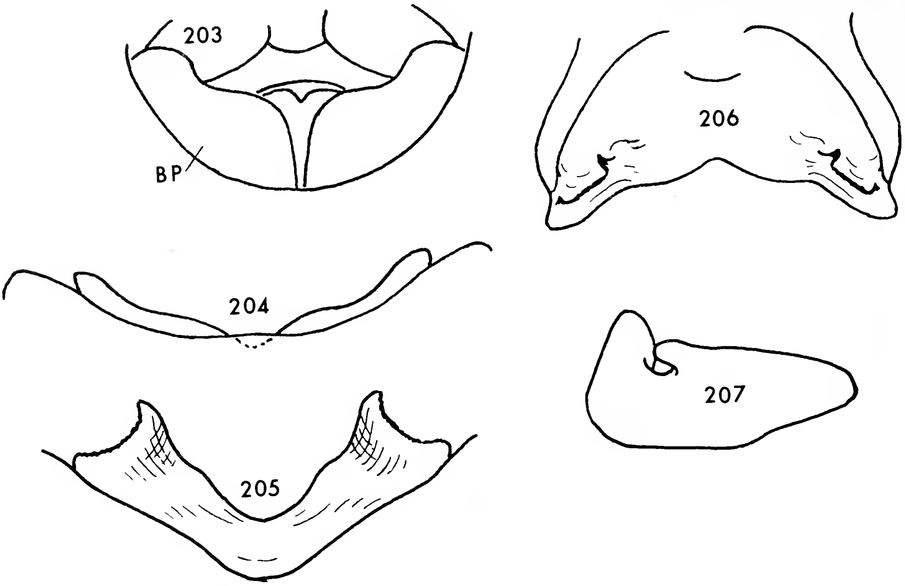
No paratypes.

Comment. This species is dedicated to Fritz Plaumann, whose industry in collecting over many years has made the insect fauna of Santa Catarina the best known in South America.

Acrosternum (*Chinavia*) *dallasi* (Distant, 1900)
(Figs. 203–207)

Rhaphigaster marginatus: Dallas, 1851, p. 277 (misdetermination).
Nezara marginata: Stål, 1872, p. 43 (listed).
Nezara dallasi Distant, 1900, p. 392.
Nezara (*Acrosternum*) *dallasi:* Kirkaldy, 1909, p. 118.
Acrosternum dallasi: Rolston, 1976, p. 3 (generic placement).

Diagnosis. Yellowish green above with head, anterior disk of pronotum, base of scutellum and median broad line thereon, connexiva excepting border entirely or predominantly tan; venter and legs mostly tan or entirely green except as noted below. Posterior margin of connexival segments narrowly black bordered. Humeral angles rounded, little produced laterad. Abdominal spine compressed, subacute apically, reaching between metacoxae. Spiracles black, unaccompanied by callus. Ostiolar ruga on each side extending about three-fourths of distance from mesial margin of ostiole to lateral thoracic margin. Rostrum terminating near posterior limit of metacoxae. Cicatrices with small black macule at mesial and lateral limits. Basal angle of scutellum marked with black foveate spot. Dorsal punctation dense, color of punctures similar to surrounding area. Posterior margin of basal plates from caudal



Figs. 203–207. *A. dallasi.* 203. Basal plates, caudal view (BP). 204. Pygophore, ventral view. 205. Pygophore, caudal view. 206. Genital cup. 207. Paramere.

view bent dorsad near lateral angle, fitting into concavity of 9th paratergites (Fig. 203). Posterior walls of genital cup dorsally diagonal on each side; dorsal rim concave, roughened, anteromesial corner bearing small tooth directed anterolaterad (Figs. 205, 206). Little of pygophore exposed from ventral view (Fig. 204). Length about 10.5–14 mm.

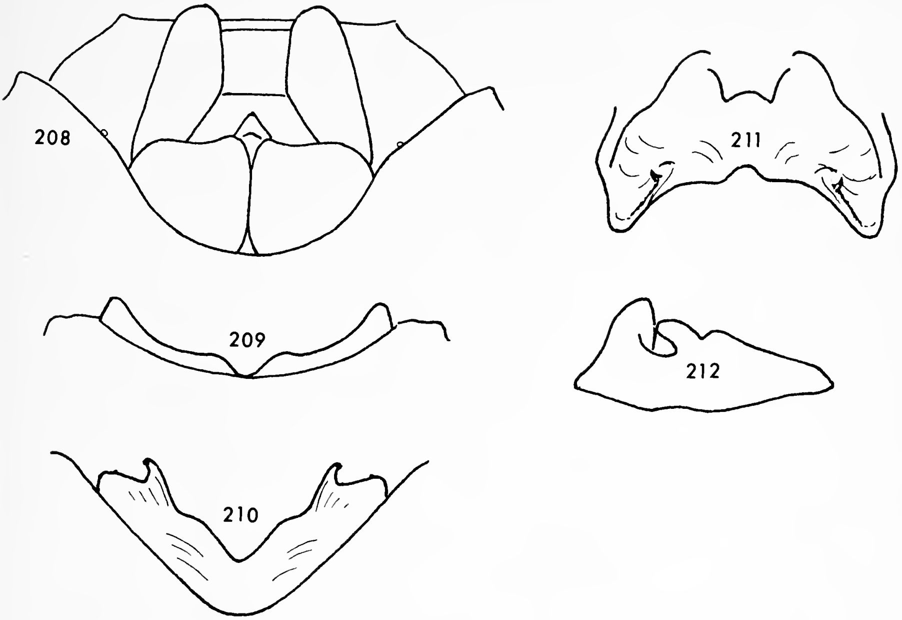
Distribution. Brazil (Goiaz, Minas Gerais), Colombia.

Type. Described from 2 specimens, only one of which was located and is here designated LECTOTYPE: ♀, labeled (a) "Type" (b) "*Rhaphigaster marginatus*" (c) "b."

Acrosternum (*Chinavia*) *bipunctulum* (Stål, 1872)
(Figs. 208–212)

Nezara (*Acrosternum*) *bipunctula* Stål, 1872, p. 42.

Diagnosis. Humeri rounded, not produced laterad. Abdominal tubercle compressed, reaching posterior limit of metacoxae. Connexival segments narrowly bordered posteriorly with black. Spiracles black, on weak sometimes yellow callus. Ostiolar ruga on each side extending about 0.55 to 0.65 distance from mesial margin of ostiole to lateral margin of thorax. Small black spot present at mesial limit of cicatrices, another often present at lateral limit of cicatrices and at basal angles of scutellum. Basal plates weakly convex, posterior margin slightly concave near mesial angle (Fig. 208). Male



Figs. 208–212. *A. bipunctulum.* 208. Genital plates, caudoventral view. 209. Pygophore, ventral view. 210. Pygophore, caudal view. 211. Genital cup. 212. Paramere.

genitalia as in Figures 209–212. Posterior wall of genital cup on each side diagonal dorsally, dorsal rim concave, weakly denticulate, terminating anteriorly in stout curved denticle directed anterolaterad (Figs. 210, 211).

Length about 10–12.5 mm.

Distribution. Brazil (Bahia, Ecuador, Peru (Amazonas).

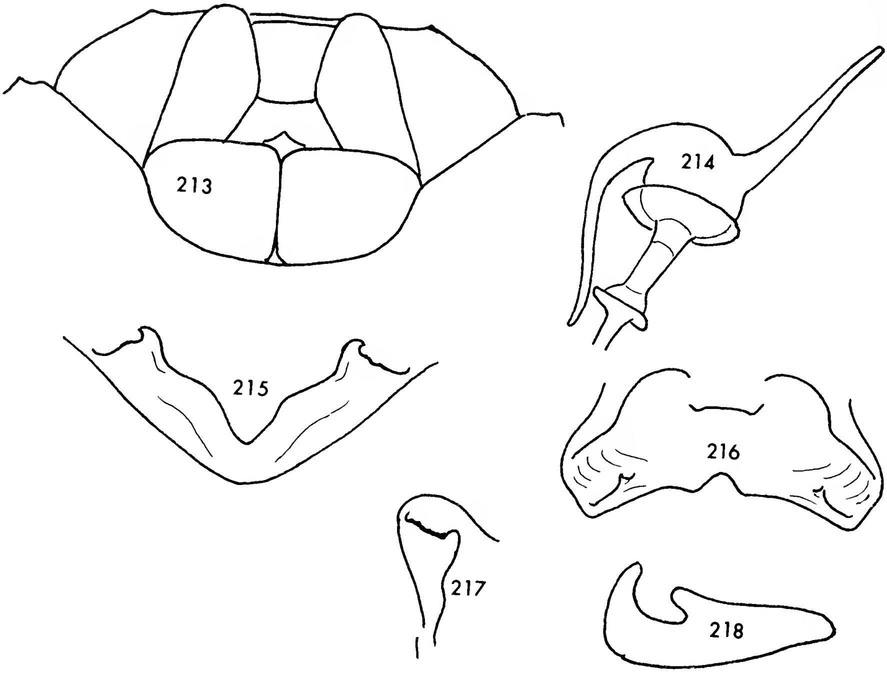
Types. Lectotype, here designated, ♀, labeled (a) "Bahia" (b) "Lindg" (c) "Type" (d) "Allotypus" (e) "111/79" (f) "Riksmuseum Stockholm". Paralectotype, here designated, ♂ with pygophore missing, labeled (a) "Bahia" (b) "Type" (c) "Typus" (d) "112/79" (e) "Riksmuseum Stockholm".

Comment. An occasional specimen of *A. laetum* has connexival markings like *A. bipunctulum* and a dark dot at the mesial limits of the cicatrices as well. Such specimens may be recognized by the well developed callus around each spiracle, yellowish macules along the base of the scutellum, and the posterior margin of the basal plates or outline of the pygophore from a caudal view.

Acrosternum (*Chinavia*) *impicticorne* (Stål, 1872)
(Figs. 213–218)

Nezara (*Acrosternum*) *impicticornis* Stål, 1872, p. 42.

Nezara vicina Berg, 1892, pp. 8–9; Pirán, 1963, p. 337 (record) (synonymized by Grazia, 1980).

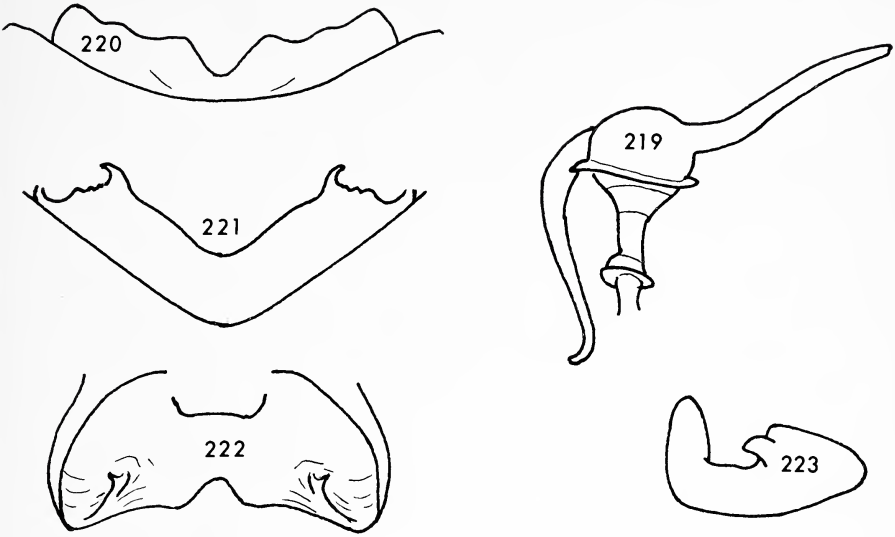


Figs. 213–218. *A. impicticorne.* 213. Genital plates, caudoventral view. 214. Spermathecal bulb and pump. 215. Pygophore, caudal view. 216. Genital cup. 217. Posterior wall, left side, dorsomesial view. 218. Paramere.

Acrosternum impicticorne: Grazia, 1977, p. 163 (records); Grazia, 1980, p. 234, fig. 1 (lectotype designated).

Diagnosis. Humeri rounded, not produced laterad. Abdominal tubercle reaching posterior limit of metacoxae, its anterior margin subvertical. Each connexival segment narrowly bordered in black posteriorly; black spot present in posterolateral angles of sternites. Area about each spiracle weakly calloused, not strongly differentiated by color; peritremes usually pale, rarely thinly circled with black. Ostiolar ruga on each side extending about three-fourths distance from mesial margin of ostiole to lateral margin of thorax. Small black spot usually present at basal angles of scutellum, another often present at mesial limit of cicatrices and occasionally at lateral limits also. Posterior margin of basal plates nearly transverse mesad of lateral angles from caudoventral view (Fig. 213); dorsal edge of basal plates transverse from caudal view. Spermatheca as in Figure 214. Male genitalia as in Figures 215–218. Posterior wall of genital cup diagonal dorsally with dorsal rim finely and irregularly denticulate, bearing large denticle anteriorly.

Distribution. Argentina, Paraguay, Brazil, Peru, Ecuador, Surinam, Colombia.



Figs. 219–223. *A. herbidum.* 219. Spermathecal bulb and pump. 220. Pygophore, ventral view. 221. Pygophore, caudal view. 222. Genital cup. 223. Paramere.

Types. One syntype of *N. impicticornis* lacks the dark spot in the basal angles of the scutellum, and this spot is faint in the other syntypes.

Comments. Dr. J. Grazia first called my attention to the synonymy of *N. impicticornis* and *N. vicina.*

In all but one of the 61 specimens examined, other than the syntypes of *N. impicticornis,* the scutellar spots are quite clear. The occasional specimen lacking the scutellar spots will run to *A. pengue* in the key, but it will not agree with this species in genitalia or markings at the incisures of the abdominal venter.

The type of *N. vicinia* as well as the syntypes of *N. impicticornis* were examined.

Acrosternum (*Chinavia*) *herbidum* (Stål, 1859)
(Figs. 219–223)

Rhaphigaster herbidus Stål, 1859, p. 229.

Nezara (*Acrosternum*) *herbida:* Stål, 1872, p. 42 (keyed).

Nezara herbida: Berg, 1878, p. 28 (reprinted 1879, p. 58); Berg, 1883, pp. 212–213 (description; reprinted 1884, pp. 28–29); Berg, 1892, p. 6 (description).

Acrosternum herbida: Ruffinelli and Pirán, 1959, p. 11.

Acrosternum herbidus: Grazia, 1980, p. 236, fig. 2 (lectotype designated).

Diagnosis. Humeri rounded, not produced laterad. Abdominal tubercle reaching between metacoxae to anterior limit of trochanters, rarely just past metacoxae. Connexival segments bordered posteriorly with black, border sometimes incomplete but covering lateral half of at least some segments. Spiracles pale, surrounding area weakly or not calloused and concolorous with adjacent part of sternites. Ostiolar ruga on each side extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax. Neither pronotum nor scutellum marked with black. Dorsal border on outer margins absent or inconspicuous, narrow, pale yellow. Anterolateral margins of pronotum weakly convex. Posterior margin of basal plates from caudoventral view nearly straight excepting lateral angles. Spermatheca as in Figure 219. Male genitalia as in Figures 220–223. Dorsal rim of posterior wall of genital cup diagonally oriented from dorsal view, anteriorly bearing large denticle curving anterolaterad and posteriorly small denticles.

Distribution. Argentina, Brazil, Peru, Surinam.

Comments. The syntypes were examined.

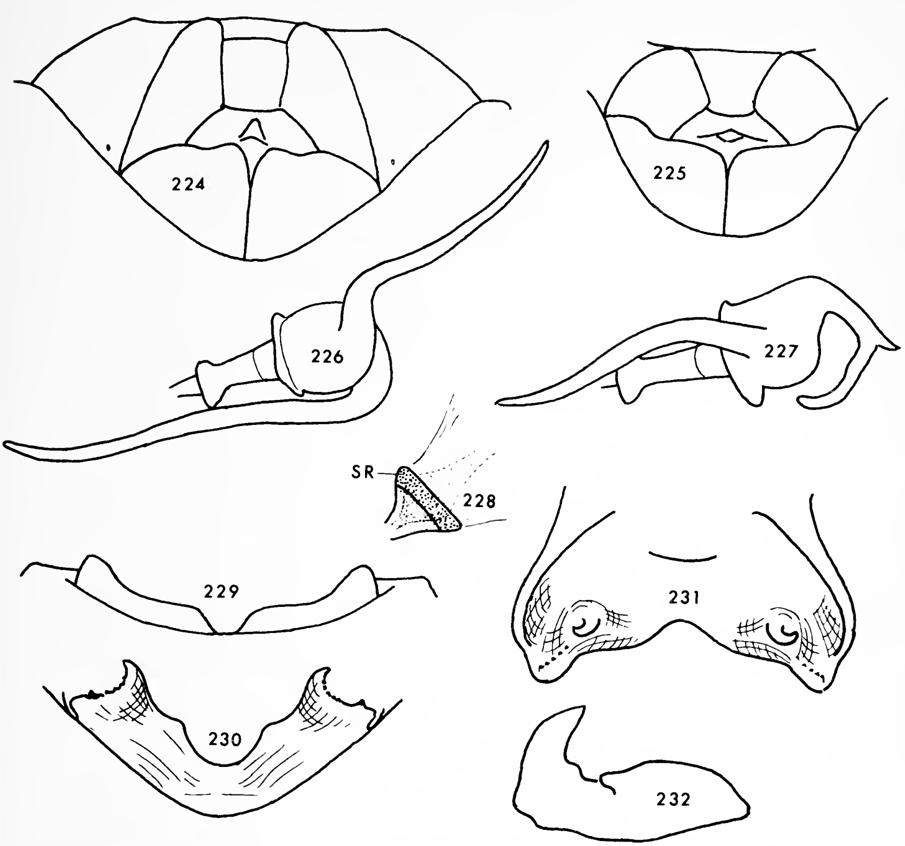
Dr. P. H. Van Doesburg called my attention to an apparently consistent difference in the pygophore of specimens from the north–south extremes of this species' range. In the south, the genital cup rim is infolded near the posterolateral corners. These projections, which vary in size and shape, have a finely denticulate and usually infuscated edge. In the north, the genital cups is unelaborated at these corners (Fig. 222). Whether this difference indicates variation, subspecies or sibling species cannot be determined from the material available to me. I have taken the conservative course, treating the difference as interspecific and geographically undefined variation.

A. herbidum and *A. occultum,* the latter known only from females, seem indistinguishable excepting the shorter abdominal spine in *A. herbidum.*

Acrosternum (Chinavia) pengue, new species
(Figs. 224–232)

Description. Light green above and below with narrow crimson border along outer margins. Posterior margins of connexival segments narrowly black bordered, this band continuing onto sternites about halfway to spiracular line. An elongated black macule present at base of antennifers on superior surface. Occasionally dark mark present at mesial limit of cicatrices, less frequently at lateral limit as well. Basal angles of scutellum immaculate. Antennae dark green. Legs pale green with rufous tint. Spiracles green to brown; area around spiracles sometimes paler, not or weakly calloused.

Head 2.6–2.9 mm wide across eyes, 2.0–2.3 mm long. Antennal segments 0.5–0.6, 0.9–1.1, 1.2–1.4, 1.3–1.8, 1.8–2.1 mm long. Rostral segments 2 through 4 about 1.4–1.7, 1.1–1.2, 0.9–1.1 mm long; rostrum reaching between metacoxae.



Figs. 224–232. *A. pengue.* 224. Genital plates, caudoventral view. 225. Same, caudal view. 226. Spermathecal bulb and pump. 227. Abnormal spermathecal bulb. 228. Proximal end of dilation of spermathecal duct; sclerotized ring (SR). 229. Pygophore, ventral view. 230. Pygophore, caudal view. 231. Genital cup. 232. Paramere.

Pronotum 6.6–7.6 mm wide at humeri, 2.6–3.1 mm long at meson. Humeri rounded, not or barely produced laterad; a short line on anterolateral edge black. Anterolateral margins of pronotum slightly convex.

Scutellum 4.2–5.0 mm wide at base, 4.7–5.6 mm long.

Abdominal tubercle compressed, reaching between metacoxae. Ostiolar ruga extending about 0.7 distance from mesial margin of ostiole to lateral margin of thorax. Posterior margin of basal plates slightly concave mesad of 9th paratergites from caudoventral view (Fig. 224), strongly concave from caudal view (Fig. 225). Spermatheca as in Figure 226. A sclerotized ring present at base of spermathecal dilation (Fig. 228).

Male genitalia as in Figures 229–232. Posterior wall of genital cup dorsally diagonal on each side; dorsal rim concave, denticulate with large tooth at anteromesial end and smaller tooth posterolateral end.

Length about 10–13 mm.

Distribution. Argentina (Misiones) and Brazil (Santa Catarina).

Holotype. ♂, labeled "Brasilien, Nova Teutonia. 27° 11′B, 52° 23′L, Fritz Plaumann", on one edge "10 I 1942", on other edge "300–500 M". Deposited in American Museum of Natural History.

Paratypes. 8♂♂, 7♀♀, same data as holotype except dates "I-1976" (♂ USNM), "VI-1975" (2♂♂ LHR), "XII-1975" (♂, ♀ LHR); "Eldorado, Misiones, Argentina", "4-IX-1967" or "16-IX-1967" (3♂♂ AMNH); "Misiones, Argentina" (♂ RNH); "Argentina, Eldorado, Misiones, X-15-1964, A. Kovacs" (♀ AMNH); as preceding except date "IX-16-1964" (♀ AMNH); "Museum Leiden, Argentina, Dos de Mayo, Prov. Misiones, XII-1964, F. H. Walz" (♀ RNH); "Museum Leiden, Argentina, Misiones, Loreto, IX-1955, F. H. Walz" (3♀♀ RNH).

Comment. An anomalous condition consisting of a bifurcate spermathecal diverticulum was found in one specimen (Fig. 227).

An occasional specimen *A. impicticorne* which lacks the black spot in the basal angles of the scutellum will key to *A. pengue.* However, the genitalia and markings at the incisures of the abdominal venter distinguish such specimens from *A. pengue.*

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PATHOGENICITY OF THE FUNGUS *ENTOMOPHTHORA CULICIS* FOR ADULT MOSQUITOES: *ANOPHELES STEPHENSI* AND *CULEX PIPIENS QUINQUEFASCIATUS*

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Abstract.—The pathogenicity of *Entomophthora culicis* for the mosquitoes *Anopheles stephensi* and *Culex pipiens quinquefasciatus* was determined by exposing healthy adults to conidial showers from cadavers of naturally infected *Chironomus decorus* and from cultures grown *in vitro.* While 100 percent of the *A. stephensi* succumbed to infection, only 20 percent of the *C. pipiens quinquefasciatus* did so. Explanations for these differences are suggested. Some morphological characteristics of the *E. culicis* used in this study are presented.

Adult *Aedes aegypti* exposed to conidia of the fungus *Entomophthora culicis* originating from field-collected cadavers of the midge *Chironomus decorus* or from experimentally infected *A. aegypti* or from yolk cultures can develop a fatal mycosis (Kramer, 1982). The present study extends our understanding of this fungus and its disease-causing abilities in two more medically important mosquito species; namely, *Anopheles stephensi* and *Culex pipiens quinquefasciatus.* The former is an important vector of malarial parasites from the middle East to India while the latter is a principal developmental host of the filarial worm *Wuchereria bancrofti* in Southeast Asia (Harwood and James, 1979).

MATERIALS AND METHODS

Sources of conidia. E. culicis conidia from two sources were used in this study. These were field-collected cadavers of naturally infected adult *Chironomus decorus* found in Ithaca, New York and mycelial mats produced from conidia discharged from *C. decorus* cadavers onto the egg-yolk medium of Müller-Kögler (1959). Fresh whole cadavers were placed on 1.5 percent water agar in small plastic dishes to promote the development of the fungus. The discharge of conidia commenced within 24 hours. Small chunks of mycelial mats taken from yolk cultures, 7 to 10 days old, were also placed on water agar. The discharge of conidia from these chunks usually began

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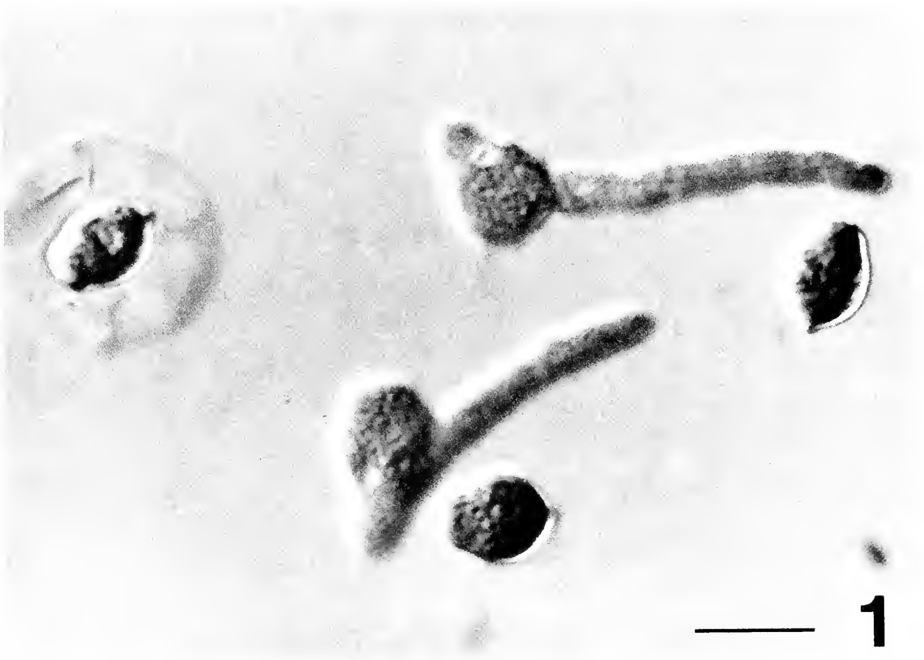

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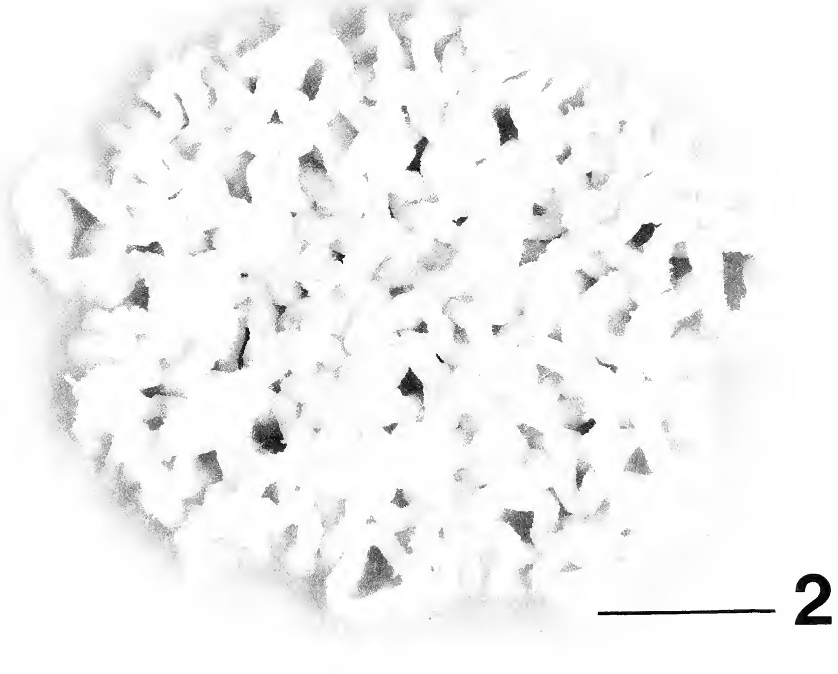

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within 48 hours. Dishes containing cadavers or chunks of mats were held at 20 ± 2°C in closed chambers containing moist filter paper.

Testing procedures. Adult mosquitoes 24 to 48 hours old from disease-free insectary cultures were placed in cylindrical transparent plastic cages (height 35 mm, width 30 mm), having two large mesh-covered windows and mesh-covered tops and bottoms. A small plastic dish containing water agar with several cadavers or chunks of mycelial mats was inverted over each cage to allow the conidia being discharged to fall through the mesh-covered top into the cage of mosquitoes. These cages with dishes were housed in glass battery jars containing a layer of wet sand. The jars, tightly closed with polyethylene wrap, were held in cabinets at 20 ± 2°C with an 18:6 photoperiod. After 48 hours the mosquitoes were transferred to glass-covered carton cages provisioned with bottles of a 3 percent sucrose solution. These cages, held at 20 ± 2°C with an 18:6 photoperiod, were checked daily for dead mosquitoes. The dead ones were placed on water agar and examined for external growth of *E. culicis* at irregular intervals up to 48 hours. Only those cadavers that produced a bloom of *E. culicis* on their exteriors by the 48th hour, were scored as infected. Female and male mosquitoes were present in equal numbers in each test group. No attempt was made to determine whether one sex or the other was more susceptible because of the small numbers of individuals used in each test.

RESULTS AND DISCUSSION

Representative conidia of the *E. culicis* used in this study are depicted in Figure 1. The binucleate primary conidia are broadly ellipsoidal with a papillate apex and a flattened base. Their size depends upon the substrate from which they developed. Those discharged from cadavers were about 14 to 16 by 10 to 11 μm, while those produced *in vitro* were consistently larger, measuring about 17 to 19 by 12 to 15 μm. In both shape and size these primary conidia are virtually identical to the *E. culicis* conidia described by Gustafsson (1965) and others (see MacLeod et al., 1976). The primary conidium produces a binucleate secondary conidium which is ovoid with a rounded apex; such conidia range in size from 11 to 14 by 8 to 11 μm. Secondary conidia produced one to four long germ tubes which are sometimes branched. Tertiary conidia were not observed. Conidia discharged

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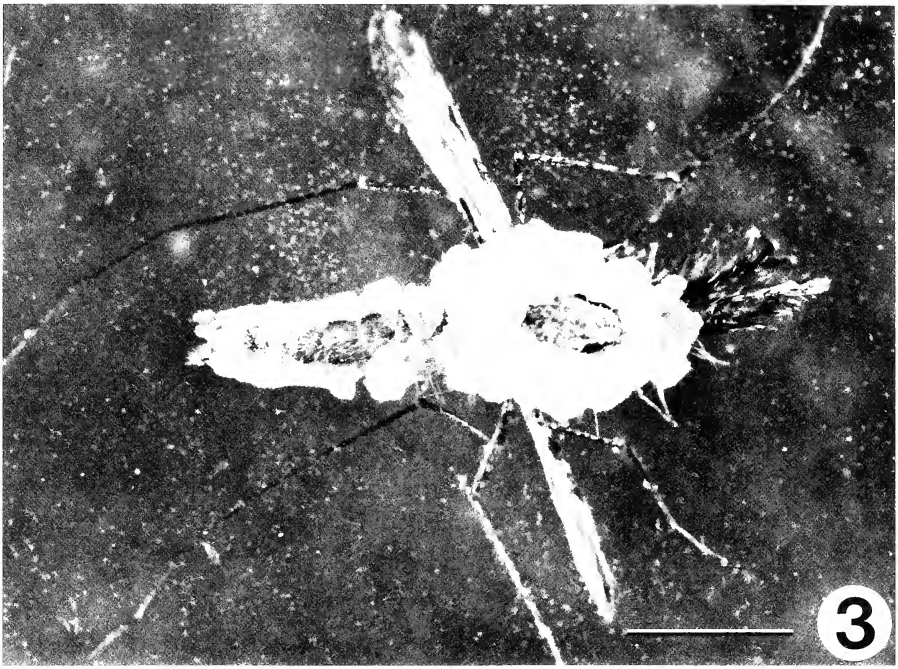
Figs. 1, 2. Fig. 1. Conidia of *Entomophthora culicis.* Note primary conidium surrounded by protoplasmic layer (at left), two secondary conidia with long germ tubes, and two primary conidia without protoplasmic layer. Bar equals 15 μm. Fig. 2. *In vitro* culture of *Entomophthora culicis* showing its typically convoluted growth pattern. Bar equals 0.75 mm.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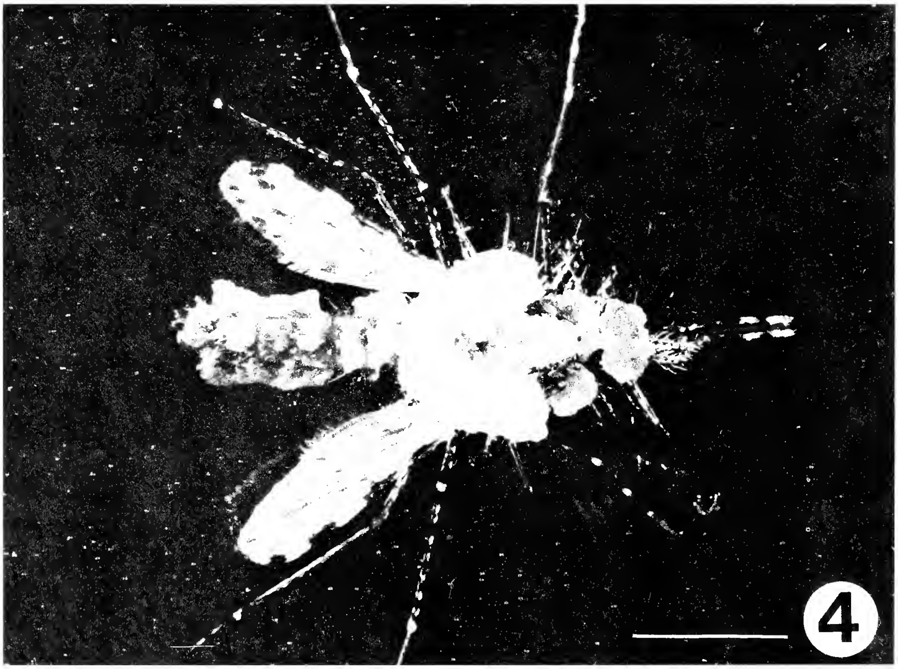
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Table 1. Mortality at post-inoculation day 6 among adult mosquitoes experimentally infected with *Entomophthora culicis.*

	Sources of conidia		
Species of mosquito	*Chironomus decorus* cadavers	Egg-yolk cultures	Both sources
Anopheles stephensi	100% (18/18)	100% (33/33)	100% (51/51)
Cx. p. quinquefasciatus	11% (4/38)	8% (2/26)	9% (6/64)

onto yolk agar produce glassy, greyish-white cerebriform colonies in 10 days to two weeks at 20 ± 2°C (Fig. 2). Chunks of these colonies placed on water agar generally developed a velvety hymenium after 24 to 48 hours.

Test mosquitoes and E. culicis. The post-mortem appearance of mosquitoes that succumbed to an *E. culicis* infection is shown in Figures 3 and 4. The fungal outgrowths so prominent on these cadavers occur only when the dead mosquito rests upon a moist surface. In nature midges with fatal *E. culicis* infections seek out shaded moist surfaces on which to die and thereby contribute to the survival and perpetuation of the agent responsible for their deaths (Kramer, 1981). It is conceivable that this pattern of behavior would also occur among mosquitoes with *E. culicis* infections in nature.

The results of the infectivity tests indicate that adults of both mosquito species are susceptible to infection by *E. culicis* (Table 1). The relative susceptibilities of these two hosts are, however, quite different. While 100 percent of the *A. stephensi* succumbed to infection by the end of post-inoculation day 6, only about 9 percent of the *C. p. quinquesfasciatus* had done so in this time period. By post-inoculation day 10 mortality in the *Culex* group reached about 20 percent; many adults in this group lived for more than 10 days but never developed the mycosis. The observed differences in susceptibility may be attributed in part to the fact that *A. stephensi* is the smaller and more delicate of the two species at risk. *A. stephensi* may also be less efficient in dislodging conidia during the grooming process. Whether conidia originated from a cadaver or from an artificial substrate did not alter their relative ability to fatally infect host mosquitoes (Table 1). The time of death of infected *Anopheles* ranged from 3 to 6 days with 50 percent dying on day 3 (Table 2). For the *Culex* that became infected the

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Figs. 3, 4. Cadavers of *Anopheles stephensi* displaying post-mortem changes caused by *Entomophthora culicis.* 1. Male with typical wreath-like growth of fungus surrounding the thorax. Bar equals 2.5 mm. 2. Female with atypical crescent-like growth around posterior part of the thorax. Bar equals 3.0 mm.

Table 2. The temporal distribution of deaths among adult mosquitoes dying of the mycosis caused by *Entomophthora culicis.*

Species of mosquito	Number infected	Post-inoculation days of death* 1–2	3	4	5	6	7	8	9	10	11–30
Anopheles stephensi	(50)	0	50	8	18	24	0	0	0	0	0
Cx. p. quinquefasciatus	(24)	0	0	0	25	8	42	0	17	8	0

* Daily distribution in percentages.

time of death ranged from 5 to 10 days with 50 percent mortality occurring by day 7 (Table 2). If these patterns of mortality took place in nature, they would enhance the pathogen's chances for survival by keeping a supply of fresh conidia in the habitat of potential hosts over a period of several days.

In his review of methods for the mass production of *E. culicis* and other pathogens, Nolan (1981) suggests that this fungus may find place in the applied control of black flies. His conjecture can be expanded to include mosquitoes as well.

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THE GENUS *PARALINCUS* (HEMIPTERA: PENTATOMIDAE)

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Abstract.—The genus *Paralincus* is diagnosed, the type species redescribed and the species keyed. One new species, *Paralincus silvae* Rolston, is described and the nominal genus *Vauriana* Ruckes relegated to the status of a junior synonym of *Paralincus* Distant.

The genus *Paralincus* is among those pentatomid genera recently transferred from Halyini in Pentatominae to Ochlerini in Discocephalinae (Rolston and McDonald, 1979; Rolston, 1981). Until now this genus has been monotypic, but during work on the ochlerines new generic synonymy and a new species of *Paralincus* were discovered, bringing the known number of species in this genus to three. These findings are reported here, a diagnosis of the genus is provided and the type species is redescribed.

The location of the eyes, separated from the anterior pronotal margin by about one half the eye diameter, together with the femoral armature distinguish this genus from other ochlerines.

Paralincus Distant

Paralincus Distant, 1911, pp. 246–247.
Vauriana Ruckes, 1958, pp. 10–12. **New Synonymy.**

Diagnosis. Femora armed distally on inferior surface with small tubercles, these obscure or reduced in size and number on posterior femora. Eyes separated from pronotum by about half the diameter of an eye (Fig. 1). Interocular distance greater than distance across ocelli from lateral limit of one to lateral limit of other. Juga exceeding tylus, convergent apically, without anteocular process or subapical tooth. Antennae 5-segmented, basal segment slightly surpassing apex of head. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second segment reaching mesocoxae; last segment extending onto sternites 4–6. Anterior margin of pronotum shallowly concave. Coria surpassing apex of scutellum. Prosternum concave, meso- and metasterna thinly carinate along meson.

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Comment. Females have not been associated definitely with males.

Type species. Paralincus: Ochlerus terminalis Walker, 1867, p. 195, by original designation. *Vauriana: Vauriana bimaculata* Ruckes, 1958, pp. 12–14, by original designation.

KEY TO MALES OF *Paralincus* SPECIES

1. Parameres capitate; antennal segments 2 and 3 subequal in length, segments 4 and 5 each about ¼ longer than 2 or 3 and subequal in length .... *terminalis* (Walker)
– Parameres laminate; antennal segments 2, 4 and 5 approximately same length, longer than 3 2
2. Lateral pygophoral emargination arcuately concave (Fig. 5); head of parameres visible in emargination suboval, curving laterad apically .... *silvae,* new species
– Lateral pygophoral emargination angular (Fig. 6); head of paramere visible in emargination subquadrangular .... *bimaculatus* (Ruckes)

Paralincus terminalis (Walker)

Ochlerus terminalis Walker, 1867, p. 195.
Paralincus terminalis: Distant, 1911, p. 247.

Redescription. Head 2.9 mm across eyes, 2.2 mm long; interocular width 1.4 mm; distance across ocelli from lateral limit of one to lateral limit of other 1.3 mm. Antennal segments 0.8, 1.3, 1.2, 1.7, 1.7 mm in length. Rostral segments 2–4 about 2.5, 2.2, 1.8 mm. Pronotum 6.9 mm wide at humeri, 3.0 mm long at meson. Scutellum 4.2 mm wide at base, 5.0 mm long. Length about 13 mm.

Vertex of head elevated, with double row of punctures on each side; U-shaped row of punctures from lateral margin of elevated vertex passing around ocellus and terminating at eye. Jugal surface impressed submarginally before eye where lateral margin concave. Apical third of antennal segment 4 and all of 5 pale. Rostrum brownish yellow.

Small tooth at anterolateral angles of pronotum narrowly rounded; anterolateral pronotal margin slightly sigmoid; humeri scarcely produced, weakly emarginated. Disk rugose, deeply punctured between rugae; collar reflexed as far laterad as ocelli, bordered where reflexed by dense punctation; cicatrices not well delineated, somewhat elevated.

Fovea in basal angles of scutellum rather large, with one deep impression and a few strong punctures. Base of scutellum marked mesially with small brownish yellow macule. Rugae and punctation of disk similar basally to that on scutellum, becoming less prominent beyond frena.

Costal angle of coria lying above penultimate abdominal segment; junction with membrane sinuous; inner angle broadly rounded. Endocoria each bearing large rufous macule; punctation moderately strong, weaking apically. Membrane dark, with about 12 veins. Connexivum partially exposed, fuscous, finely and somewhat sparsely punctate.

Punctation of pleura rather uniform, moderately strong, somewhat sparse. Coxae, trochanters and tarsi brownish yellow. Tubercles on inferior surface of front and middle femora in 2 irregular rows, obscure on hind femora.

Abdominal venter with broad shallow median sulcus on all but last segment, elsewhere with large shallow circular depressions centered on short seta. Brownish yellow band located submarginally on each side of abdominal venter interrupted broadly at sutures.

Pygophore deeply, arcuately emarginate from caudal view (Fig. 8). Interior ridge trisinuate, shallowly concave mesially. Head of parameres capitate with granulated area apically, visible from lateral view in convex emargination of extracted pygophore (Fig. 7).

Distribution. Known only from holotype, which came from an unspecified locality in Brazil.

Paralincus silvae, new species
(Figs. 2–5)

Head 3.0–3.2 mm wide across eyes, 2.5–2.6 mm long; interocular width 1.6–1.7 mm; distance across ocelli from lateral limit of one to lateral limit of other 1.45–1.5 mm. Antennal segments 0.9–1.0, 1.6–1.8, 1.3–1.4, 1.9, 1.6–1.8 mm long. Rostral segments 2–4 about 2.4–2.8, 2.2–2.3, 2.0–2.1 mm long. Pronotum 7.6–7.9 mm wide at humeri, 3.4–3.6 mm long at meson. Scutellum 4.8–5.0 mm wide at base, 5.4–5.5 mm long. Length about 13.5–14.5 mm.

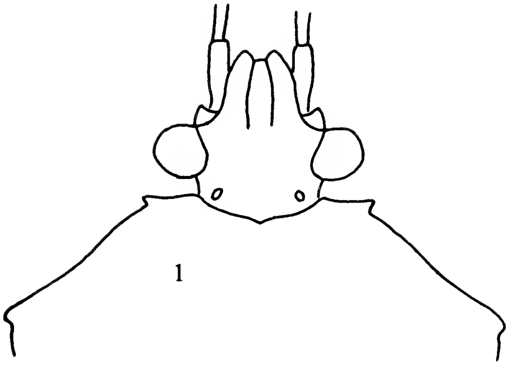
Aside from measurements, conforming to description of *P. terminalis* except as follows: A row of transversely elongated punctures on each side of head bordering elevated vertex which is rugosely and irregularly punctate. Abdominal venter entirely fuscous, lacking paler submarginal band on each side. Coxae, trochanters and tarsi dark brown to fuscous. All femora clearly tuberculate on inferior surface, the number of tubercles fewest on hind femora.

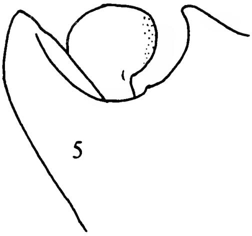
Lateral emargination of pygophore smoothly arcuate, with tiny acute tooth on cephalic edge of emargination (Fig. 5). Parameres laminate, curving laterad apically, granular on cephalic margin of lateral face (Figs. 2, 3). Theca without appendages; conjunctiva moderately sclerotized, bearing small dorsolateral lobe on each side and medioventral lobe; penisfilum nearly straight, slightly flanged apically (Fig. 4).

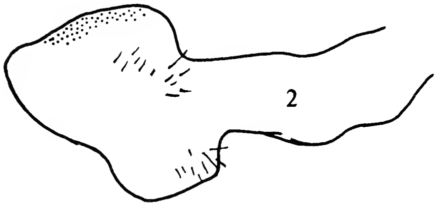
Holotype. ♂, labeled "Brazil, Para, Belem-Utinga. 07. IV. 1978. R. Neto." Deposited in Rijksmuseum van Natuurlijke Historie.

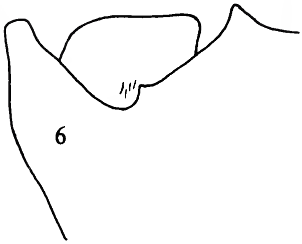
Paratypes. 2♂♂, "Surin. [illegible] 10 III 58 ([illegible]" (LHR); (a) "Ter. Ampa, Rio Ampari, J. Lane, Co." (b) [illegible] "16. VI. 65." (c) "Colecao J. Lane" (Museum de Zoologia de São Paulo).

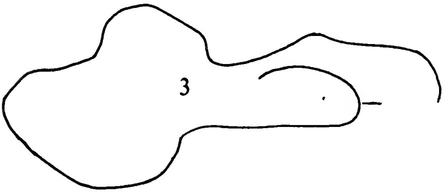
Comments. Aside from substantial differences in the form of the pygophore and parameres, this species seems indistinguishable from *P. bimaculatus.* It

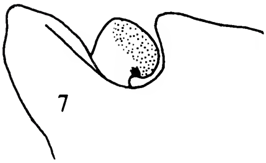


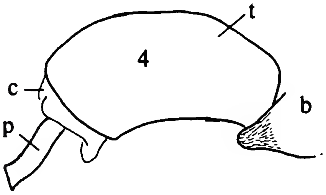












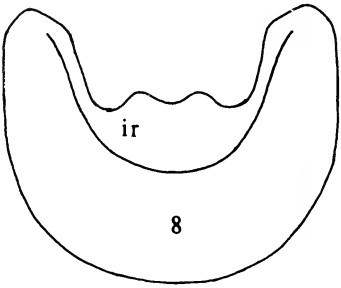


Fig. 1. *P. terminalis.* Head and pronotum in part.

Figs. 2–5. *P. silvae.* 2. Right paramere, lateral surface. 3. Same, rotated 180°, mesial surface. 4. Aedeagus; theca (t), penisfilum (p), conjunctiva (c), basal plate in part (b). 5. Lateral emargination of pygophore and head of paramere.

Fig. 6. *P. bimaculatus.* Lateral emargination of pygophore and distal part of paramere.

Figs. 7, 8. *P. terminalis.* 7. Lateral emargination of pygophore and head of paramere. 8. Caudal view of pygophore, parameres and proctiger omitted; inferior ridge (ir).

differs notably from *P. terminalis* in these respects also, and in the relative lengths of the antennal segments.

Paralincus bimaculatus (Ruckes), **New Combination**
(Fig. 6)

Vauriana bimaculata Ruckes, 1958, pp. 12–14, fig. 1.

Ruckes (1958) described this species in detail and provided a habitus drawing. Other than the male genitalia, *P. bimaculatus* seems indistinguishable from the preceding species, *P. silvae.* The holotype of *Vauriana bimaculata* was examined and the genitalia figured (Fig. 6).

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BOOK REVIEW

Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society.—V. A. Funk and D. R. Brooks (eds.). 1981. New York Botanical Garden, New York. 250 pp. $29.50.

The Proceedings of the First Meeting of the Willi Hennig Society are appropriately titled *Advances in Cladistics.* Much of the debate concerning cladistics over the last few years has comprised repetition of arguments (e.g., Mayr, 1981), many of which have been repeatedly refuted. As J. S. Farris indicates in the Founder's Address, the Hennig Society will serve as a forum for advancing phylogenetic systematics as a science, by providing an opportunity for diverse workers to debate within a cladistic framework. The 13 papers contained herein form an interesting cross-section of current research in theory and application, and show that there are many areas for further development. The meetings from which these papers were drawn (which occurred in October of 1980) have been reviewed by Schuh (1981).

The papers are grouped in four sections. In the first, "Cladistics and Molecular Biology", Farris provides a landmark paper on the use of distance data in phylogenetic analysis. He discusses techniques for analyzing immunological distances, then examines various other types of biochemical distances, and concludes with a general treatment of distance measures. He first devotes considerable space to refutation of the contention of Prager and Wilson (1978) for general superiority of the Fitch-Margoliash method to the Distance Wagner procedure of Farris. After showing their comparisons to be improper he alters his algorithm to fit branch lengths so as to allow better fit in terms of percent standard deviation (i.e., negative branch lengths). This leads to discussion of the bases for measuring fit, and from that he proceeds to consider the effect of nonmetricity on distance measures. As he demonstrates, this vitiates the interpretation of such measures as amounts of evolutionary change between taxa, to the extent of rendering them useless for constructing evolutionary trees. Therefore the concept of a molecular clock as drawn from studies using immunological and Nei's distances is unsupported (since a measure must be ultrametric to show clocklike behavior). He then shows that Euclidean metrics are not interpretable as change either, and that whereas the Manhattan metric is, it can be misleading in terms of treatment of homoplasious characters. Further, sequence differences and the Manhattan metric applied to frequency data are shown to lead to uninterpretable branch lengths. From these conclusions he is led to recommend analyzing character data directly rather than via distance techniques.

Farris' paper has already had a pronounced effect on approaches to genetic distance data. For example, J. Felsenstein at the Evolution meetings in June of 1982 suggested changing the interpretation of the distances from actual phenetic distance to expected (in the statistical sense) distance, and thus permitting branch length fitting. This is in line with Felsenstein's inveterate approach to phylogenetic analysis as a statistical problem, but even if his interpretation is adopted, any molecular clock still needs repair.

D. L. Swofford's paper describes a modification of Farris' Distance Wagner procedure to incorporate all three addition criteria described by Farris in 1972 simultaneously. He then outlines a method for optimizing Distance branch lengths after the initial construction of the tree which allows proper comparison in terms of the "F" statistic of Prager and Wilson (1978). His procedure is quite different from Farris' in the foregoing paper, but his results in re Prager and Wilson are the same. Their logic was flawed and their comparisons when properly done show general superiority for Distance Wagner. Swofford amplifies on certain points made by Farris, and concludes that a defined algorithm such as Distance Wagner is generally more efficient than trial-and-error methods. He rationalizes the use of distance data on the pragmatic grounds that biochemical systematists will undoubtedly continue to rely on distance measures, which is no doubt true. However, in view of the enormous sums expended on such studies they ought to be encouraged to concoct some better justification. Swofford and Selander (1981) describe a Fortran program that will perform his modified procedure.

M. F. Mickevich and C. Mitter, in the third and final paper in this section, compare methods for coding characters of terminal taxa when the characters vary within taxa. Together with Mickevich's paper on quantitative biogeography, this represents the first published exposition of Mickevich's "transformation series analysis" (the term is somewhat sententiously capitalized everywhere in the book except the index). The method is a further formalization for assigning polarities to multistate characters so as to obtain best fit to a given cladogram, ordering states without requiring a pre-defined polarity. In the application to coding the authors first outline the three optimality criteria they use: consistency (degree of fit between classification-implied and data character distributions), boldness (ability to specify a hierarchy) and "Occam's Probative" (which might be characterized as constraining results to the possible) and then compare three coding methods using electromorph data. These are 1) "Independent alleles", where the alleles are the characters and any one can evolve into any other at the same locus. They consider treating combinations of these as quantitative characters, or as binary characters. 2) "Shared alleles", in which the locus is the character and the allelic combinations its states. When more than two alleles occur they are ordered such that states are linked to those with which they share the most alleles. 3) The locus is the character and allelic combinations the states, with order inferred by transformation series analysis. Using a variety of data sets, they show a better performance for the third coding method. They conclude by emphasizing the applicability of this method to other sorts of polymorphic characters, and in an intriguing idea, suggest comparing this method with other types of coding methods developed on the basis of evolutionary assumptions about particular characters as tests of those assumptions.

The second section, "Theoretical Cladistics", is monobasic, comprising D. R. Brooks' paper on treating classifications as languages. He suggests various criteria for best classification from an application of an entropy concept. This approach is here more successful than in Wiley and Brooks (1982). The criteria converge on parsimony, and he concludes by analogizing his approach with those of Nelson (1979) and Farris (1969). His treatment is more general than that of Farris (1979), in that he considers aspects of the information within the terminal taxa, whereas Farris treated this as a constant and analyzed transmission of this information, but it is less applicable in that his criteria could be argued (I suppose) and there is ambiguity in the relationship of the measures for minimum entropy he compares (e.g., his treatment of Nelson's "term information").

The next section, "Botanical Cladistics", includes five papers. Three of these (Sanders, Bolick and Churchill) are cladistic analyses of various plant groups, and are presumably included in this volume in order to demonstrate that, yes, phylogenetic systematics can be done with plants. However, at least the synopsis provided by Churchill (complete with the Latin diagnoses of new taxa) seems quite out of place. There are scattered fallacies throughout some of these papers: Sanders lists four assumptions of Hennigian cladistics, none of which are necessary; he and Funk frequently use "outgroup" for "sister-group"; Churchill speaks of methods that employ the axioms of evolution; Sanders terms bushes resolved; Funk states that a cladistic analysis involving non-monophyletic groups is futile; synapomorphy and autapomorphy are frequently confused; etc. These statements, recalling as they do the misunderstandings prevalent in *Systematic Zoology* debates of ten years ago, indicate that botanists are not very advanced in their understanding of the methods. Although there has of late been considerable print expended on the issue of whether cladistics has somehow been transformed from Hennig's methods, the transformation has been in perception. The methods are just that, a variety of analytical procedures that may be applied to a given data set. Whether or not that data set is evolutionarily clean is irrelevant. Further, the general tenor to the arguments in favor of applying cladistic methods, implying that zoological studies are easy by comparison, is occasionally aggravating.

Withal, certain aspects of these papers are instructive. Funk has an extended discussion of the treatment of putative hybrids in an analysis, concluding, as does Wagner (1980), that they should be removed prior to the construction of the cladogram, to which they can be added like so many ornaments afterwards. This problem is more thoroughly examined here than in theoretical treatments by zoologists. Bremer and Wanntorp give an interesting comparison of cladistic and traditional classifications of major groups of organisms, arguing for progress in classification.

The final section, "Biogeography and Cladistics", contains 4 papers. In the first, Brooks, T. B. Thorson and M. A. Mayes present a study of freshwater stingray biogeography, testing four narrative hypotheses, each encompassing several points, such as the monophyly and origin of the group, on the basis of assertions about the parasite fauna of these fish. They construct cladograms for helminth parasites, show Pacific relationships and are able to define areas of endemism that correspond to those shown by other fishes. They further suggest that an outgroup genus of stingrays may be paraphyletic because of the pattern of interrelationships shown by the parasites. However, only two of the parasite groups force this interpretation (figs. 6 and 11). All in all, an excellent example of the "coevolutionary" approach.

C. J. Humphries also presents an interesting study, on the celebrated *Nothofagus.* Constructing a cladogram of the species and then a reduced area cladogram, he compares this with four geological cladograms and is able to show only a Laurasia/Gondwanaland pattern. Comparison with reduced area cladograms of a variety of other organisms shows considerable incongruence. Thus *Nothofagus* is relatively uninformative about interrelationships of the southern land masses. Throughout his paper there is a very good emphasis that acceptance of continental drift only provides a plausible dispersal route for a non-analytic biogeography.

Mickevich contributes an important paper on quantitative biogeography. In it she shows how transformation series analysis (which is explained by examples and figures that allow one to perform the procedure) can be of great use in biogeography. The method can extract the general pattern (a "biogeographic map") from a set of area cladograms. It is a logical extension of parsimony algorithms to analytic biogeography, which may thus be automated. Readers attempting to follow her example drawn from Rosen (1978) should note that there are several typos and there are missing values for row "D" in Table II: the 4 should be a 2. Also her exclusion of area 7 on the *Heterandria* cladogram (fig. 7a) from the transformation into area states may be an oversight, but points out some ambiguity in this part of the process (cf. her assignments of area states with figs. 1 and 2 in Platnick's paper).

Platnick has the final say in a paper explicating the thoughts of Nelson and Platnick (1981) on dealing with widespread taxa in biogeography. He too uses the example from Rosen (1978), analyzing the cladograms under two different assumptions about the history of the groups. It is interesting that Mickevich's method, when area states are defined as she does and area 7 omitted, gives the same pattern under both assumptions. This again shows ambiguity in the assignment of area states. If the localities are used as area states (only areas 2 and 10 overlap), the problem of combinability discussed by Platnick remains. Whether the greater informativeness under Platnick's second assumption (amounting here to disjunction, then fusion of areas) is more than *ad hoc* can at least be tested as he suggests.

In summary, as published symposia go, the quality of papers in this book is quite good. In these days of offset printing of this type of publication, it is refreshing to see superb quality paper and excellent binding for a paperback. However, the rather exorbitant price ($29.50) illustrates why offset printing is used so widely for symposia. Considering that there are no entomological papers in the book, readers of this journal interested in these proceedings are likely to be systematists interested in some of the theoretical papers. That being the case, they would probably be better off photocopying about three or four papers and the unified bibliography than purchasing the whole volume.—*James M. Carpenter, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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The *Journal of the New York Entomological Society* is devoted to the advancement and dissemination of knowledge of insects and related taxa. The Journal will consider for publication all manuscripts dealing with original research in entomology. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

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EXOTIC INSECTS REPORTED NEW TO NORTHEASTERN UNITED STATES AND EASTERN CANADA SINCE 1970[1]

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Abstract.—To promote interest in the detection of exotic insects, we provide a list of species accidentally introduced to North America and reported since 1970 as new to the Western Hemisphere, United States, or Canada. The area of detection is limited to eastern Canada (Ontario, Quebec, Newfoundland, and the Maritime Provinces) and the U.S. from Maine to Virginia and west to Pennsylvania and West Virginia. Included for each immigrant species are the country or area of probable origin, collection data relating to detection, host and habitat preferences (if known) in the area of endemism, economic importance in North America, and subsequent references to distribution or habits in North America. The list includes 70 species new to the Western Hemisphere; 6, to the United States; and 7, to Canada. The 70 insects new to the Western Hemisphere include 22 Coleoptera, 14 Hemiptera-Heteroptera, 10 Hymenoptera, 7 Lepidoptera, 7 Diptera, 6 Hemiptera-Homoptera, and 1 each for Dictyoptera, Psocoptera, Thysanoptera, and Neuroptera.

The importance of detecting exotic insects in North America, especially plant pests, has long been recognized. Since colonial times, man's activities and commerce have enhanced the passive, worldwide movement of insects and other invertebrates. In eastern North America many of the most important pests are immigrants from Europe or Asia, principally because of the large volume of Eurasian–North American traffic. Sailer (1978) analyzed the immigrant fauna (by insect order only) in the contiguous United States. His comprehensive study further stimulated interest in detection and focused more attention on several questions such as where have introduced insects originated, what areas of North America are most susceptible to invasion by exotic species, and where have they been first detected?

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[1] The original version of this paper was presented as a report of the Committee on Insect Detection, Evaluation and Prediction (IDEP), Eastern Branch, Entomological Society of America, September 29, 1982, Hartford, Connecticut.

Insect detection generally is the responsibility of the U.S. Department of Agriculture, state departments of agriculture, Agriculture Canada, and other cooperating agencies and professionals (see Wheeler and Nixon, 1979). Even with increased vigilance at the international ports of entry, new discoveries will be made. The prompt detection of invaders, pest species or otherwise, continues as one of the vital needs for agriculture in the United States and Canada. Plans now are underway to develop the first computerized database of essential information on insects and their allies introduced into the Western Hemisphere, with emphasis on North America, especially the U.S. (L. Knutson, *in litt.*). A forthcoming book on exotic pests in North American agriculture by C. L. Wilson and C. L. Graham (U.S. Department of Agriculture) also should draw attention to pest detection.

Although detection is acknowledged as a national priority, some would consider it one of the less glamorous aspects of entomology, sometimes eliciting disdain from those who pursue more "sophisticated" activities. But even in integrated pest management, currently a popular area of research, detection should play a role. In citing criteria for implementing new pest management strategies, Kim (1979) emphasized the detection of exotic pests. Too often, however, it is slighted in favor of assessment and forecasting. The monitoring of pests obviously is crucial to management strategies, but an overemphasis on "key pests" without considering other members of the agroecosystem is not conducive to an appropriate level of detection. We recognize that the disparate objectives of assessment and detection may be incompatible in some crop monitoring systems, or probably cannot be employed each time a crop is sampled. Ideally, however, scouts who evaluate only the most economically important species should also be familiar with the "typical" or characteristic arthropods associated with the host crop. With such knowledge, plus some curiosity, a scout is apt to spot some anachronism—to suspect that a particular species is out of place in the crop being surveyed. Eventually, a few of these apparently unusual insect inhabitants, that is, ones appearing unfamiliar to a well-trained observer, will prove interesting—maybe only an undescribed species of interest to taxonomic specialists of the group, but perhaps a native insect that recently has changed its host preference, a resurgent pest, or an immigrant that has gone undetected.

From our general collecting of insects in the Northeast since the mid-1970's, we have discovered several species new to the Western Hemisphere, or immigrants known only from a few North American localities. Such collecting, plus detections made during the "High Hazard Pest Survey" conducted by USDA-APHIS, has emphasized our inadequate knowledge of North American insects, or what Turnbull (1979) has called an ". . . ignorance of the recent changes in the insect fauna." As Sailer (1978) noted, ". . .

while we are painfully aware of those species that are pests, and know something of those that are beneficial, few people, aside from taxonomists, are aware of the large number having little or no known importance."

To promote interest in insect detection—among systematists as well as those involved in pest management and other applied aspects of entomology—we have compiled and listed relevant information on insect detection in the northeastern U.S. and eastern Canada since 1970. Any attempt to document all known introductions is at best preliminary because of the scattered literature in which new records are published, thus making omissions inevitable.

In the following list, we include all insect species considered *accidentally* introduced into North America (thus species thought to be naturally Holarctic or deliberately introduced are excluded) and reported in the literature since 1970 as new Western Hemisphere [W. Hem.], United States [U.S.], or Canadian [Can.] records from states composing the Eastern Branch, Entomological Society of America, or from eastern Canada.[2] For each exotic species we give (1) the country or area of probable origin, (2) information on first detection including locality, dates, and other collection data, (3) host preferences or habitat if known in the area of endemism (most often Europe), (4) economic importance, and (5) subsequent references to distribution or life history in North America. The arrangement is by insect orders and families, with taxa listed alphabetically under the family-group names.

DICTYOPTERA

ECTOBIIDAE

Ectobius sylvestris (Poda) [W. Hem.]

Probable origin. Europe.

Detection. Geneva, New York (Ontario County), June 1980, and between May 25 and July 16, 1981; in a private home (in kitchen) and out-of-doors.

Host preference(s)/habitat. Various habitats; commonly on the ground in forests, particularly in mountainous areas.

Economic status. Probably noneconomic.

Reference(s). Hoebeke, E. R. and D. A. Nickle. 1981. The forest cockroach, *Ectobius sylvestris* (Poda), a European species newly discovered in North America (Dictyoptera: Blattoidea: Ectobiidae). Proc. Entomol. Soc. Washington 83:592–595.

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[2] Eastern Branch States: Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, Virginia, and West Virginia; eastern Canada: New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, and Quebec.

PSOCOPTERA

ELIPSOCIDAE

Cuneopalpus cyanops (Rostock) [W. Hem.]

Probable origin. Western Europe.

Detection. Prospect Park, Brooklyn, New York, summer 1950; from conifers.

Host preference(s)/habitat. Various conifer spp.

Economic status. Probably noneconomic.

Reference(s). New, T. R. and A. M. Nadler. 1970. A North American record of *Cuneopalpus cyanops* (Rostock) (Psocoptera). Entomologist 103:44.

THYSANOPTERA

THRIPIDAE

Tmetothrips subapterus (Haliday) [W. Hem.]

Probable origin. Europe.

Detection. Rew, Pennsylvania (McKean County), July 27, 1975; on *Stellaria graminea* L. (little starwort).

Host preference(s)/habitat. Various plants including *Plantago maritima* L. (European seaside plantain), *Stellaria media* (L.) Vill. (chickweed), *Galium palustre* L. (marsh bedstraw), *Juncus* sp. (a rush), *Lolium perenne* L. (perennial ryegrass), *Clematis vitalba* L. (travelersjoy), *Lonicera caprifolium* L. (sweet honeysuckle), and *Robinia pseudoacacia* L. (black locust).

Economic status. Probably noneconomic.

Reference(s). Anonymous. 1976. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 1(43):798.

HEMIPTERA-HETEROPTERA

MICROPHYSIDAE

Loricula pselaphiformis Curtis [W. Hem.]

Probable origin. Europe.

Detection. Halifax, Nova Scotia, July 22, 1976; on trunks of European beech (*Fagus sylvatica* var. *purpurea* Ait.), at Point Pleasant Park.

Host preference(s)/habitat. Among lichens on trunks of trees such as *Betula, Crataegus, Fagus,* and *Juniperus*; also on *Acer, Buxus, Fraxinus, Malus, Quercus, Salix, Sambucus, Tilia, Ulmus, Abies,* and *Pinus.* This species is predaceous on small arthropods.

Economic status. Probably noneconomic.

Reference(s). Kelton, L. A. 1980. First record of a European bug, *Loricula pselaphiformis,* in the Nearctic region (Heteroptera: Microphysidae). Canad. Entomol. 112:1085–1087.

Myrmedobia exilis (Fallen) [W. Hem.]

Probable origin. Europe.

Detection. St. John's, Newfoundland, July 20, 1980; "collected by sweeping ground cover on the east side of Gibbet Hill just west of the Information Centre (Signal Hill National Historic Park) . . . ."

Host preference(s)/habitat. Among mosses and lichens on trees such as *Pinus, Abies, Larix, Quercus,* and *Fagus*; also among moss and grass roots on the ground. This species is predaceous on small arthropods.

Economic status. Probably noneconomic.

Reference(s). Kelton, L. A. 1982 (1981). First record of a European bug, *Myrmedobia exilis* (Heteroptera: Microphysidae), in the Nearctic region. Canad. Entomol. 113:1125–1127.

MIRIDAE

Camptozygum aequale (Villers) [W. Hem.]

Probable origin. Europe.

Detection. 11 counties in central and western Pennsylvania in 1971 and 1972; from seedlings and trees of Scotch pine (*Pinus sylvestris* L.) and seedlings of Austrian pine (*P. nigra* Arnold); red pine (*P. resinosa* Ait.); Swiss mountain pine (*P. mugo* Turra); and western yellow pine (*P. ponderosa* Douglas).

Host preference(s)/habitat. Conifers, mainly *Pinus* spp.

Economic status. Probably noneconomic.

Reference(s). Wheeler, A. G., Jr. and T. J. Henry. 1973. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 23(16):228; Wheeler, A. G., Jr. and T. J. Henry. 1973. *Camptozygum aequale* (Villers), a pine feeding mirid new to North America (Hemiptera: Miridae). Proc. Entomol. Soc. Washington 75:240–246; Wheeler, A. G., Jr. 1979. A comparison of the plant-bug fauna of the Ithaca, New York area in 1910–1919 with that in 1978. Iowa St. J. Res. 54:29–35; Henry, T. J. and A. G. Wheeler, Jr. 1979. Palearctic Miridae in North America: records of newly discovered and little-known species (Hemiptera: Heteroptera). Proc. Entomol. Soc. Washington 81:257–268; Wheeler, A. G., Jr. 1980. Plant bugs at Cornell: a changing fauna. Cornell Plantations 36(1): 3–8.

Dicyphus rhododendri Dolling [W. Hem.]

Probable origin. Great Britain.

Detection. Several localities in Pennsylvania (Centre, Dauphin, Luzerne, Philadelphia, and Schuylkill counties) during June 1977 to July 1975; also Cleveland, Ohio (Cuyahoga County), June 24, 1933 (specimens in the USNM colln.); on flowers of native and cultivated *Rhododendron maximum* L. and mountain laurel (*Kalmia latifolia* L.). Because the closest relatives apparently are in the New World, Dolling suggested that *rhododendri* is a Nearctic endemic which has been introduced to England.

Host preference(s)/habitat. Rhododendron spp.

Economic status. Probably noneconomic.

Reference(s). Henry, T. J. and A. G. Wheeler, Jr. 1976. *Dicyphus rhododendri* Dolling, first records from North America (Hemiptera: Miridae). Proc. Entomol. Soc. Washington 78:108–109.

Megalocoleus molliculus (Fallen) [Can.]

Probable origin. Europe.

Detection. "Southeastern Ontario"; from Canada goldenrod (*Solidago canadensis* L.).

Host preference(s)/habitat. Composites (Asteraceae), particularly *Achillea* L. and *Tanacetum* L.

Economic status. Probably noneconomic.

Reference(s). Reid, D. G., C. C. Loan and R. Harmsen. 1976. The mirid (Hemiptera) fauna of *Solidago canadensis* (Asteraceae) in south-eastern Ontario. Canad. Entomol. 108:561–567.

Orthotylus nassatus (F.) [W. Hem.]

Probable origin. Europe.

Detection. Allentown, Pennsylvania (Lehigh County), July 5, 1973; and 3 miles south of Hershey, Pennsylvania (Dauphin County), July 4, 1977; on pear, *Pyrus* sp., heavily infested with pear psylla (*Psylla pyricola* Foerster) at Allentown, and at blacklight south of Hershey.

Host preference(s)/habitat. On *Fraxinus, Quercus, Salix,* and *Tilia.*

Reference(s). Henry, T. J. 1977. *Orthotylus nassatus,* a European plant bug new to North America (Heteroptera: Miridae). U.S. Dept. Agric., Coop. Plant Pest Rep. 2(31):605–608; Henry, T. J. and A. G. Wheeler, Jr. 1979. Palearctic Miridae in North America: records of newly discovered and little-known species (Hemiptera: Heteroptera). Proc. Entomol. Soc. Washington 81:257–268; Kelton, L. A. 1982. New records of European *Pilophorus* and *Orthotylus* in Canada (Heteroptera: Miridae). Canad. Entomol. 114:283–287.

Orthotylus viridinervis (Kirschbaum) [W. Hem.]

Probable origin. Europe.

Detection. Niagara Falls, Ontario, June 17, 1978; on American elm, *Ulmus americana* L., heavily infested with woolly elm aphid, *Eriosoma americanum* (Riley).

Host preference(s)/habitat. On Wych or Scotch elm (*Ulmus glabra* Huds.), and on *Alnus, Corylus, Quercus,* and *Salix.*

Economic status. Probably noneconomic.

Reference(s). Henry, T. J. and A. G. Wheeler, Jr. 1979. Palearctic Miridae in North America: records of newly discovered and little-known species (Hemiptera: Heteroptera). Proc. Entomol. Soc. Washington 81:257–268; Kelton, L. A. 1982. New records of European *Pilophorus* and *Orthotylus* in Canada (Heteroptera: Miridae). Canad. Entomol. 114:283–287.

Pilophorus confusus (Kirschbaum) [W. Hem.]

Probable origin. Europe.

Detection. Kentville, Nova Scotia (Research Station, Agriculture Canada), July 10–14, 1976; in orchard on plum trees heavily infested with aphids.

Host preference(s)/habitat. Various deciduous trees and shrubs, including *Alnus, Crataegus, Populus, Ribes, Salix,* and *Tilia*; feeds mainly on aphids.

Economic status. Probably noneconomic.

Reference(s). Kelton, L. A. 1982. New records of European *Pilophorus* and *Orthotylus* in Canada (Heteroptera: Miridae). Canad. Entomol. 114: 283–287.

Pinalitus rubricatus (Fallen) [W. Hem.]

Probable origin. Europe.

Detection. Wayne County, Pennsylvania, June 26, 1974; on white spruce (*Picea glauca* (Moench) Voss).

Host preference(s)/habitat. Various conifers, mainly spruces (*Picea* spp.)

Economic status. Probably noneconomic.

Reference(s). Henry, T. J. and A. G. Wheeler, Jr. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(11):103; Henry, T. J. and A. G. Wheeler, Jr. 1974. *Sthenarus dissimilis* and *Orthops rubricatus*: conifer-feeding mirids new to North America (Hemiptera: Miridae). Proc. Entomol. Soc. Washington 76: 217–224; Wheeler, A. G., Jr. 1979. A comparison of the plant-bug fauna of the Ithaca, New York area in 1910–1919 with that in 1978. Iowa St. J. Res. 54:29–35; Wheeler, A. G., Jr. 1980. Plant bugs at Cornell: a changing fauna. Cornell Plantations 36(1):3–8.

Plagiognathus vitellinus (Scholtz) [W. Hem.]

Probable origin. Europe.

Detection. 17 counties in Pennsylvania during 1972–1973; on Douglas fir (*Pseudotsuga menziesii* (Mich.) Franco); European larch (*Larix decidua* Mill.), Norway spruce (*Picea abies* (L.) Karst.), Colorado spruce (*P. pungens* Engelm.), and white spruce (*P. glauca*).

Host preference(s)/habitat. Spruce (*Picea* spp.) and larch (*Larix* spp.).

Economic status. Probably noneconomic.

Reference(s). Henry, T. J. and A. G. Wheeler, Jr. 1973. *Plagiognathus vitellinus* (Scholtz), a conifer-feeding mirid new to North America (Hemiptera: Miridae). Proc. Entomol. Soc. Washington 75:480–485; Henry, T. J. and A. G. Wheeler, Jr. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(11): 103; Henry, T. J. and A. G. Wheeler, Jr. 1979. Palearctic Miridae in North

America: records of newly discovered and little-known species (Hemiptera: Heteroptera). Proc. Entomol. Soc. Washington 81:257–268; Wheeler, A. G., Jr. 1979. A comparison of the plant-bug fauna of the Ithaca, New York area in 1910–1919 with that in 1978. Iowa St. J. Res. 54:29–35; Wheeler, A. G., Jr. 1980. Plant bugs at Cornell: a changing fauna. Cornell Plantations 36(1): 3–8.

Psallus variabilis (Fallen) [W. Hem.]

Probable origin. Europe.

Detection. Planting Fields Arboretum, Oyster Bay, Long Island (Nassau County), New York, June 6, 1979.

Host preference(s)/habitat. Mainly reproductive structures of oaks (*Quercus* spp.), and recorded from *Populus, Salix,* and *Tilia*; also predaceous on small insects.

Economic status. Probably noneconomic.

Reference(s). Hoebeke, E. R. 1980. U.S. Dept. Agric., Coop. Plant Pest Rep. 5(33):628; Wheeler, A. G., Jr. and E. R. Hoebeke. 1982. *Psallus variabilis* and *P. albipennis,* two European plant bugs established in North America, with notes on taxonomic changes (Hemiptera-Heteroptera: Miridae). Proc. Entomol. Soc. Washington 84:690–703.

Sthenarus dissimilis Reuter [W. Hem.]

Probable origin. Europe.

Detection. 5 counties in southeastern Pennsylvania from early May to late June 1973; on balsam fir (*Abies balsamea* (L.) Mill.), concolor fir (*A. concolor* (Gord.) Ldl.), and Nordmann fir (*A. nordmanniana* (Stev.) Spach).

Host preference(s)/habitat. Fir (*Abies* spp.).

Economic status. Probably noneconomic.

References. Henry, T. J. and A. G. Wheeler, Jr. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(11):103; Henry, T. J. and A. G. Wheeler, Jr. 1974. *Sthenarus dissimilis* and *Orthops rubricatus*: conifer-feeding mirids new to North America (Hemiptera: Miridae). Proc. Entomol. Soc. Washington 76: 217–224; Wheeler, A. G., Jr. 1979. A comparison of the plant-bug fauna of the Ithaca, New York area in 1910–1919 with that in 1978. Iowa St. J. Res. 54:29–35; Wheeler, A. G., Jr. 1980. Plant bugs at Cornell: a changing fauna. Cornell Plantations 36(1):3–8.

Sthenarus rotermundi (Scholtz) [W. Hem.]

Probable origin. Europe.

Detection. Monroeville, Pennsylvania (Allegheny County), May 24–26, 1977; near Wilkes-Barre (Luzerne County), May 7, 1978; and Niagara Falls, Ontario, June 17, 1978; from quaking aspen (*Populus tremuloides* Michx.), large-tooth aspen (*P. grandidentata* Michx.) and from seeds of silver poplar (*P. alba* L.).

Host preference(s)/habitat. White or silver poplar (*Populus alba*) and also *P. canescens* Smith and *Alnus glutinosa* (L.) Gaertn.

Economic status. Probably noneconomic.

Reference(s). Henry, T. J. and A. G. Wheeler, Jr. 1979. Palearctic Miridae in North America: records of newly discovered and little-known species (Hemiptera: Heteroptera). Proc. Entomol. Soc. Washington 81:257–268.

RHOPALIDAE

Rhopalus (Brachycarenus) tigrinus (Schilling) [W. Hem.]

Probable origin. Europe.

Detection. North Vineland, New Jersey (Cumberland County), August 18, 1977; from wheat (*Triticum aestivum* L.) on a farm.

Host preference(s)/habitat. Various crucifers (Brassicaceae).

Economic status. Probably noneconomic.

Reference(s). Hoebeke, E. R. 1977. U.S. Dept. Agric., Coop. Plant Pest Rep. 2(40):802; Hoebeke, E. R. 1978. U.S. Dept. Agric., Coop. Plant Pest Rep. 3(40–41):579; Hoebeke, E. R. and A. G. Wheeler, Jr. 1982. *Rhopalus* (*Brachycarenus*) *tigrinus,* recently established in North America, with a key to the genera and species of Rhopalidae in eastern North America (Hemiptera: Heteroptera). Proc. Entomol. Soc. Washington 84:213–224.

CYDNIDAE

Aethus nigritus (F.) [W. Hem.]

Probable origin. Europe.

Detection. Townsend, Delaware (New Castle County), June 8, 1977; from soybeans on a farm.

Host preference(s)/habitat. Sandy areas, associated with roots of weeds and grasses, particularly *Corynephorus canescens* L. (Beauv.) (Poaceae).

Economic status. Probably noneconomic.

Reference(s). Hoebeke, E. R. 1978. U.S. Dept. Agric., Coop. Plant Pest Rep. 3(29):376; Hoebeke, E. R. 1980. U.S. Dept. Agric., Coop. Plant Pest Rep. 5(36):691.

PENTATOMIDAE

Picromerus bidens (L.) [Can.]

Probable origin. Europe.

Detection. Lennoxville, Quebec, in 1968, and Ascot Corner, Quebec, in 1969.

Host preference(s)/habitat. A well-known predator of coleopterous and lepidopterous larvae.

Economic status. Potentially beneficial.

Reference(s). Kelton, L. A. 1972. *Picromerus bidens* in Canada (Heteroptera: Pentatomidae). Canad. Entomol. 104:1743–1744; Larochelle, A. 1979. Les punaises a bouclier (Hemiptera: Scutelleroidea) du Quebec. Cordulia, Suppl. 11:1–84; Larochelle, A. 1980. *Picromerus bidens* L. (Heteroptera: Pentatomidae) en Amerique du Nord: repartition geographique, habitat et biologie. Bull. Invent. Ins. Quebec 2:10–18.

HEMIPTERA-HOMOPTERA

CICADELLIDAE

Anoscopus albifrons (L.) [W. Hem.]

Probable origin. Europe.

Detection. Greenwood, Kings Co., Nova Scotia, August 12, 1973; and also Marion Co., Oregon, July 23, 1974.

Host preference(s)/habitat. Mostly dry localities, with *Agrostis tenuis* Sibth., *Anthoxanthum, Luzula, Holcus mollis* L., etc.

Economic status. Probably noneconomic.

Reference(s). Hamilton, K. G. A. 1975. A review of the northern hemisphere Aphrodina (Rhynchota: Homoptera: Cicadellidae), with special reference to the Nearctic fauna. Canad. Entomol. 107:1009–1027.

Eupteryx atropunctata (Goeze) [U.S.]

Probable origin. Europe.

Detection. Willimantic, Connecticut (Windham County), July 3, 1979; on beans (*Phaseolus vulgaris* L.) in garden.

Host preference(s)/habitat. Especially species of Labiatae (mints), but also on some Asteraceae, Scrophulariaceae, Verbenaceae, Solanaceae, and Chenopodiaceae.

Economic status. Potentially economic.

Reference(s). Hoebeke, E. R. 1980. U.S. Dept. Agric., Coop. Plant Pest Rep. 5(29):547; Hoebeke, E. R. and A. G. Wheeler, Jr. In press. *Eupteryx atropunctata*: North American distribution, seasonal history and host plants, and description of fifth-instar nymph (Hemiptera-Homoptera: Cicadellidae). Proc. Entomol. Soc. Washington.

Planaphrodes bifasciata (L.) [W. Hem.]

Probable origin. Europe.

Detection. St. John's, Newfoundland, July 26, 1967; in a Malaise trap.

Host preference(s)/habitat. Dry meadows.

Economic status. Probably noneconomic.

Reference(s). Hamilton, K. G. A. 1975. A review of the northern hemisphere Aphrodina (Rhynchota: Homoptera: Cicadellidae), with special reference to the Nearctic fauna. Canad. Entomol. 107:1009–1027.

PSYLLIDAE

Psylla mali (Schmidberger) [U.S.]

Probable origin. Europe.

Detection. Camden, Maine (Knox County), June 27, 1980; from apple leaves (*Malus sylvestris* Mill.) in organically grown orchard.

Host preference(s)/habitat. Malus sylvestris (apple), *Prunus* sp. (plum), *Cydonia oblonga* Mill. (quince), and *Sorbus aucuparia* L. (European mountain ash).

Economic status. Economic.

Reference(s). Anonymous. 1981. Serious European apple pest new in the U.S. U.S. Dept. Agric., Plant Pest News 1(2):2.

APHIDIDAE

Brachycolus asparagi (Mordvilko) [W. Hem.]

Probable origin. Mediterranean area and eastern Europe.

Detection. Orient, Long Island, New York (Suffolk County), July 20, 1969, and New Brunswick, New Jersey (Middlesex County), August and November 20, 1969; on red top (*Agrostis alba* L.) and asparagus (*Asparagus officinalis* L.).

Host preference(s)/habitat. Asparagus (*Asparagus* sp.).

Economic status. Economic.

Reference(s). Leonard, M. D. 1970. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 20(11):156.

Coloradoa tanacetina (Walker) [W. Hem.]

Probable origin. Europe.

Detection. Veazie, Maine (Penobscot County), August 13, 1977; from *Tanacetum vulgare* L. (common tansy).

Host preference(s)/habitat. Tansy (*Tanacetum vulgare*).

Economic status. Probably noneconomic.

Reference(s). Smith, C. F. 1978. U.S. Dept. Agric., Coop. Plant Pest Rep. 3(11):89.

Hyadaphis tataricae (Ajzenberg) [W. Hem.]

Probable origin. Northern and western Asia.

Detection. Numerous localities in Quebec since 1976; from honeysuckle (*Lonicera* spp.).

Host preference(s)/habitat. Lonicera spp., particularly *L. tatarica* L. and *L. bella* Zabel.

Economic status. Economic.

Reference(s). Boisvert, J.-M., C. Cloutier and J. McNeil. 1981. *Hyadaphis tataricae* (Homoptera: Aphididae), a pest of honeysuckle new to North America. Canad. Entomol. 113:415–418; Voegtlin, D. 1981. Notes on a

European aphid (Homoptera: Aphididae) new to North America. Proc. Entomol. Soc. Washington 83:361–362; Voegtlin, D. 1982. The distribution and spread of *Hyadaphis tataricae* (Homoptera: Aphididae) in the north-central states with notes on its hosts, biology, and origin. Great Lakes Entomol. 15: 147–152.

PSEUDOCOCCIDAE

Chaetococcus phragmitis (Marchal) [W. Hem.]

Probable origin. Europe.

Detection. 1 mile east of Tuckerton, New Jersey (Ocean County), July 21, 1975; on *Phragmites communis* Trin. (common reed).

Host preference(s)/habitat. Phragmites spp.

Economic status. Probably noneconomic.

Reference(s). Nakahara, S. 1975. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 25(45–48):875.

NEUROPTERA

CONIOPTERYGIDAE

Aleuropteryx juniperi Ohm [W. Hem.]

Probable origin. Europe.

Detection. Harrisburg, Pennsylvania (Dauphin County), July 21, 1968 and 6 other Pennsylvania counties; on scale-infested juniper (*Juniperus* spp.).

Host preference(s)/habitat. Juniperus spp.; larvae prey on juniper scale (*Carulaspis juniperi* (Bouche)).

Economic status. Beneficial.

Reference(s). Henry, T. J. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(33):659; Anonymous. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(35):703; Henry, T. J. 1976. *Aleuropteryx juniperi*: a European scale predator established in North America (Neuroptera: Coniopterygidae). Proc. Entomol. Soc. Washington 78:195–201; Wheeler, A. G., Jr. 1981. Updated distribution of *Aleuropteryx juniperi* (Neuroptera: Coniopterydiae), a predator of scale insects on ornamental juniper. Proc. Entomol. Soc. Washington 83:173.

COLEOPTERA

CARABIDAE

Harpalus rufipes DeGeer [U.S.]

Probable origin. Europe.

Detection. Orono, Maine (Penobscot County), May 4 and 29, 1970; on the banks of the Penobscot River.

Host preference(s)/habitat. Open, moderately dry country, especially cultivated fields, waste places, feeding largely upon seeds; a pest of strawberries.

Economic status. Potentially economic.

Reference(s). Larochelle, A. 1976. Premiere mention de l'*Harpalus rufipes* DeGeer (Coleoptera) pour les Etats-Unis d'Amerique. Cordulia 2:121–122; Dunn, G. A. 1981. Distribution of *Haraplus rufipes* DeGeer in Canada and United States (Coleoptera; Carabidae). Entomol. News 92:186–188; Larson, D. J. and D. W. Langor. 1982. Carabid beetles of insular Newfoundland (Coleoptera: Carabidae: Cicindelidae)—30 years after Lindroth. Canad. Entomol. 114:591–597.

Leistus ferrugineus (L.) [W. Hem.]

Probable origin. Europe.

Detection. Northwest St. John's, Newfoundland, August–October 1977; under stones and in litter or humus lying over well-drained, moist, gravelly soil in mixed *Abies-Alnus-Prunus* forest.

Host preference(s)/habitat. Open, dry country, often in moss and grass tufts.

Economic status. Probably noneconomic.

Reference(s). Larson, D. J. 1978. *Leistus ferrugineus* (L.) (Coleoptera: Carabidae), new to North America. Coleopt. Bull. 32:307–309; Larson, D. J. and D. W. Langor. 1982. Carabid beetles of insular Newfoundland (Coleoptera: Carabidae: Cicindelidae)—30 years after Lindroth. Canad. Entomol. 114:591–597.

STAPHYLINIDAE

Sepedophilus marshami (Stephens) [W. Hem.]

Probable origin. Europe.

Detection. Cap Rouge, Quebec, June 19, 1959 and subsequently from Sydney, Nova Scotia, and additional localities in Quebec along the St. Lawrence and Ottawa river valleys from Quebec City to Hull.

Host preference(s)/habitat. Under logs and loose bark, in rotting wood, in leaf litter, under stones, at plant roots, etc.

Economic status. Noneconomic.

Reference(s). Campbell, J. M. 1976. A revision of the genus *Sepedophilus* Gistel (Coleoptera: Staphylinidae) of America north of Mexico. Mem. Entomol. Soc. Canad., no. 99:89 pp.

Tachinus corticinus Gravenhorst [W. Hem.]

Probable origin. Europe.

Detection. Near Montreal, Quebec, November 21, 1970 and September 2, 1972; and St. Cyrville, Quebec (Drummond County), April 8, 1967.

Host preference(s)/habitat. Under rotting matter, including compost, hay and straw; under moss and decaying leaves.

Economic status. Probably noneconomic.

Reference(s). Campbell, J. M. 1975. New species and records of *Tachinus* (Coleoptera: Staphylinidae) from North America. Canad. Entomol. 107:87–94.

PSELAPHIDAE

Euplectus* (*Diplectellus*) *karsteni (Reichenbach) [W. Hem.]

Probable origin. Europe.

Detection. Specimens examined from Montreal, Quebec, June 29, 1898; Tilbury, Essex Co., Ontario, March 26, June 2 and September 5, 1967; Long Island, New York; Washington, D.C., September 2, 1964; Latrobe, St. Vincent, Westmoreland Co., Pennsylvania; and from numerous localities in Ohio, Michigan, Illinois, Iowa, Wisconsin, and Minnesota.

Host preference(s)/habitat. Frequently found in composted or well-rotted haystacks, corncob piles, horse manure, and occasionally in tree holes.

Economic status. Probably noneconomic.

Reference(s). Wagner, J. A. 1975. Review of the genera *Euplectus, Pycnoplectus, Leptoplectus,* and *Acolonia* (Coleoptera: Pselaphidae) including Nearctic species north of Mexico. Entomol. Amer. 49:125–207.

Euplectus* (*Diplectellus*) *signatus (Reichenbach) [W. Hem.]

Probable origin. Europe.

Detection. Specimens examined from Laurentide Park, Camp Le Relais, Quebec, August 29, 1956, from wood shavings and straw compost near domestic rabbit hatch; Barre, Washington Co., Vermont, July 7, 1961, from cow manure mixed with sawdust; Tilbury, Essex Co., Ontario, June 2, 1967, from manure; and Illinois and Wisconsin.

Host preference(s)/habitat. Restricted to rich domestic or farm compost, especially that with much fungal mycelia.

Economic status. Probably noneconomic.

Reference(s). Wagner, J. A. 1975. Review of the genera *Euplectus, Pycnoplectus, Leptoplectus,* and *Acolonia* (Coleoptera: Pselaphidae) including Nearctic species north of Mexico. Entomol. Amer. 49:125–207.

ELATERIDAE

Melanotus dichrous (Erichson) [W. Hem.]

Probable origin. Southern Europe.

Detection. Adjacent to Pier No. 1, Clinton Street, Canton pier area of Baltimore City, Maryland, late June 1965 to mid-July 1970, in blacklight trap.

Host preference(s)/habitat. Nocturnal, attracted to lights. Little or nothing is known about biology.

Economic status. Probably noneconomic.

Reference(s). Ford, E. J., Jr. 1973. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 23(29):472; Becker, E. C. 1973. A European species of *Melanotus* now established at Baltimore, Maryland (Coleoptera: Elateridae). Proc. Entomol. Soc. Washington 75:454–458.

DERMESTIDAE

Attegenus lobatus Rosenhauer [W. Hem.]

Probable origin. Europe.

Detection. New York, New York, May 15, 1964; in building. Also found at Detroit, Michigan, February 2, 1960; in building.

Host preference(s)/habitat. In nests of desert owls (*Athene noctua bactriana* Hutt.), Old World jumping rats or gerbils (Gerbillinae), long-clawed ground squirrels (*Spermophilopsis leptodactylus* Licht.), and various predatory mammals such as foxes and badgers; a pest of skins, furs, feathers, woolen goods, grain, and red pepper.

Economic status. Economic.

Reference(s). Beal, R. S., Jr. 1970. A taxonomic and biological study of species of Attegenini (Coleoptera: Dermestidae) in the United States and Canada. Entomol. Amer. 45:141–235.

MELYRIDAE

Troglops cephalotes Erichson [W. Hem.]

Probable origin. Central Europe.

Detection. Bedford, Massachusetts (Middlesex County), May 18, 1974 and May 20, 1975; at window.

Host preference(s)/habitat. Little or nothing is known about biology.

Economic status. Probably noneconomic.

Reference(s). Wittmer, W. 1975. First records of the genus *Troglops* Er. (Coleoptera: Malachiidae) in the United States. Coleopt. Bull. 29:250.

EUCNEMIDAE

Dirrhagofarsus lewisi (Fleutiaux) [W. Hem.]

Probable origin. Japan.

Detection. Leakin Park, Baltimore, Maryland, in 1976; larvae and pupae collected from fallen, dead beech tree (*Fagus grandifolia* Ehr.) between 4 March and 11 August 1976.

Host preference(s)/habitat. Little or nothing is known about biology and habits in Japan.

Economic status. Probably noneconomic.

Reference(s). Ford, E. J., Jr. and T. J. Spilman. 1979. Biology and immature stages of *Dirrhagofarsus lewisi,* a species new to the United States (Coleoptera, Eucnemidae). Coleopt. Bull. 33:75–83.

COCCINELLIDAE

Coccinella septempunctata (L.) [W. Hem.]

Probable origin. Europe.

Detection. Near Lyndhurst, New Jersey (Bergen County), June 28, 1973; in Hackensack Meadowlands. Beginning in 1956, the Beneficial Insects Research Laboratory, USDA-ARS, Newark, Delaware, released this species in the eastern U.S., but no recoveries were made to indicate its establishment.

Host preference(s)/habitat. Predaceous on numerous species of aphids and coccids, as well as larvae of some lepidopterous and weevil pests of agricultural crops.

Economic status. Beneficial.

Reference(s). Anonymous. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(33):659; Angalet, G. W. and R. L. Jacques. 1975. The establishment of *Coccinella septempunctata* L. in the continental United States. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 25(45–48):883–884; Larochelle, A. and M.-C. Lariviere. 1979. *Coccinella septempunctata* L. (Coleoptera; Coccinellidae) au Quebec: repartition geographique, habitat et biologie. Bull. Invent. Ins. Quebec 1(4):68–76; Hoebeke, E. R. and A. G. Wheeler, Jr. 1980. New distribution records of *Coccinella septempunctata* L. in the eastern United States (Coleoptera: Coccinellidae). Coleopt. Bull. 34:209–212.

Propylea quatuordecimpunctata (L.) [W. Hem.]

Probable origin. Europe.

Detection. Montreal: Ile de Montreal; Montmorency No. 2: Saint Jean-d'Orleans; Portneuf: Saint-Augustin; and Quebec: Lorette, Sainte-Foy.

Host preference(s)/habitat. Predaceous on various aphid species.

Economic status. Beneficial.

Reference(s). Landry, L.-P. 1979. Interessantes recoltes d'Insectes a Trois-Rivieres. Fabreries 5(1):8–10; Larochelle, A. 1979. Repartition de Coleopteres Coccinellidae au Quebec. Fabreries 5(2):26–33; Larochelle, A. 1979. Les Coleopteres Coccinellidae du Quebec. Cordulia, Suppl. 10:1–111; Larochelle, A. and M.-C. Lariviere. 1980. *Propylea quatuordecimpunctata* L. (Coleoptera: Coccinellidae) en Amerique du Nord: etablissement, habitat et biologie. Bull. Invent. Ins. Quebec 2(1):1–9.

Scymnus (Pullus) suturalis Thunberg [W. Hem.]

Probable origin. Europe.

Detection. 11 specimens examined from various localities in Pennsylvania July 1972; on various species of pine (reported as *S. coniferarum* Crotch).

Host preference(s)/habitat. Feeds mainly or entirely on aphids infesting conifers.

Economic status. Potentially beneficial.

Reference(s). Gordon, R. D. 1976. The Scymnini (Coleoptera: Coccinellidae) of the United States and Canada: key to genera and revision of *Scymnus, Nephus* and *Diomus.* Bull. Buffalo Soc. Nat. Sci. 28:1–362; Gordon, R. D. 1982. An Old World species of *Scymnus* (*Pullus*) established in Pennsylvania and New York (Coleoptera: Coccinellidae). Proc. Entomol. Soc. Washington 84:250–255.

Subcoccinella vigintiquatuorpunctata (L.) [W. Hem.]

Probable origin. Europe.

Detection. Southcentral Pennsylvania in August 1972 and in the Hackensack Meadowlands (Bergen County), New Jersey, in June 1973; on crownvetch (*Coronilla varia* L.).

Host preference(s)/habitat. Approximately 70 host plants, mainly species of Caryophyllaceae, Chenopodiaceae, and Leguminosae; a pest of alfalfa (*Medicago sativa* L.).

Economic status. Potentially economic.

Reference(s). Anonymous. 1974. European alfalfa beetle in the U.S.—1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(36):731–734; Anonymous. 1975. Distribution of European alfalfa beetle, *Subcoccinella vigintiquatuorpunctata.* U.S. Dept. Agric., Coop. Econ. Ins. Rep. 25(11):184; Wheeler, A. G., Jr. and T. J. Henry. 1981. Seasonal history and habits of the European alfalfa beetle, *Subcoccinella vigintiquatuorpunctata* (L.) (Coleoptera: Coccinellidae). Coleopt. Bull. 35:197–203.

LATHRIDIIDAE

Adistemia watsoni (Wollaston) [Can.]

Probable origin. Europe?

Detection. Ottawa, Ontario, February 1974; on the wall of an office building.

Host preference(s)/habitat. Feeds on spores and hyphae of various species of fungi (molds) which infest seed and herbarium specimens.

Economic status. Potentially economic.

Reference(s). Becker, E. C. 1977. New and noteworthy records of Coleoptera in Canada (1). Ann. Entomol. Soc. Quebec 22:14–17.

CHRYSOMELIDAE

Chaetocnema concinna (Marsham) [W. Hem.]

Probable origin. Europe.

Detection. Hingham, Massachusetts (Plymouth County), June 26, 1979; from sudangrass forage (*Sorghum sudanense* (Piper) Stapf) on farm.

Host preference(s)/habitat. Known from *Beta vulgaris* L. (beets and mangles), *Brassica* spp. (kale and rutabaga), *Chenopodium alba* L. (common lambsquarters), *Fragaria* sp. (strawberry), etc.

Economic status. Potentially economic.

Reference(s). Hoebeke, E. R. 1980. U.S. Dept. Agric., Coop. Plant Pest Rep. 5(20):374.

Longitarsus luridus (Scopoli) [U.S.]

Probable origin. Europe.

Detection. Amston, Connecticut (Tolland County), July 20, 1979; on beans in a garden.

Host preference(s)/habitat. Numerous hosts, including plants of Boraginaceae, Lamiaceae, Asteraceae, and Plantaginaceae.

Economic status. Probably noneconomic.

Reference(s). Anonymous. 1981. New U.S. detection in high hazard area. U.S. Dept. Agric., Plant Pest News 1(2):2–3; Anonymous. 1981. *Longitarsus luridus* extends range. U.S. Dept. Agric., Plant Pest News 1(3):2.

Psylliodes affinis (Paykull) [Can.]

Probable origin. Europe.

Detection. Between Hamilton and Burlington, Ontario (Halton Co.), June 13, 1981; from foliage of bitter nightshade (*Solanum dulcamara* L.).

Host preference(s)/habitat. Solanaceous plants, including bitter nightshade (*Solanum dulcamara*), potato (*Solanum tuberosum* L.), tobacco (*Nicotiana* spp.), tomato (*Lycopersicon esculentum* L.), black henbane (*Hyoscyamus niger* L.), *Lycium* sp., and occasionally hops (*Humulus* sp., Cannabinaceae). Apparently prefers *S. dulcamara.*

Economic status. Potentially economic.

Reference(s). Wheeler, A. G., Jr. and E. R. Hoebeke. In press. New records of a Palearctic flea beetle, *Psylliodes affinis,* in eastern North America. Proc. Entomol. Soc. Washington.

Psylliodes napi (F.) [W. Hem.]

Probable origin. Europe.

Detection. Ithaca, New York (Tompkins County) area during 1966–1969; also in Berkshire County, Massachusetts in early June 1968; on collard (*Brassica oleracea* L.) and on yellow rocket (*Barbarea vulgaris* L.).

Host preference(s)/habitat. Various wild crucifers.

Economic status. Potentially economic.

Reference(s). Tahvanainen, J. O. and R. B. Root. 1970. The invasion and population outbreak of *Psylliodes napi* (Coleoptera: Chrysomelidae) on yellow rocket (*Barbarea vulgaris*) in New York. Ann. Entomol. Soc. Amer. 63: 1479–1480.

Psylliodes picina (Marsham) [W. Hem.]

Probable origin. Europe.

Detection. Near Ulster, Pennsylvania (Bradford County), July 6, 1978; from corn (*Zea mays* L.) on farm.

Host preference(s)/habitat. Known from *Cirsium palustre* (L.) Scop. (a thistle), *Lysimachia vulgaris* L. (garden loosestrife), *Lythrum salicaria* L. (purple loosestrife) and *Quercus* (oaks).

Economic status. Probably noneconomic.

Reference(s). Hoebeke, E. R. 1979. U.S. Dept. Agric., Coop. Plant Pest Rep. 4(14):202.

Pyrrhalta viburni (Paykull) [W. Hem.]

Probable origin. Eurasia.

Detection. Ottawa, Ontario and Hull, Quebec, summer 1978; from foliage of *Viburnum opulus* L., also on ornamental plantings of *V. lantana* L. and *V. dentatum* L. and on native *V. rafinesquianum* Schultes.

Host preference(s)/habitat. *Viburnum* spp.

Economic status. Economic.

Reference(s). Becker, E. C. 1979. *Pyrrhalta viburni* (Coleoptera: Chrysomelidae), a Eurasian pest of *Viburnum* recently established in Canada. Canad. Entomol. 111:417–419.

CURCULIONIDAE

Calomycterus setarius Roelofs [Can.]

Probable origin. Japan.

Detection. Lanark, Ontario, August 1974; in and around a house, and "fairly abundant along the roadside."

Host preference(s)/habitat. Variety of herbaceous plants.

Economic status. Probably noneconomic.

Reference(s). Becker, E. C. 1977. New and noteworthy records of Coleoptera in Canada (1). Ann. Entomol. Soc. Quebec 22:14–17.

Larinus carlinae (Olivier) [W. Hem.]

Probable origin. Europe.

Detection. Maugansville, Maryland (Washington County), June 15, 1971; on thistle (*Cirsium* sp.).

Host preference(s)/habitat. Composites, including *Carduus, Cirsium, Carlina,* and *Centaurea.*

Economic status. Potentially beneficial.

Reference(s). White, J. C. 1972. A European weevil, *Larinus carlinae* Olivier, collected in Maryland. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 22(26):418. [D. R. Whitehead (USDA, Systematic Entomology Laboratory) considers *L. planus* (F.) as the correct name.]

Otiorhynchus clavipes Bonsdorff [W. Hem.]

Probable origin. Western Europe.

Detection. "Newport County, Rhode Island, July 16, 1942."

Host preference(s)/habitat. Adults feed on leaves of many fruit trees and vines, and larvae eat roots of lilac (*Syringa*), raspberry (*Rubus*), strawberry (*Fragaria*), smooth sumac (*Rhus glabra* L.), European cranberry bush (*Viburnum opulus* L.), bigsting nettle (*Urtica dioica* L.), curly dock (*Rumex crispus* L.), Japanese aucuba (*Aucuba*), and honeysuckle (*Lonicera*). A serious pest of strawberries.

Economic status. Economic.

Reference(s). Warner, R. E. and F. B. Negley. 1976. The genus *Otiorhynchus* in America north of Mexico (Coleoptera: Curculionidae). Proc. Entomol. Soc. Washington 78:240–262.

Otiorhynchus ligustici (L.) [Can.]

Probable origin. Europe.

Detection. Wolfe Island (in the St. Lawrence River), near Kingston, Ontario, "about 1965 and later."

Host preference(s)/habitat. Numerous plants; a serious pest of alfalfa (*Medicago sativa*).

Economic status. Economic.

Reference(s). Warner, R. E. and F. B. Negley. 1976. The genus *Otiorhynchus* in America north of Mexico (Coleoptera: Curculionidae). Proc. Entomol. Soc. Washington 78:240–262; Becker, E. C. 1977. New and noteworthy records of Coleoptera in Canada (1). Ann. Entomol. Soc. Quebec 22:14–17.

Polydrusus cervinus (L.) [W. Hem.]

Probable origin. Europe.

Detection. Moorestown?, New Jersey (Burlington County), 1969; Hanover, New Hampshire (Grafton County), August 1963; and environs of Hanover, late April to mid-October 1963; from the windshield of a car, and probably from birch (*Betula* sp.) that "margined the lacrosse playing fields of Dartmouth College."

Host preference(s)/habitat. Larvae live in the roots of orchard grass, *Dactylis glomerata* L., and the adults feed on leaves of birch, oak, hazel, and maple.

Economic status. Probably economic.

Reference(s). Warner, R. E. 1971. *Polydrusus cervinus* (L.), a European weevil discovered in North America (Coleoptera: Curculionidae). Proc. Entomol. Soc. Washington 73:57; Hoebeke, E. R. 1980. U.S. Dept. Agric., Coop. Plant Pest Rep. 5(29):540.

Campylirhynchus bruchoides (Herbst) [W. Hem.]

Probable origin. Europe.

Detection. Bear, Delaware (New Castle County), July 25, 1979, and Potomac, Maryland (Montgomery County) in 1979; from alfalfa.

Host preference(s)/habitat. Host plants include *Polygonum* (*P. lapathifolium* L., *P. persicaria* L., and *P. hydropiper* L.), and species of *Oenanthe* and *Chaerophyllum* (Apiaceae).

Economic status. Probably noneconomic.

Reference(s). Hoebeke, E. R. and D. R. Whitehead. 1980. New records of *Rhinoncus bruchoides* (Herbst) for the Western Hemisphere and a revised key to the North American species of the genus *Rhinoncus* (Coleoptera: Curculionidae: Ceutorhynchinae). Proc. Entomol. Soc. Washington 82:556–561.

SCOLYTIDAE

Xyleborus validus Eichhoff [W. Hem.]

Probable origin. Japan.

Detection. Old Westbury, Long Island, New York (Nassau County), May 1976; from infested grove of mature beech trees and possibly a young Norway maple in arboretum.

Host preference(s)/habitat. Hosts include *Abies, Pinus, Tsuga, Fagus, Prunus,* and *Quercus.*

Economic status. Potentially economic.

Reference(s). Willson, H. R. 1976. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 1(37):610; Wood, S. L. 1977. Introduced and exported American Scolytidae (Coleoptera). Great Basin Nat. 37:67–74; Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. Mem., no. 6:1–1359.

LEPIDOPTERA

OCHSENHEIMERIIDAE

Ochsenheimeria vacculella F. Von Roesslerstamm [W. Hem.]

Probable origin. Eurasia.

Detection. Specimens collected from unspecified locality in New York in 1968, and from near Ithaca, New York (Tompkins Co.) in August 1973; from Slippery Rock, Pennsylvania (Butler Co.) in August 1971; and also from unspecified locality in Geauga County, Ohio, in 1964, and in Cuyahoga County, Ohio, in 1967.

Host preference(s)/habitat. Larval host plants include various cereals and a number of wild grass species.

Economic status. Potentially economic.

Reference(s). Davis, D. R. 1975. A review of Ochsenheimeriidae and the introduction of the cereal stem moth *Ochsenheimeria vacculella* into the United States (Lepidoptera: Tineoidea). Smith. Contrib. Zool., no. 192:20

pp.; Ellis, C. R. 1978. First record of the cereal stem moth, *Ochsenheimeria vacculella* (Lepidoptera: Ochsenheimeriidae) in Canada. Proc. Entomol. Soc. Ontario 109:82–83.

OECOPHORIDAE (ETHMIIDAE)

Ethmia bipunctella (F.) [W. Hem.]

Probable origin. Europe.

Detection. Laval and Philipsburg, Quebec, May–August 1965–1969, and also Pincourt, Ile Perrot, August 1969.

Host preference(s)/habitat. Larval host plants are *Echium vulgare* L., and species of *Symphytum, Cynoglossum, Anchusa,* and *Lithospermum* (all Boraginaceae).

Economic status. Probably noneconomic.

Reference(s). Sheppard, A. C. 1970. Palearctic Lepidoptera new to the province of Quebec. Ann. Entomol. Soc. Quebec 15:14–16; Powell, J. A. 1973. A systematic monograph of New World ethmiid moths (Lepidoptera: Gelechioidea). Smith. Contrib. Zool., no. 120:302 pp.; Heppner, J. B. and J. A. Powell. 1974. *Ethmia bipunctella* in Maryland, Pennsylvania and West Virginia: the expanding range of an introduced European moth (Gelechioidea). J. Lepid. Soc. 28:302–305.

TORTRICIDAE

Cnephasia stephensiana (Doubleday) [W. Hem.]

Probable origin. Europe.

Detection. 5 specimens collected in Nova Scotia in 1954 (CNC collection), from Prince Edward Island and Quebec in 1978, and from the vicinity of Ottawa, Ontario, in 1979.

Host preference(s)/habitat. Larvae polyphagous on herbaceous plants, including *Chrysanthemum, Inula, Hieracium, Taraxacum, Centaurea, Sonchus, Heracleum, Vicia, Chenopodium, Rumex, Ranunculus, Plantago*; occasionally on cultivated peas and beans.

Economic status. Potentially economic.

Reference(s). Mutuura, A. 1982. *Cnephasia stephensiana,* a species newly recorded from Canada and compared with the previously recorded *C. interjectana* (Lepidoptera: Tortricidae). Canad. Entomol. 114:667–671.

Grapholita delineana (Walker) [W. Hem.]

Probable origin. Eurasia.

Detection. Earliest label dates are New York, New York in 1944, and Madison, Wisconsin and Lexington, Kentucky in 1943; present distribution records include Minnesota, Iowa, Missouri, Wisconsin, Illinois, Kentucky, and New York.

Host preference(s)/habitat. Wild hops (*Humulus lupulus* L.), as well as hemp (both Cannabinaceae); larvae feed in stems, inflorescences, and developing seeds.

Economic status. Economic.

Reference(s). Miller, W. E. 1982. *Grapholita delineana* (Walker), a Eurasian hemp moth, discovered in North America. Ann. Entomol. Soc. Amer. 75:184–186.

GEOMETRIDAE

Chloroclystis rectangulata (L.) [W. Hem.]

Probable origin. Europe.

Detection. The following localities in Nova Scotia, summer 1970: Smiley Brook Provincial Park, near Brooklyn, Hants Co., July 20; Middle River, Victoria Co., Cape Breton Island, July 27; Baddeck River, near Baddeck Bridge, Victoria Co., July 29; and the Hants Co. locality, July 23, 1972.

Host preference(s)/habitat. Primary larval hosts include species of *Crataegus, Prunus* and *Pyrus,* and blossoms of wild and cultivated apple.

Economic status. Potentially economic.

Reference(s). Ferguson, D. C. 1972. The occurrence of *Chloroclystis rectangulata* (L.) in North America (Geometridae). J. Lepid. Soc. 26:220–221; Neil, K. 1980. The occurrence of *Chloroclystis rectangulata* (Geometridae) in New Brunswick. J. Lepid. Soc. 34:75.

Eulithis mellinata (F.) (=**Lygris associata** (Bkh.)) [W. Hem.]

Probable origin. Europe.

Detection. Laval (Ile Jesus), Quebec, July 10, 1967, and June 24 and July 1, 1973; captured at light in a garden at rear of a home.

Host preference(s)/habitat. Larval host plants are red and black currant (*Ribes rubrum* L. and *R. nigrum* L.).

Economic status. Probably noneconomic.

Reference(s). Sheppard, A. C. 1975. *Lygris associata* Bork., a new record for North America (Lepidoptera: Geometridae). Ann. Entomol. Soc. Quebec 20:7; Neil, K. 1978. A second locality for *Eulythis mellinata* (Geometridae) in North America. J. Lepid. Soc. 32:224–225.

NOCTUIDAE

Noctua pronuba L. [W. Hem.]

Probable origin. Europe.

Detection. West end Halifax, Nova Scotia, August 8, 1979; under a house porch light.

Host preference(s)/habitat. Numerous larval hosts include *Poa annua* L., *Rumex, Polygonum, Atriplex, Myosotis, Taraxacum* spp., and various Brassicaceae.

Economic status. Probably noneconomic.

Reference(s). Neil, K. 1981. The occurrence of *Noctua pronuba* (L.) (Noctuidae) in Nova Scotia: a new North American record. J. Lepid. Soc. 35: 248.

DIPTERA

CHIRONOMIDAE

Orthocladius* (*Orthocladius*) *dentifer Brundin [W. Hem.]

Probable origin. Europe.

Detection. Jock River, near Munster Hamlet, Ontario, May 1973; Lake Ontario, Sta. X, May 1968; Leeds Co., St. Lawrence Nat'l. Pk., center of Grenadier Isl., May 1975; known also from other northcentral and western North American localities.

Host preference(s)/habitat. Pupae and adults in and around lakes.

Economic status. Noneconomic.

Reference(s). Soponis, A. R. 1977. A revision of the Nearctic species of *Orthocladius* (*Orthocladius*) Van der Wulp (Diptera: Chironomidae). Mem. Entomol. Soc. Canad., no. 102:187 pp.

CECIDOMYIIDAE

Coccopsis marginata de Meijere [W. Hem.]

Probable origin. Europe.

Detection. "New York"; in light trap.

Host preference(s)/habitat. Little or nothing is known about biology.

Economic status. Probably noneconomic.

Reference(s). Gagne, R. J. 1976. New Nearctic records and taxonomic changes in the Cecidomyiidae (Diptera). Ann. Entomol. Soc. Amer. 69:26–28.

Colomyia hordei Barnes [W. Hem.]

Probable origin. Europe.

Detection. "New Jersey"; in light trap.

Host preference(s)/habitat. Little or nothing is known about biology.

Economic status. Probably noneconomic.

Reference(s). Gagne, R. J. 1976. New Nearctic records and taxonomic changes in the Cecidomyiidae (Diptera). Ann. Entomol. Soc. Amer. 69:26–28. [R. J. Gagne (USDA, Systematic Entomology Laboratory) feels that both cecidomyiids represent "widespread Holarctic species" rather than introductions.]

RHAGIONIDAE

Rhagio strigosus Meigen [W. Hem.]

Probable origin. Europe.

Detection. Bergen, New York (Genesee County), around August 8, 1981; from garage window. Additional dead and damaged specimens collected from garage window sill at same site in summer 1982.

Host preference(s)/habitat. Little or nothing is known about biology.

Economic status. Noneconomic.

Reference(s). Pechuman, L. L. and E. R. Hoebeke. In press. European Rhagionidae in eastern North America: records of newly discovered species (Diptera, Brachycera). Entomol. News.

Rhagio tringarius L. [U.S.]

Probable origin. Europe.

Detection. Lenox (Eastover), Massachusetts (Berkshire County), July 7, 1982 and Jam Pond Bog near German, New York (Chenango County), August 7, 1980.

Host preference(s)/habitat. Among shrubs on damp ground.

Economic status. Noneconomic.

Reference(s). Pechuman, L. L. and E. R. Hoebeke. In press. European Rhagionidae in eastern North America: records of newly discovered species (Diptera, Brachycera). Entomol. News.

SPHAEROCERIDAE

Apteromyia claviventris (Strobl) [W. Hem.]

Probable origin. Europe.

Detection. Ontario: Guelph, 4-XI-1981, ex decaying mushroom; Guelph, IX-1979; Dundas, Royal Botanical Gardens, 10-IX-1982, ex decaying coral fungus; and New Brunswick: St. Andrews, 5-V-1978, ex pan trap in seaweed; St. Andrews, 15-VIII-1978, ex carrion trap.

Host preference(s)/habitat. Adults associated with compost piles, also found in rabbit, mouse, and mole nests; bred from decomposing narcissus bulbs.

Economic status. Probably noneconomic.

Reference(s). Marshall, S. A. and J. R. Rohacek. 1982. Two new species and a new Nearctic record in genera *Apteromyia* and *Nearcticorpus* (Diptera: Sphaeroceridae). Ann. Entomol. Soc. Amer. 75:642–648.

AGROMYZIDAE

Agromyza frontella (Rondani) [Can.]

Probable origin. Europe.

Detection. Near St. Armand, Quebec, less than 3 miles from the Vermont border, June 29, 1972; on alfalfa (larvae reared). First reported in U.S. (Massachusetts) as *Agromyza* sp.; now well established in northeastern states.

Host preference(s)/habitat. Host plants are various species of *Medicago* (*M. falcata* L., *M. lupulina* L., *M. sativa*), *Melilotus*, and *Trifolium*; preferred host is apparently alfalfa, *M. sativa.*

Economic status. Economic.

Reference(s). Harcourt, D. G. 1973. *Agromyza frontella* (Rond.) (Diptera: Agromyzidae): a pest of alfalfa new to Canada. Ann. Entomol. Soc. Quebec 18:49–51.

ANTHOMYIIDAE

Delia coarctata (Fallen) [W. Hem.]

Probable origin. Europe.

Detection. First documented occurrence at Cap Chat, Quebec, 21–29 July 1954; additional collections in 1954 and 1971 from Quebec and New Brunswick, and 1980 from Nova Scotia, Prince Edward Island, and Maine.

Host preference(s)/habitat. Primary wild host is couch grass (*Agropyron repens* (L.) Beauv.); also important pest of winter wheat, and will infest barley and rye.

Economic status. Economic.

Reference(s). McAlpine, J. F. and C. Slight. 1981. The wheat bulb fly, *Delia coarctata,* in North America (Diptera: Anthomyiidae). Canad. Entomol. 113:615–621.

Emmesomyia socia (Fallen) [W. Hem.]

Probable origin. Europe.

Detection. South of Auburn, New York (Cayuga County), August 6 and 8, 1970; from cells of *Oxybelus uniglumis quadrinotatus* Say (a sphecid wasp).

Host preference(s)/habitat. Adults attracted to animal dung and other decaying animal matter; larvae develop in dung.

Economic status. Probably noneconomic.

Reference(s). Anonymous. 1971. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 21(1):5. [F. C. Thompson (USDA, Systematic Entomology Laboratory) believes that this record should be referred to the closely related species *E. villica* (Meigen).]

HYMENOPTERA

TENTHREDINIDAE

Allantus viennensis (Schrank) [W. Hem.]

Probable origin. Europe.

Detection. Several localities in Tompkins County, New York (vicinity of the Cornell University campus and Ludlowville) from June 1967 to August 1968; from flowers of *Rosa* sp. and *Rubus* sp.

Host preference(s)/habitat. Larval hosts include foliage of *Rosa* spp., and also *Rubus* and *Ribes.*

Economic status. Potentially economic.

Reference(s). Smith, D. R. 1975. A rose sawfly new to North America (Hymenoptera: Tenthredinidae). U.S. Dept. Agric., Coop. Econ. Ins. Rep. 25(10):163–165.

BRACONIDAE

Chorebus rondanii (Giard) [U.S.]

Probable origin. Europe.

Detection. South Deerfield, Massachusetts (Franklin County), May 1973; reared from puparia of asparagus miner (*Ophiomyia simplex* (Loew)) (Agromyzidae).

Host preference(s)/habitat. Known host is *Ophiomyia simplex.*

Economic status. Potentially beneficial.

Reference(s). Anonymous. 1973. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 23(43):729.

ICHNEUMONIDAE

Homotherus magus (Wesmael) [W. Hem.]

Probable origin. Europe.

Detection. "Newfoundland"; collections made in July and August 1973, and June–August 1974.

Host preference(s)/habitat. Little or nothing is known about biology.

Economic status. Probably noneconomic.

Reference(s). Heinrich, G. H. 1975. Synopsis of Nearctic Ichneumoninae Stenopneusticae with particular reference to the northeastern region (Hymenoptera). Supplement 5: Ichneumoninae of the island of Newfoundland. Natur. Canad. 102:753–782.

EULOPHIDAE

Tetrastichus rhosaces (Walker) [W. Hem.]

Probable origin. Europe.

Detection. Winchester, Virginia (Frederick County), July 6, 1973; from *Cassida rubiginosa* F. (a chrysomelid beetle) on *Carduus nutans* L.

Host preference(s)/habitat. Four species of *Cassida* have been recorded as hosts.

Economic status. Potentially beneficial.

Reference(s). Anonymous. 1974. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 24(14):203.

PTEROMALIDAE

Trichomalus statutus (Foerster) [W. Hem.]

Probable origin. Europe.

Detection. Blacksburg, Virginia (Montgomery County), August 28, 1970; emerged from pupae of the frit fly, *Oscinella frit* (L.) (Chloropidae).

Host preference(s)/habitat. Known host is *Oscinella frit.*

Economic status. Beneficial.

Reference(s). Allen, W. A. 1971. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 21(23):400.

EUCOILIDAE

Hexacola hexatoma (Hartig) [W. Hem.]

Probable origin. Europe.

Detection. Blacksburg, Virginia (Montgomery County), September 3, 1970; emerged from pupae of the frit fly, *Oscinella frit.*

Host preference(s)/habitat. Known host is *Oscinella frit.*

Economic status. Beneficial.

Reference(s). Allen, W. A. 1971. U.S. Dept. Agric., Coop. Econ. Ins. Rep. 21(23):400.

VESPIDAE

Polistes gallicus (L.) [W. Hem.]

Probable origin. Europe.

Detection. Cambridge, Somerville, Belmont, and Newton (Boston area), Massachusetts in 1981; also in Cambridge in 1980.

Host preference(s)/habitat. Nests constructed in enclosed places, such as metal containers and gutter pipes; or in the open, hanging from eaves, branches, or other protective horizontal structures.

Economic status. Probably noneconomic.

Reference(s). Hathaway, M. A. 1981. *Polistes gallicus* in Massachusetts (Hymenoptera: Vespidae). Psyche 88:169–173.

Vespula germanica (F.) [W. Hem.]

Probable origin. Europe.

Detection. Earliest known record is Ithaca, New York (Tompkins County), August 18, 1891; other records include vicinity of Ithaca from 1920–1950; and Walkersville, Maryland (Frederick County) in 1968. (Previous reports of *germanica* in North America have been discounted as they were probably based on misidentifications of the North American species *V. maculifrons* (de Buysson).)

Host preference(s)/habitat. Nests are usually subterranean, but may be aerial or in roofs, attics, and between walls of houses; workers prey on wide variety of arthropods and also are opportunistic in exploiting food sources.

Economic status. Economic.

Reference(s). Menke, A. S. and R. Snelling. 1975. *Vespula germanica* (Fabricius), an adventive yellow jacket in the northeastern United States (Hymenoptera: Vespidae). U.S. Dept. Agric., Coop. Econ. Ins. Rep. 25(11): 193–200; Akre, R. D., A. Greene, J. F. MacDonald and others. 1981. The yellowjackets of America north of Mexico. U.S. Dept. Agric., Sci. and Educ. Admin., Agriculture Handbook, no. 552:102 pp.

MEGACHILIDAE

Chelostoma campanularum (Kirby) [W. Hem.]

Probable origin. Europe.

Detection. Schoharie, Tompkins, Ontario, Schuyler, and Jefferson counties, New York, since 1973, from July 1–July 27; from inflorescences of bellflower, *Campanula* spp. (Campanulaceae).

Host preference(s)/habitat. Strictly oligolectic for pollen of bellflowers, *Campanula* spp.; nests constructed in pre-existing cavities, such as holes in old wood, including stumps, posts, and structural timbers.

Economic status. Probably noneconomic.

Reference(s). Eickwort, G. C. 1980. Two European species of *Chelostoma* established in New York State (Hymenoptera: Megachilidae). Psyche 87: 315–323.

Chelostoma fuliginosum (Panzer) [W. Hem.]

Probable origin. Europe.

Detection. Schoharie, Tompkins, and Ontario counties, New York, since 1962, from June 4–July 2; from inflorescences of bellflower, *Campanula* spp.

Host preference(s)/habitat. Strictly oligolectic for pollen of bellflowers, *Campanula* spp.; nests constructed in pre-existing cavities such as holes in old wood, including stumps, poles, and structural timbers.

Economic status. Probably noneconomic.

Reference(s). Eickwort, G. C. 1980. Two European species of *Chelostoma* established in New York State (Hymenoptera: Megachilidae). Psyche 87: 315–323.

Lithurge chrysurus Fonscolombe [W. Hem.]

Probable origin. Western Mediterranean area.

Detection. Phillipsburg, New Jersey (Warren County), June 1977 (the Phillipsburg nest site is only 150 feet from the railroad which serves industries along the Delaware River); from nests in house siding, consisting of a 4 mm outer layer of asphalt-impregnated wood fiber.

Host preference(s)/habitat. Gathers pollen of spotted knapweed (*Centaurea maculosa* (Lamarck)) (Asteraceae), and also from star thistle (*C. calcitrapa* L.).

Economic status. Probably noneconomic.

Reference(s). Roberts, R. B. 1978. The nesting biology, behavior and immature stages of *Lithurge chrysurus,* an adventitious wood-boring bee in New Jersey (Hymenoptera: Megachilidae). J. Kansas Entomol. Soc. 51:735–745.

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THE TYPES OF CERCERINE WASPS DESCRIBED BY NATHAN BANKS (HYMENOPTERA: PHILANTHIDAE)[1]

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Abstract.—A study of the type material of the 52 species-group taxa of *Cerceris* and one species of *Eucerceris* described by Nathan Banks is reported. Lectotypes of 25 species-group taxa of *Cerceris* are designated. Banks designated holotypes in his original descriptions for two species of *Cerceris,* and the types of the remaining 25 species-group taxa of *Cerceris* and one species of *Eucerceris* are accepted as holotypes since the original descriptions state or imply that only one specimen was involved and only one specimen was found.

In a series of nine papers from 1912 to 1947 Nathan Banks described 52 species-group taxa in the genus *Cerceris* and one species of *Eucerceris.* In only two cases did he unambiguously designate a holotype in the original description. He states the number of specimens in the type series in some cases but not in others. Most, but not all, specimens comprising syntype series are conspecific. Type material for 49 of Banks' taxa is in the Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ), type material of three species is in the American Museum of Natural History, New York (AMNH), and one species is represented by type specimens in both institutions.

Lectotypes are designated below for 25 taxa. Holotypes of two species were designated by Banks in the original descriptions. The remaining 26 taxa are represented by holotypes since only one type specimen was found and the original description either states or implies that only one specimen was involved.

In the MCZ each holotype and each specimen in a syntype series bears a red MCZ label with the printed word TYPE and the type number handwritten below it. Each specimen in a syntype series carries the same type number. In his 1917 and 1947 papers Banks stated the MCZ type number for each newly described species, but he did not do so in his other papers.

For the taxa described from 1912 to 1917 there is usually a small, red

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label with only the handwritten word "type" on one, and only one, specimen of a syntype series in addition to the red MCZ type label. For the taxa described from 1912 to 1919 subscript numbers are usually found written below the letter "E" of the printed word "TYPE" on the red MCZ label. One specimen of a syntype series is always without a subscript number. The subscript numbering starts with "2" and proceeds consecutively according to the number of specimens in the syntype series. Where the small, red handwritten type label also occurs, it is always on the specimen without a subscript number. I assume that the presence of the small, red handwritten type label and/or the absence of a subscript number signifies Banks' intention that the specimen so labelled be regarded as the type. To the extent possible I have been guided by the above labelling in selecting lectotypes. In some cases there are no such clues. In two cases I have deviated from the above guideline because of the seriously damaged condition of the specimens which I would have otherwise selected.

Except as otherwise noted, when a single specimen was found, and nothing in the original description indicates that more than one specimen was involved, that specimen is accepted as the holotype. With the exception of *Cerceris huachuca,* all holotypes and lectotypes are in conformity with the original descriptions.

Each holotype and one specimen of each syntype series carries a determination label in Banks' handwriting. With one exception (*C. semiatra*) the word "Type" is written on the label. These "header" labels usually have several pinholes, and it cannot be assumed that the specimen on which the header label now occurs is the one on which it was placed by Banks. The present placement of these header labels on specimens within syntype series is not always consistent with the occurrence of the small, red handwritten type label or the presence or absence of the subscript numbers discussed above. These header labels have largely been ignored in selection of lectotypes.

Individual specimens of eight species bear a curious blue "Paratype" label in a handwriting that does not appear to be that of Banks. There is no apparent pattern as to the specimen in a syntype series on which this label appears. Hathaway (1981) states "No one here [MCZ] knows anything about the blue paratype labels". These labels have been ignored in lectotype selection.

Synonymy and taxonomic status of the 52 species of *Cerceris* described by Banks will be treated in a forthcoming synonymic check-list of North and Central American *Cerceris.*

Cerceris abbreviata Banks, 1919:84

Described from "Males from Yakima River, Little Spokane and Umatilla, Washington. June and July (S. Henshaw)". Number of specimens and MCZ type number not stated. Five conspecific syntype males are in the MCZ with the type number 13794 labelled as above. One specimen labelled "Yakima R., W. T., Nelson's, July 4,5, '82" is without a subscript number on the MCZ type label and is designated lectotype. The other four specimens have subscript numbers 2, 3, 4, 5 respectively.

Cerceris alaope Banks, 1912:22

Described from both sexes "From Falls Church, Va., 5 June on *Ceanothus*". Number of specimens and MCZ type number not stated. The male is described first in the original description, and the female is given rather cursory treatment. A male and a female in the MCZ with type number 13784 are labelled as above except that the male carries the date "5 July" and the female the date "26 June". The date of "5 June" in the original description is considered to be a *lapsus.* The male bears a small, red handwritten type label in addition to the MCZ type label and is designated lectotype. The female is not conspecific but is a specimen of *Cerceris clypeata* Dahlbom with reduced pale markings on the posterior terga.

Cerceris ampla Banks, 1912:16

Described from both sexes from "Fedor, Lee County, Texas (Birkman)". Number of specimens and MCZ type number not stated. A female and a conspecific male are in the MCZ with type number 13769. The female with a small, red handwritten type label and a MCZ type label without a subscript number is designated lectotype. The male has the subscript number 2 on the MCZ type label.

Cerceris arelate Banks, 1912:18

Described from the female "From Great Falls, Va., 20 June". Number of specimens and type number not stated. One female in the MCZ labelled as above with type number 13779 is accepted as the holotype.

Cerceris (*Apiratrix*) [sic] *arizonella* Banks, 1947:32

Described from "One male from Tempe, Arizona, 1 August (Bequaert). Type M.C.Z. no. 23538". One male in the MCZ labelled as above is accepted as the holotype.

Cerceris arno Banks, 1947:19

Described from two conspecific females "From Colton, Calif. (Pilate), Eddy Collection, and mountains near Claremont (Baker). Type M.C.Z. no. 23542". The two females labelled as above are in the MCZ. The female from Colton carries both a red MCZ Paratype label with the number 23542 and a MCZ Holotype label with the "Holo" handwritten before the printed word TYPE. The anterior four legs and most of the antennae are missing from this specimen. The second specimen is labelled "Mts. near Claremont, Cal. Baker" and bears a MCZ type 23542 label as well as a small, white handwritten "*ferruginior*" label. Although the gaster is glued to the second label, the specimen from "Mts. near Claremont" is in much better condition and is designated lectotype.

Cerceris astarte Banks, 1913b:424

Described from the female from "Falls Church, Va., 7 and 8 Sept. 1912". Number of specimens and type number not stated. One female is in the MCZ labelled "Falls Church, Va., 7-IX" with the type number 13788 and a small, red handwritten type label. Since two collection dates were given in the original description, it is presumed that more than one specimen was involved. The above labelled specimen is designated lectotype.

Cerceris athene Banks, 1947:20

Described from the female "From Claremont, Calif. (Baker). Type M.C.Z. no. 23537". Number of specimens not stated. One female in the MCZ with the above labelling is accepted as the holotype.

Cerceris atramontensis Banks, 1913b:425

Described from the female "From Valley of Black Mts., N. Car., 23 July, 1906 (Beutenmuller)". Number of specimens and type number not stated. One specimen is in the AMNH with the above labelling and bears a label "*Cerceris atramontensis* Bks.—Type" in Banks handwriting. It has a red "Type AMNH" label with no number plus a label reading "Am. Mus. Nat. Hist., Dept. Invert. Zool. No. 21180", and it is accepted as the holotype.

Cerceris belfragei Banks, 1917:114

Described from both sexes from "Type.—M.C.Z. 10029. Texas. G. W. Belfrage. Coll. Peabody Academy Science, Salem. Four specimens". Three females and one male are in the MCZ with the above type number. One female labelled "Tex." lacks a subscript number on the MCZ type label and is designated lectotype. The male has subscript number 2, and two females have subscript numbers 3 and 4 respectively. The four specimens are conspecific. The female with subscript number 3 has the blue paratype label described in the introductory discussion.

Cerceris calodera Banks, 1947:22

Described from "One [male] from Jacumba, Calif., 12 August 1917. Type M.C.Z. no. 27622". One male in the MCZ with the above labelling is accepted as the holotype.

Cerceris jucunda carolina Banks, 1912:26

Described from specimens "From Southern Pines". Number of specimens, sex and MCZ type number not stated. Reference in the original description to the mesosternal processes indicates that he had males. Three conspecific males from "Southern Pines, N.C." are in the MCZ with the type number 13785. A male with the collection date "VI-4-09", a small, red handwritten type label and the MCZ type label lacking a subscript number is designated lectotype. It also carries the blue paratype label described earlier. The other two males have collection dates of "VI-4-10" and "VII-12-09", and bear subscript numbers 2 and 3 respectively on the MCZ type labels.

Cerceris carrizonensis Banks, 1915:403
Described from the male from Uvalde, Texas (misspelled Walde in the original description). Number of specimens and MCZ type number not stated. One male in the MCZ with type number 13772 labelled "Uvalde, Texas, June 19–20, 930 ft." is accepted as the holotype.

Cerceris catawba Banks, 1912:25
Described from both sexes "From Southern Pines, N. Car. June, (Manee)". Number of specimens and MCZ type number not stated. A female and a conspecific male with the above labelling in the MCZ have the type number 13787. The female bears a small, red handwritten type label in addition to the MCZ label, the latter being without a subscript number. The specimen is labelled "Southern Pines, N.C., VI-5-09" and is designated lectotype. The male has a collection date of "VI-4-09", and the MCZ type label has the subscript number 2.

Cerceris chryssipe Banks, 1912:18
Described from both sexes from "Falls Church, Va. in July on *Cicuta*". Number of specimens and MCZ type number not stated. One female and six conspecific males are in the MCZ with type number 13791. The female has a small, red handwritten type label in addition to the MCZ label, the latter being without a subscript number. It is labelled "Falls Church, Va., 30-VII" and is designated lectotype. The males have the subscript numbers 2, 3, 4, 5, 6, and 8 on the MCZ type lables. The specimen with subscript number 7 has been found in the U.S. National Museum, Washington.

Cerceris clymene Banks, 1912:20
Described from both sexes "From Glencarlyn, Va., 23 June, (*Ceanothus*), and Falls Church, Va., 30 July". Number of specimens and MCZ type number not stated. One female and three conspecific males are in the MCZ with type number 13789. All are from "Falls Church, Va., 30-VII", there being no specimen from Glencarlyn, Va. The female bears a small, red handwritten type label, lacks a subscript number on theMCZ type label, and is here designated lectotype. The males have the subscript numbers 2, 3, and 4 respectively.

Cerceris completa Banks, 1919:83
Described from "Male from Claremont, California (Baker)". MCZ type number not stated. One male labelled as above in the MCZ with type number 13767 is accepted as the holotype.

Cerceris dakotensis Banks, 1915:402
Described from both sexes "From Fargo, N. Dak., July 7 to Sept. 6 (Stevens

coll.)". Number of specimens and MCZ type number not stated. A female and two conspecific males are in the MCZ with type number 13770. The female has a small, red handwritten type label and the MCZ label is without a subscript number. It is labelled "Fargo, N.D., Jul. 9, 1911, O. A. Stevens, *Melilotus alba*" and is designated lectotype. Males have subscript numbers 2 and 3 on the MCZ label and have collection dates of "July 7, 1911", and "Aug. 2, 1913", respectively. The collection date of "Sept. 6" is not represented in the type material.

Cerceris denticularis Banks, 1917:113

Described from both sexes from "Type—M.C.Z. no. 10,028. Oregon: Umatilla, June, 1882; Washington: Lone Tree, Yakima River, 30 June, 1882. Samuel Henshaw. Nine specimens." Four females and two males, all conspecific, with the above type number are in the MCZ. A female labelled "Umatilla, Or., June 24, '82" is without a subscript number on the MCZ type label and is designated lectotype. Three females have the subscript numbers 2, 3, and 6, respectively, and two males have the subscript numbers 7 and 8, respectively. The male with subscript number 7 is labelled "Spokane, W. T., July 27, '82", a locality not mentioned in the original description. The subscript numbers 4 and 5 are not represented.

Cerceris englehardti Banks, 1947:12

Described from "A male from St. John, Arizona, 27 July, 1931 (G. P. Englehardt). Type M.C.Z. no. 27638". One male labelled as above is in the MCZ, but the MCZ label states "MCZ Paratype 27638". Since the original description states "a male" and only one specimen was found, I regard the red paratype label as a *lapsus* in labelling and accept the specimen as the holotype.

Cerceris eurymele Banks, 1947:11

Described from "The female holotype from Davis, Calif., 30 June (Bohart), M.C.Z. no. 23546, and males from El Cajon, Calif., May 1 (Van Duzee), and Santa Barbara, Calif., 18 July (Cockerell), Riverside, Calif., 4 Oct. (Melander)". The female holotype as designated above is labelled with a red MCZ holotype label in addition to the MCZ 23546 type label. Three males each carry a red MCZ paratype label with the type number 23546.

Cerceris floridensis Banks, 1915:403

Described from the male "From Gulfport, Fla. (Reynolds)". Number of specimens and MCZ type number not stated. One male labelled as above in the MCZ with the type number 13765 is accepted as holotype.

Cerceris gnarina Banks, 1913a:237

Described from the female "From Vinita, Indian Terr., 7 June (Wickham), Colorado Springs, Colo., 16 June (Wickham), and Chimney Gulch, Golden, Colo. (Oslar). Type American Mus. Nat. Hist. Co-type, Author's Collection". Number of specimens and type number not stated. The above record of type material does not indicate which specimen was placed in the AMNH. A female in the AMNH with the labelling "Vinita, Ind. T., June 7, 8, '99" and "*Cerceris gnarina* Banks—Type" in Banks' handwriting is designated lectotype. An identically labelled specimen is in the MCZ except that it bears a red MCZ type label with number 13768 and is without a subscript number. It also bears a label in Banks' handwriting "*Cerceris gnarina* Bks.—Co-type". Another female in the MCZ from "Chimney Gulch, Golden, Colorado", has the subscript number 2 on the MCZ type label. The Colorado Springs locality mentioned in the original description is not represented. The three specimens examined are conspecific.

Cerceris grandis Banks, 1913b:423

Described from the female "From Ft. Yuma, Arizona; Amer. Mus. Nat. Hist.". Number of specimens not stated. One female in the AMNH with the above labelling and with "*Cerceris grandis* Bks.—Type" in Banks' handwriting is accepted as the holotype.

Cerceris halone Banks, 1912:24

Described from the female "From Falls Church, Va." Number of specimens and type number not stated. One female in the MCZ from the above locality with the type number 13777 and bearing a small, red handwritten type label is accepted as the holotype.

Cerceris hesperina Banks, 1917:115

Described from "Type—M.C.Z. 10,031. Washington: Yakima, July, 1882; Ainsworth, July, 1882. Samuel Henshaw. Four specimens". A female and three males, all conspecific, are in the MCZ with the above labelling. The female from "Ainsworth, W. T., July 20, '82" without a subscript number on the MCZ type label is designated lectotype. The males have subscript numbers 2, 3 and 4 respectively. The male with subscript number 3 is labelled "Yakima City, W. T." whereas the others are from "Ainsworth, W. T." Scullen (1965) incorrectly stated that the female was from Yakima, Washington.

Cerceris (*Apiratrix*) [sic] *huachuca* Banks, 1947:29

Described from the male "From Patagonia, Arizona, 20 August (Bequaert). Type M.C.Z. no. 27636". Number of specimens not stated. One specimen labelled as above is in the MCZ. The thorax and gaster, in one piece, are glued to a point with a head glued separately to the same point. The head is that of a species different from that of the thorax and gaster. The thorax and gaster agree with Banks' original description, but the head does not. The specimen as represented by the thorax and gaster, but not the head, is accepted as the holotype. I have placed a "note" on the specimen referring to a memorandum on file at the MCZ detailing my reasons for concluding that the parts of the specimen are not conspecific.

Cerceris illota Banks, 1947:23

Described from an unstated number of males "From Tucson, Arizona, August (Bequaert), also Patagonia, Arizona, 20 August (Bequaert), and Colton, Southern California, 16 August (Pilate); also two from Palmerlee, Arizona (Biedermann). Type M.C.Z. no. 23541". Eleven conspecific males are in the MCZ with the type number 23541, six from Tucson, one from Patagonia, two from Palmerlee and two from Colton. The specimens from Patagonia, Palmerlee and Colton have MCZ type 23541 labels with the specimen from Patagonia having two such identical labels. Three specimens from Tucson have a MCZ type 23541 label, and two specimens from Tucson have a MCZ paratype 23541 label. The sixth specimen labelled "Tucson, Ariz. VIII" with a MCZ holotype 23541 label is designated lectotype.

Cerceris interjecta Banks, 1919:84

Described from "Male from Lake Point, Utah, 18 July (Titus)". MCZ type number not stated. The male in the MCZ labelled as above with the type number 13766 is accepted as the holotype.

Cerceris irene Banks, 1912:26

Described from the female "From Fedor, Lee County, Texas, 25 June (Birkman)". Number of specimens and MCZ type number not stated. One female in the MCZ with the above labelling and MCZ type number 13781 is accepted as the holotype.

Cerceris isolde Banks, 1947:24

Described from the male "From Palmerlee, Arizona, Biedermann coll. Type M.C.Z. no. 23540". One male in the MCZ labelled as above is accepted as the holotype.

Cerceris melanthe Banks, 1947:21

Described from the female "From Apache Co., Santa Catalina Mts., Ariz., 25 July, 5500 ft., J. Bequaert collector. Type M.C.Z. no. 23539". One female in the MCZ labelled as above is accepted as the holotype.

Cerceris nigritula Banks, 1915:402

Described from the male "From Colden, N.Y., July 3 (M. C. Van Duzee)". Number of specimens and type number not stated. A male in the MCZ with the type number 13782 and labelled as above is accepted as the holotype.

Cerceris finitima nigroris Banks, 1912:27

Described from the male "From Falls Church, Va., in August". Number of specimens and MCZ type number not stated. Two males are in the MCZ labelled as above with the type number 13786. One male, dated "7 Aug." with a small, red handwritten type label and no subscript number on the MCZ type label is designated lectotype. The second male is dated "27-VIII" and has the subscript number 2 on the MCZ type label.

Cerceris nitida Banks, 1913b:424

Described from an unstated number of both sexes "From Valley of Black Mts., N. Car., 12 to 22 July, 1906 (Beutenmuller)". A female labelled as above, except the date is "June 24, 1906", bearing a "*Cerceris nitida* Bks. — Type" label in Banks' handwriting is in the AMNH and is designated lectotype. The discrepancy in date is considered to be a *lapsus*. The male was not found.

Cerceris orestes Banks, 1947:13

Described from an unstated number of both sexes "From Patagonia, Arizona, 1 to 14 August (Bequaert). Type M.C.Z. no. 27637". One female in the MCZ with the above labelling and type number is designated lectotype. There is no subscript number on the MCZ type label. The male was not found.

Cerceris orphne Banks, 1947:15

Described from "One male from Jemez Springs, N. Mex., 2 July (Englehardt). Type M.C.Z. no. 23536". A male in the MCZ with the above labelling is accepted as the holotype.

Cerceris posticata Banks, 1916:64

Described from the male "From Jemez Mountains, New Mexico, 11 July (Woodgate)". Number of specimens and MCZ type number not stated. One male in the MCZ with the above labelling bearing the MCZ type number 13771 is accepted as the holotype.

Cerceris prominens Banks, 1912:19

Described from both sexes "From Falls Church, Va., September and October". Number of specimens and MCZ type number not stated. Three females and two males, all conspecific, are in the MCZ with the above labelling and bear the MCZ type number 13790. One female with a small, red handwritten type label and the MCZ type label without a subscript number is designated lectotype. The other two females have subscript numbers 2 and 3 respectively, and the males have subscript numbers 4 and 5 respectively.

Cerceris psamathe Banks, 1912:21

Described from the female "From Fedor, Lee County, Texas (Birkman)". Number of specimens and MCZ type number not stated. One female in the MCZ with type number 13780 bearing the above labelling is accepted as the holotype.

Cerceris salome Banks, 1923:21

Described from the female "From Long Island, and Nyack, N.Y., Wellesley, Mass. (Morse); and Jones' Creek, Lee Co., Va.". Number of specimens and MCZ type number not stated. Three conspecific females are in the MCZ with the type number 14705 without subscript numbers on the type labels. One specimen is simply labelled "N.Y.". A second specimen has a label "Coll. A. P. M., Lot 11" and a second label "Coll. A. P. M., Lot 30". A third specimen is labelled "Jones' Cr., Lee Co., Va." and is designated lectotype since this is the only specimen in unambiguous agreement with the original description.

Cerceris sayi Banks, 1923:21

Described from both sexes "From Steele, N. Dakota, July 13 (Stevens)". Number of specimens and type number not stated. One female in the MCZ labelled as above with type number 14706 is designated lectotype. The male was not found.

Cerceris semiatra Banks, 1947:25

Described from "One male from Patagonia, Arizona, 20 August (Bequaert). Type M.C.Z. no. 27620". A male in the MCZ with the above labelling is accepted as the holotype. The header label in Banks' handwriting spells the name "*semiater*" and lacks the word "type".

Cerceris (*Apiratrix*) [sic] *seminigra* Banks, 1947:33

Described from "One male from Patagonia, Arizona, 20 August (Bequaert). Type M.C.Z. no. 27621". A male in the MCZ labelled as above is accepted as the holotype.

Cerceris sextoides Banks, 1947:10

Described from "Holotype female from Lone Tree, Yakima River, Wash., 30 June 1882 (S. Henshaw); allotype and paratypes from Nelson's, Yakima River, 4–5 July, and Camp Umatilla, 26 June, both Washington and by Mr. Henshaw; also from Davis, Calif., 1 July (Bohart), and one 'California'. Type M.C.Z. no. 23547." The female holotype labelled as above is in the MCZ and bears a MCZ holotype label in addition to the MCZ 23547 label. Four males bear MCZ 23547 paratype labels, and one of these labelled "Yakima R., W. T. Nelson's, July 4,5 '82" bears a MCZ allotype label in addition to the paratype 23547 label.

Cerceris snowi Banks, 1919:84

Described from an unstated number of males "From Tucson, Arizona (Snow) and San Diego Co., Cal. (Van Duzee)". MCZ type number not stated. Three conspecific males are in the MCZ with the type number 13764. One male from "Tucson, Ariz." is without a subscript number on the MCZ label, but the specimen consists only of a pinned thorax with a head glued to the top label. The head is without antennae and the gaster is missing. A male from "San Diego Co., Cal.", has the subscript number 2. Another male labelled "Tucson, Ariz., F. H. Snow" bears the subscript number 3 on the MCZ label and is designated lectotype due to the badly damaged condition of the specimen without a subscript number.

Cerceris stevensi Banks, 1923:22
Described "From Steele, N. Dakota, Aug. 10 (Stevens)". Sex, number of specimens and MCZ type number not stated. Reference to the clypeal process indicates a female. One female labelled as above in the MCZ with the type number 14707 is accepted as the holotype.

Cerceris stigmosalis Banks, 1916:64
Described from the male "From Fargo, North Dakota, September, on *Solidago* (Stevens)". Number of specimens and MCZ type number not stated. One male in the MCZ labelled as above with type number 13778 is accepted as the holotype.

Cerceris thione Banks, 1947:18
Described from an unstated number of males "From Colton, Calif. (Pilate), Eddy Collection, 24 August and 4 September, and Claremont, Calif. (Baker). One specimen from Colton is only 8 mm. long. Type M.C.Z. no. 23593 [sic]". The type number "23593" of the original description is a typographical error as the specimens are labelled "23543" and the MCZ log indicates "23543". Four conspecific males are in the MCZ with the above labelling. One specimen from "Colton, Calif.", with the date "8-24" and a red MCZ holotype label in addition to the MCZ 23543 label is designated lectotype. The remaining three males have red MCZ paratype 23543 labels.

Cerceris vanduzeei Banks, 1917:114
Described from the female from "Type—M.C.Z. 10,030. Calif.: San Diego, June. E. P. Van Duzee. One specimen [sic]". Despite the statement "one specimen" there are two females in the MCZ with identical labelling as above except that one has a small, red handwritten type label and the MCZ label is without a subscript number. It is designated lectotype. The second specimen lacks the small, red handwritten type label and has the subscript number 2 on the MCZ label. I interpret the statement "one specimen" in the original description as a *lapsus.*

Cerceris (*Apiratrix*) [sic] *vierecki* Banks, 1947:30
Described from the female "From Tempe, Arizona, 1 August (Bequaert). Type M.C.Z. no. 23544". Number of specimens not stated. One female in the MCZ with the above labelling is accepted as the holotype. In addition there are two males in the MCZ from Tempe, Arizona, with collection dates "2-VIII" and "31-VII" bearing red MCZ 23544 paratype labels. Since the

male was not mentioned in the original description, these specimens are without status. They are conspecific with *C. arizonella* Banks described from a male from the same locality.

Cerceris zelica Banks, 1912:23

Described from both sexes, the male "From Fedor, Lee County, Texas, 7 June (Birkmann)", and the female "From Lee County, Texas, 7 July (Birkmann)". Number of specimens and MCZ type number not stated. A female and a male in the MCZ with the above labelling and the MCZ type number 13773 are not conspecific. The female with a small, red handwritten type label and the MCZ label without a subscript number is designated lectotype. The male bears the subscript number 2 on the MCZ label, and the gaster is glued to the top label. It is a male of *C. squamulifera* Mickel.

Eucerceris apicata Banks, 1915:404

Described from the male "From Yuma, Arizona". Number of specimens and MCZ type number not stated. One male in the MCZ labelled as above with the type number 13742 is accepted as the holotype.

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TWO NEW SPECIES AND SYNONYMY OF THREE SPECIES OF NORTH AMERICAN *CERCERIS* (HYMENOPTERA: PHILANTHIDAE)[1]

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Abstract.—A study of the relevant types in the genus *Cerceris* has resulted in the following synonymy (junior subjective synonyms in parentheses): *C. acanthophila* Cockerell (=*C. chilopsidis* Viereck and Cockerell), *revised synonymy*; *C. cockerelli* Viereck, *revised status* (=*C. minax* Mickel), *new synonymy*; *C. gandarai* Rohwer (=*C. micheneri* Scullen), *new synonymy.* Two species are left without names and are described as *C. grisselli* Ferguson n. sp. (=*C. minax,* sensu Bohart and Grissell, nec Mickel) and *C. rohweri* Ferguson n. sp. (=*C. gandarai,* sensu Scullen, nec Rohwer).

Five species of North American *Cerceris* are discussed. A study of the types representing the six names previously applied to these five species shows that the six names apply to only three of the species, leaving two species without names. These two species are described as new to provide names for a forthcoming synonymic list of North American *Cerceris,* and the synonymy for the other three species is presented.

Cerceris acanthophila Cockerell

Cerceris acanthophilus (sic) Cockerell, 1897:135 (Male lectotype, Deming, New Mexico; ANSP); Viereck and Cockerell, 1904:138; Cresson, 1928:48; Banks, 1947:30; Scullen, 1951:1004, 1972:17.

Cerceris chilopsidis Viereck and Cockerell, 1904:136 (Female holotype, Rincon, New Mexico; ANSP); Cresson, 1928:48; Scullen, 1951:1005, 1965:365; Bohart and Grissell, 1975:42; Bohart and Menke, 1976:578; Krombein, 1979:1731. **Revised Synonymy.** Synonymy first proposed by Banks (1947).

Banks (1947) first recognized that *C. acanthophila* and *C. chilopsidis* were the male and female, respectively, of the same species. However, Scullen

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(1960, 1965) misidentified *C. acanthophila* and used the name for the species discussed below as *C. cockerelli.* Scullen (1972) reversed himself and recognized *C. chilopsidis* as the female of *C. acanthophila.* Bohart and Grissell (1975) characterized and keyed both sexes of this species under the name of *C. chilopsidis.*

Cerceris cockerelli Viereck, **Revised Status**

Cerceris cockerelli Viereck, 1902:731 (Male lectotype, La Jolla, California; ANSP); Cresson, 1928:48; Banks, 1947:31; Scullen, 1951:1006, 1965:367 (as unrecognized species).

Cerceris minax Mickel, 1918:339 (Female holotype, Sacramento, California; NEB); Banks, 1947:34; Scullen, 1951:1008, 1972:18. **New Synonymy.**

Cerceris acanthophila, Scullen, 1960:75, 1965:355, in part; Krombein, 1967: 414; Bohart and Grissell, 1975:38; Bohart and Menke, 1976:576; Krombein, 1979:1729.

Scullen (1960, 1965) incorrectly applied the name *C. acanthophila* to this taxon, and this interpretation was followed by subsequent authors. Later he stated (Scullen, 1972:18) "*Cerceris chilopsidis* Viereck and Cockerell is, therefore, now considered a synonym of *C. acanthophila* Cockerell and *C. minax* Mickel is again accepted as a valid species." However, he ambiguously retained *C. minax* Mickel in his list of synonyms of *C. acanthophila.* Bohart and Grissell (1975) correctly recognized *C. cockerelli* as belonging to this taxon, but they used *C. acanthophila* as the senior name. The type of *C. minax* Mickel is conspecific with *C. cockerelli* Viereck.

Cerceris grisselli, new species

Cerceris acanthophila, Scullen, 1965:355, in part, figs. 108a, b, c.

Cerceris minax, Bohart and Grissell, 1975:49, map 36, figs. 99, 100, 124, 125; Bohart and Menke, 1976:584; Krombein, 1979:1739.

Bohart and Grissell (1975) first recognized this taxon as a species distinct from *C. cockerelli.* Although Scullen (1965) had specimens of both species before him, he did not discriminate between them. Bohart and Grissell (1975) figured and keyed the differences between the two species. Unfortunately, they used the name *C. minax* for this species, but the holotype female of *C. minax* Mickel is clearly a specimen of *C. cockerelli.* The *minax* of Bohart and Grissell (1975) is thereby left without a name.

The female pygidium in *grisselli* is abruptly constricted distally with the sides subparallel over the apical one-third, whereas in *cockerelli* the sides are rather evenly tapered toward the apex. In the male the clypeal brush of *cockerelli* is dense, rectangular, wider than long, whereas in *grisselli* the brush is rather loose and tapered toward the apex.

Description. Jugal lobe of hind wing about ⅓ as long as submedian cell; stigmal and prestigmal veins brown, slightly paler than subcosta; apicomedian fossette present on tergum I; sternum II with basal platform; complete longitudinal carina on inner ventral margin of coxa III; tegulae evenly convex, not pitted; propodeal enclosure usually weakly ridged; scutal punctures separated by 1 to 3 puncture diameters, at least across middle; propodeal punctures dense, separated by ridges of 0.3 to 0.5 puncture diameter; punctation of preapical terga as on propodeum. FEMALE: Length 8–10 mm; clypeal midsection with low, transverse lamellate process separated apically from clypeal margin by scarcely the length of flagellomere IV, apical margin of process usually emarginate with distinct apicolateral corners and about as wide as subantennal sclerite; mesopleural tubercle and precoxal carina strong; pygidium narrow, about 2.5 times as long as greatest width, constricted basally, abruptly narrowed apically with sides subparallel over apical 0.3; pygidial surface smoother on apical 0.3 than on basal portion. MALE: Length 7–9 mm; clypeal midsection with numerous to dense micropunctures between macropunctures, with 3 short, blunt teeth apically, and about as wide as midlength (width measured between tentorial pits); antennocular distance about equal to length of flagellomere I; clypeal brush scarcely as wide as least clypeo-ocular distance, tapered toward apex, hairs not agglutinated or waxed; sterna IV–VI without apicolateral teeth; pygidium subrectangular, slightly bowed outward medially. COLOR: Black with yellow markings as follows: clypeus except lip; subantennal sclerite partly or entirely; lateral sections of face from above sockets to clypeus; scape below; basal half of mandible; spot behind eye; tegulae in part; lateral stripes on pronotal collar; metanotum; spot on hypoepimeron sometimes present in female; anteriorly emarginate transverse bands on terga I–V (female) and terga I–VI (male), often reduced on tergum I and penultimate tergum, less strongly emarginate in male than in female; one or more sterna with lateral spots or transverse band; trochanter III in part or entirely; apical 0.3 to 0.5 of femora; tibiae and metatarsi. Apical 0.25 of metatarsus III and tarsomeres II–V infuscated; some tarsomeres of anterior legs tinged with red.

Holotype. Female, California, Los Angeles County, Tanbark Flat, VI-25-50 (A. T. McClay); UCD. [The holotype female is the specimen used by Scullen (1965) for his figures 108a, b, c under the name *acanthophila.*]

Paratypes. 71 males, 26 females all from California, Los Angeles County, Tanbark Flat as follows: 5 males, 8 females same date as holotype (P. D. Hurd, A. T. McClay, F. X. Williams) (UCB, UCD, CAS, MIS); 59 males, 10 females, VI-15-50 to VII-25-50 (H. M. Graham, J. C. Hall, P. D. Hurd, A. T. McClay, W. O. Marshall, K. G. Whitesell, F. X. Williams) (UCB, UCD, CAS, MIS, OSU); 4 males, 5 females, VI-29-52 to VII-13-52 (R. L. Anderson, D. E. Barcus, A. A. Grigarick, A. T. McClay, B. Miyagawa, S. Miyagawa) (UCD); 3 males, 3 females, VI-18-56 to VII-18-56 (R. C. Bechtel, R. M. Bohart, R. W. Bushing, J. I. Stage) (UCB, UCD).

Other specimens. In addition to the type series I have examined 171 males and 52 females.

Distribution. Known only from California. Bohart and Grissell (1975) provide details of distribution under the name *C. minax.* A series of specimens (OSU) from California, Modoc County, Adin Pass, 5,000 ft., July 30, 1955 (G. R. Ferguson, Joe Schuh) extends the range of the species northward.

This species is named for E. E. Grissell who, with R. M. Bohart in Bohart and Grissell (1975), first showed that it was a distinct species.

Cerceris gandarai Rohwer

Cerceris gandarai Rohwer, 1912:470 (Male holotype, Federal District, Mexico; USNM).

Cerceris micheneri Scullen, 1972:86 (Female holotype, Metachic, Chihuahua, Mexico; AMNH); Bohart and Menke, 1976:584. **New Synonymy.**

This species was described, figured and keyed by Scullen (1972) under the name of *C. micheneri.* However, a study of the male holotype of *C. gandarai* shows that Scullen (1972) misidentified Rohwer's species. It is in fact conspecific with and a senior synonym of *C. micheneri.* The type female, allotype male, and several paratypes of *C. micheneri* have been studied.

Cerceris rohweri, new species

Cerceris gandari (sic), Scullen, 1972:82, figs. 156a, b, c, d.

Cerceris gandarai, Bohart and Menke, 1976:581; Krombein, 1979:1734.

This species was described, figured and keyed by Scullen (1972) under the name *C. gandarai.* Since the name *C. gandarai* must now be applied to the species previously known as *C. micheneri,* the species treated by Scullen (1972) as *C. gandarai* is left without a name and is described here as *C. rohweri.* It and true *gandarai* belong to an as yet undefined group of small species, most of which occur in the central plateau area of Mexico and contiguous portions of the United States. In having a fossette on tergum I and a variably developed basal platform on sternum II, the group is allied to the *Cerceris finitima* group but separable by the absence of a carina on coxa III.

In both sexes *C. rohweri* lacks microridging between punctures on the scutum, whereas these microridges are conspicuous in *C. gandarai.* Female *C. gandarai* has an elevated, truncate process on the clypeal midsection; in

C. rohweri this process is absent, and, instead, there is a pair of somewhat rounded, subquadrate lobes on the apical margin of the clypeal midsection. In the male the clypeal brush of *C. gandarai* is somewhat tapered toward the apex and not wider than the distance from the tentorial pit to the eye margin; in *C. rohweri* the clypeal brush is rectangular and wider than the distance from the tentorial pit to the eye margin.

Description. Jugal lobe of hind wing 0.3 times length of submedian cell; fossette present on tergum I; carina absent on coxa III; basal platform of sternum II a low, rounded swelling in male, essentially absent in female; propodeal enclosure shiny with numerous micropunctures, median furrow complete, crenulate; tegulae longer than wide, smooth; deflected posterior portion of metasternal plate with triangles broadly fused at base, carinate between. FEMALE: Length 9–11 mm; with small, sharp mesopleural tubercle; mandible with large, broadly triangular tooth a little basad of middle; clypeal midsection evenly convex, without a projecting process, terminating apically in a pair of broad, subquadrate, slightly outturned lobes, fused at base and with a transverse depression at base of lobes; eyes slightly divergent below; macropunctures of clypeus and lower face well separated with numerous micropunctures on lateral clypeal sections and lower face; punctation denser in front of ocellar triangle than behind; scutal punctures separated by 0.5–1 puncture diameter, at least across middle; anterior part of mesopleuron with a few ridges between punctures, punctures separated by flat ridges on disc; propodeal punctures separated by many thick ridges of 0.5–1 puncture diameter on side of and behind enclosure; punctures of black portions of terga III–IV dense, some contiguous, some separated by flat, shagreened ridges of 0.25–0.5 puncture diameter, pale portions with well separated coarse punctures; pygidium narrowly oval, twice as long as midwidth, uniformly rugose without pits at base, about as wide apically as basally. MALE: Length 7–8 mm; mandible edentate; clypeal lip edentate, about as wide as subantennal sclerite; clypeal brush strong, waxed, cupped, wider than clypeal lip; clypeal midsection 1.2 times as long as width between tentorial pits; eyes parallel; punctures of clypeus and lower face separated mostly by 1 or more puncture diameters; punctures on scutum, mesopleuron, propodeum and terga as in female except ridges between punctures absent; pygidium subrectangular, 1.8 times as long as greatest width, not widened basally, slightly narrowed apically, slightly bowed out on the sides, coarsely punctate. COLOR: Black with following parts yellow: base of mandible (sometimes absent in male); clypeus except apically and basally in female and apically in male; lower face from above sockets; spot on subantennal sclerite in male; small spot behind eye in female; interrupted band on pronotum; metanotum; tegulae in part; lateral spot on propodeum of female; interrupted band or spots on tergum I, sometimes absent in male; posterior bands on preapical terga, shallowly emarginate anteriorly; lateral spots on sterna III–IV. Legs black and yellow suffused with red; tibiae I–II, except dark spot behind, and trochanter III pale; femora with narrow, red apical band in female, basal half pale in male; tarsi I–II reddish, less so in male; tarsi III infuscate. Forewings with brownish infuscation along anterior one-third; antennae with scape and pedicel black, flagellum brown below.

Holotype. Female, 17 mi. NE San Luis Potosi, S.L.P., Mexico, 6,200 ft., Sept. 6, 1963 (Scullen and Bolinger); USNM.

Paratypes. 48 males, 12 females, all from the state of San Luis Potosi, Mexico, as follows: 40 males, 7 females, same data as holotype (CAS, UCD, OSU, USNM); 2 males, 19 mi. SW San Luis Potosi, 7,200 ft., IX-4-63 (Scullen and Bolinger) (OSU); 5 males, 1 female, 40 mi. S San Luis Potosi, 5,700 ft., IX-5-63 (Scullen and Bolinger) (OSU); 2 females, 15 mi. E San Luis Potosi, 6,500 ft., X-3-57 (H. A. Scullen) (OSU); 1 female, 18 mi. SW San Luis Potosi, 7,300 ft., X-2-57 (H. A. Scullen) (OSU); 1 male, 1 female, 10 mi. NE San Luis Potosi, 6,200 ft., VIII-22-54 (R. R. Dreisbach) (MIS).

Other specimens examined. 113 males, 20 females, from several states in Mexico as follows: OAXACA: 18 males, 2 females, 5,600–6,850 ft., VI-27 to VIII-23 (OSU); PUEBLA: 9 males, 2 females, 5,380–6,900 ft., VI-7 to VIII-24 (UCB, OSU); MEXICO: 17 males, 9 females, 7,400–8,550 ft., IV-7 to VIII-30 (MIS, OSU); VERACRUZ: 1 male, 5,000 ft., VI-9 (OSU); QUERETARO: 46 males, 2 females, 6,500–7,400 ft., VI-13 to IX-19 (OSU); AGUASCALIENTES: 1 male, 1 female, VIII-3 to VIII-9 (OSU, USNM); ZACATECAS: 6 males, VII-3 to VIII-20 (MIS, OSU); DURANGO: 9 males, 2 females, 6,000–7,100 ft., VI-17 to X-23 (MIS, OSU); COAHUILA: 1 male, 4,450 ft., IX-9 (OSU); NUEVO LEON: 5 males, 2 females, 4,600–7,200 ft., VIII-30 to IX-22 (UCB, OSU, USU).

Scullen (1972) lists additional records (as *gandarai*) including a female from Brooks County, Texas.

This species is named for the late S. A. Rohwer, long time student of aculeate and other Hymenoptera, who described the species with which this species has been misidentified.

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GYNANDROMORPHIC DESERT FIRE ANT, *SOLENOPSIS AUREA* WHEELER (HYMENOPTERA: FORMICIDAE)[1]

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Abstract.—A gynandromorph of *Solenopsis aurea* Wheeler is described from an ant collected in western Texas. The specimen is predominantly that of a queen, but the head is noticeably male on the right half, female on the left half. The reproductive system, both internally and externally, is entirely female.

Gynandromorphs are individuals which have the male and female sexual characters combined discretely. The character combinations can occur as right-left halves, dorsoventral halves, antero-posterior halves, or in patches, resulting in mosaics. Female ant characters can be contributed by any of the castes present: queen-male (gynandromorph), worker-male (ergatandromorph), and soldier-male (dinergatandromorph). Combinations of worker, queen, and male are also known (Donisthorpe, 1929).

Numerous mechanisms have been proposed to explain the occurrence of gynandromorphs in animals. Most mechanisms deal either with fertilization-related phenomena or with cytogenetic complications during early embryogenesis. Morgan and Bridges (1919), Rothenbuhler et al. (1952), Brust (1966), and Wigglesworth (1972) provide useful reviews and discussions on the various mechanisms implicated in formation of insect gynandromorphs.

Gynandromorphs have been reported from 39 species in 22 genera of ants (Donisthorpe, 1929; Wheeler, 1931, 1937; Buschinger and Stoewesand, 1971; Hung et al., 1975). Two gynandromorphs have been reported from the genus *Solenopsis.* A red imported fire ant, *Solenopsis* (*Solenopsis*) *invicta* Buren, with male head, mosaic thorax, and female pedicel and gaster was described by Hung et al. (1975). A thief ant, *Solenopsis* (*Diplorhoptrum*) *fugax* Latreille, with female head and thorax, and male pedicel and gaster was reported by

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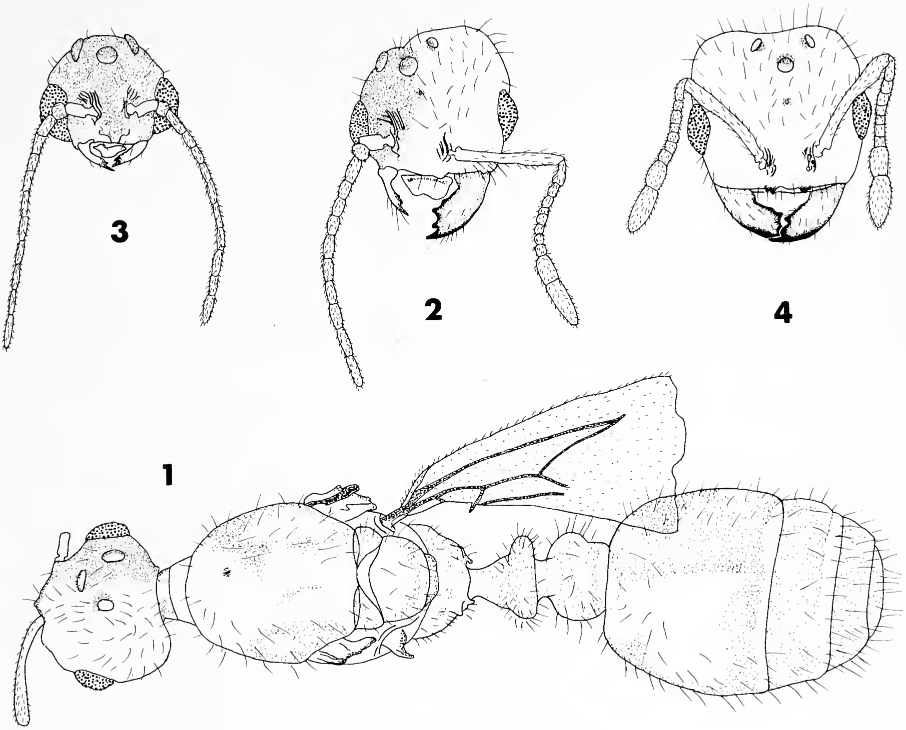

Figs. 1–4. *Solenopsis aurea.* 1. Dorsal view of gynandromorph. 2. Anterior aspect of gynandromorph head. 3. Anterior aspect of male head. 4. Anterior aspect of female head.

Santschi (1910). Another anomaly reported for the red imported fire ant is that of intercastes, female individuals exhibiting worker and queen characters (Glancey et al., 1980).

The present gynandromorph is that of a desert fire ant, *Solenopsis* (*Solenopsis*) *aurea* Wheeler, which is preserved along with normal male and female siblings (cat. no. 6461) in the Entomological collection, The Museum, Texas Tech University. Nineteen colonies of *S. aurea* where collected 2.6 miles ESE of Southland, Garza Co., Texas, on 4 June 1982 and were kept alive in the laboratory. On 15 June 1982 all the colonies were closely examined for the presence of external parasites, at which time the malformed ant was discovered. The gynandromorph and six male and female siblings were isolated on 2 July for closer observations. The gynandromorph, but not its siblings, died 6 July 1982.

The sexes of *S. aurea* are distinctive and easily separated. The gynandromorph (Figs. 1, 2) is predominantly female, with male characteristics most distinctive on the head. A normal male head (Fig. 3) is darkly pigmented and small in size. The ocelli and compound eyes are large, and the mandibles and antennal scapes are small. The number of segments in the antenna also differs between the sexes: 12 for males, 10 or 11 for females. The head of the gynandromorph (Fig. 2) is clearly asymmetrical. The right half is that of a male: dark, with large ocelli, reduced antennal scape and mandible, and with a 12-segmented antenna. The left half is distinctly female: light in color, with small ocellus, large mandible, long antennal scape, and 11-segmented antenna. The thorax and its appendages, except for minor differences, are those of a female. The wing bases appear to have been removed by the gynandromorph's siblings, or at least dealation did not occur normally. The pronotum is slightly darker on the right side, although not as dark as on males. The small ridge on the declivous face of the propodeum, characteristic of females, is absent on the right half of the postpetiole. The internal anatomy of the head, thorax, and pedicel was not examined. The abdomen is four segmented as in females (five segments in males) and shows but a slight darkening in color on the right half, although still much paler than in males. Dissection of the abdomen revealed a complete bilaterally symmetrical female reproductive system. Developing oocytes are present in the ovarioles. The spermatheca is well developed and as large as that of mated females, but no spermatozoa were found in a section of spermathecal duct stained with giemsa. The poison gland and sting are present and of normal size.

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A REDEFINITION OF *DISDERIA* AND ADDITION OF A NEW SPECIES (HEMIPTERA: PENTATOMIDAE)

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Abstract.—The genus *Disderia* is redefined and a new species from Oaxaca, Mexico, added. Parts of the male genitalia of the three known species and the genital plates of the females of *D. decorata* and *D. inornata* are figured. A key to the species is given.

Bergroth (1910) established the genus *Disderia* for *Phalaecus decoratus* Distant, and Ruckes (1959) added *D. inornata.* A third species is described here and additional details are given concerning the genitalia of the other 2 species. The genus is redefined to broaden and augment the original description.

Among the Pentatomini of the Western Hemisphere, *Disderia* may be recognized by the combination of 3-segmented tarsi and a grossly elongated abdominal spine which reaches the procoxae.

Disderia Bergroth, 1910

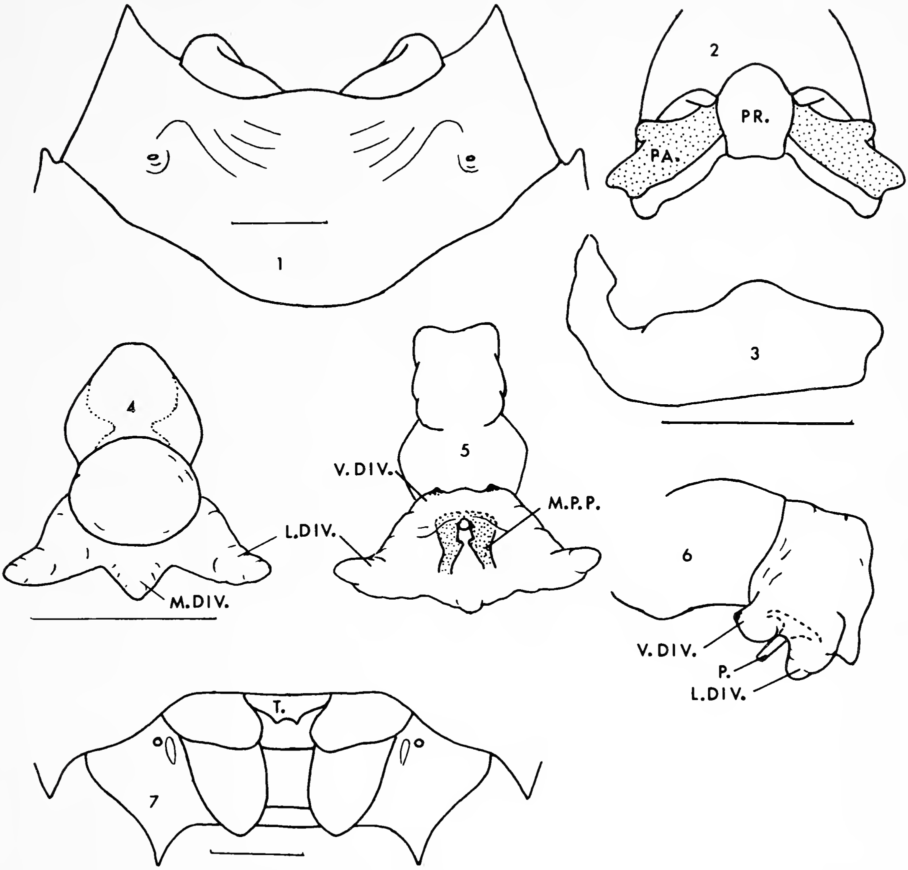
Disderia Bergroth, 1910, p. 20; Distant, 1911, p. 252; Ruckes, 1959, p. 27.

Median basal spine of abdomen reaching procoxae, depressed basally, compressed distally. Ostiolar rugae straight, extending about three-fourths of distance from inner margin of ostiole to lateral margin of metapleuron. Mesosternum and metasterum anteriorly with low median carina. Femora without apical spine or other armament. Tarsi three-segmented.

Length of head about 0.7 width across eyes; juga narrowly contiguous or nearly so at apex of head (Fig. 14); distal end of first antennal segment surpassing apex of head; bucculae evanescent at base of head, terminating near distal end of first rostral segment; apex of rostrum reaching between mesocoxae. Pronotum about 2.5 times wider than long at meson; anterior margin contiguous with and projecting a little laterad of eyes; anterolateral margins entire. Scutellum 0.1–0.2 longer than wide at base; frena extending about 0.6 length of scutellum from base toward apex.

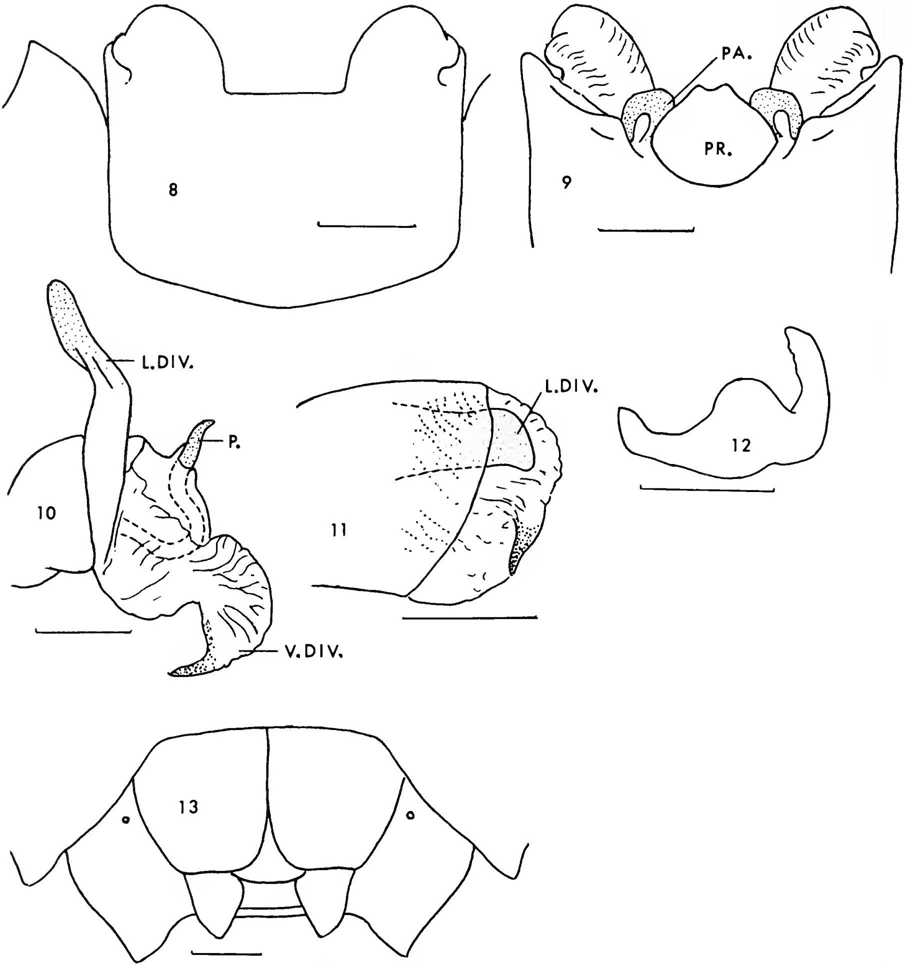
Theca of male genitalia without processes on apical margin. Eighth paratergites of female and 8th sternite of males bearing spiracles.

Type species. Phalaecus decoratus Distant by original designation.



Figs. 1–7. *D. decorata.* 1. Pygophore and last abdominal segment, ventral view. 2. Genital cup; paramere (PA); proctiger (PR). 3. Paramere, ventral view. 4. Aedeagus, dorsal view; lateral diverticula (L. DIV.); median diverticulum (M. DIV.). 5. Aedeagus, ventral view; lateral diverticula (L. DIV.); ventral diverticula (V. DIV.); median penial plates (M. P. P.). 6. Aedeagus, lateral view; lateral diverticula (L. DIV.); ventral diverticula (V. DIV.); penisfilum (P.). 7. Genital plates; triangulum (T.).

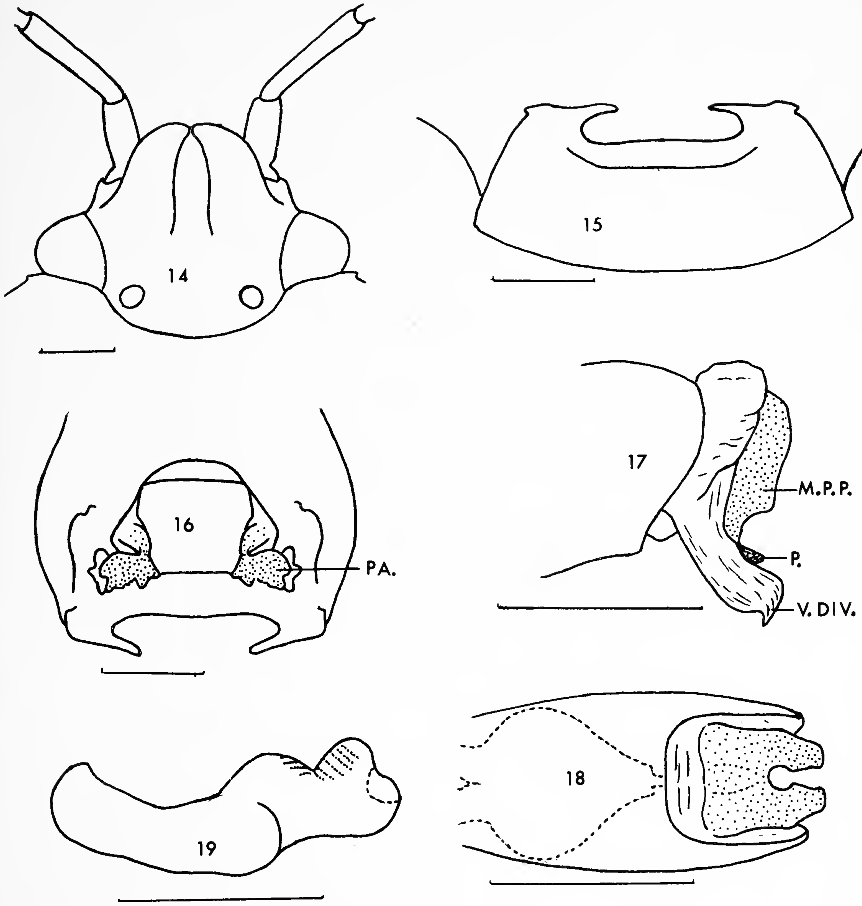
Comment. Perhaps it should be emphasized, because of conflicting statements, that Distant (1880) was correct in describing the mesosternum and metasternum as elevated (p. 83), although Bergroth (1910) may also have been correct in his belief that Distant mistook the abdominal spine for sterna. In all 3 species the mesosternum and anterior portion of the metasternum have a low median carina which is generally rather obscured by the abdominal spine.



Figs. 8–13. *D. inornata.* 8. Pygophore, ventral view. 9. Genital cup; parameres (PA); proctiger (PR). 10. Aedeagus, everted, lateral view; lateral diverticula (L. DIV.); ventral diverticulum (V. DIV.); penisfilum (P). 11. Aedeagus, uneverted; lateral diverticula (L. DIV.). 12. Paramere, ventrolateral view. 13. Genital plates.

Disderia parda, new species
(Figs. 14–19)

Description. Dorsum dark yellowish brown; punctation black, on coria especially dense, on pronotum and scutellum disposed in part as irregular



Figs. 14–19. *D. parda.* 14. Head. 15. Pygophore, ventral view. 16. Genital cup; parameres (PA). 17. Aedeagus, everted, lateral view, ventral diverticulum (V. DIV.); median penial plates (M. P. P.); penisfilum (P.). 18. Aedeagus, uneverted, ventral view. 19. Parameres, ventral view.

rows with a general transverse orientation. Venter much paler; thoracic punctures of moderate size, mostly dark, irregularly distributed; abdominal punctures for most part progressively larger darker and less numerous from lateral abdominal margins toward meson. Length of body 7.8 to 8.1 mm.

Head 1.9 mm wide across eyes, 1.4 mm long. Three basal segments of antennae concolorous with venter, bearing numerous dark dots; ultimate two segments darker, immaculate; length of segments 0.5; 0.8 to 0.9; 0.9; 1.2; 2.0 mm. Pronotum 5.0 to 5.1 mm wide, 2.0 mm long at meson; anterolateral margins slightly convex; humeri rounded, scarcely produced. Scutellum 3.1 mm wide at base, 3.5 to 3.6 mm long; basal disk darkened by diffusion of black about punctures. Coastal angle of coria reaching posterior margin of penultimate tergite; membrane of hemelytra darkly fumose, veins simple or furcate. Connexiva little to moderately exposed, black with pale marginal spot in middle of each segment.

Evaporative area large, each covering much of metapleuron and mesopleuron, matte, similar to remainder of pleura in color and punctation. Legs with fuscous dots, those on femora larger and less numerous than on tibiae; superior surface of all tibiae sulcate. Spiracular peritremes dark. Abdominal margins thinly edged in black except in middle of each segment.

Digitiform process on posterolateral angles of pygophore directed obliquely mesad (Figs. 15, 16); conspicuous impression in lateral pygophoral surface located outside of genital cup opposite apex of parameres. Parameres irregularly palmate from dorsal aspect; ventrolateral subapical surface covered with fine serrate ragae (Fig. 19). Median penial plates forming large concave area, heavily sclerotized and pigmented, with short penisfilum emerging within ventral margin; ventral conjunctival diverticulum increasingly sclerotized and pigmented toward apex, distally bifurcate, terminating on each side in hook (Fig. 17); most of conjunctiva and penisfilum retractable into theca, of pigmented parts leaving only distal part of ventral diverticulum exposed in deep ventral emargination of theca (Fig. 18).

Holotype. ♂, labeled (a) "Mexico, Oaxaca, 21.8 mi. n. Juchatengo. 7100′ III, 23, 1966, in bromeliads" (b) "George E. Ball, D. R. Whitehead, collectors". Deposited in U.S. National Museum, type no. 75558.

Paratype. ♂, labeled as holotype, in author's collection.

Discussion. Disderia has no great likeness to any other genus, as both Bergroth (1910) and Ruckes (1959) remarked, and the intrageneric dissimilarities suggest that the relationship among species is not close.

Although the tibiae of *D. decorata* are asulcate and those of the other 2 species are sulcate, the external morphology other than the genitalia is consistent with expectations for congenericity. Both *D. decorata* and *D. ornata* have eversible conjunctiva, i.e., the conjunctiva and associated phallic structures are largely contained within the theca (Figs. 11, 18), from which they may be extracted manually and from which they are presumably everted during copulation (Figs. 10, 17). This does not seem to be the case in *D. ornata.*

There are notable differences among the 3 species in the conjunctival structures. *D. decorata* has a median, conical diverticulum that is posterior to a dome shaped expanion, a pair of lateral diverticula and a pair of ventral diverticula (Figs. 4–6). These are entirely membranous with the exception of the apex of each member of the ventral pair. Small median penial plates are present at the base of the penisfilum. Both *D. inornata* and *D. parda* have an elongated ventral diverticulum that bifurcates distally with each part terminating in a hook (Figs. 10, 17). The two species diverge sharply in that *D. parda* has large median penial plates while *D. inornata* has none, and *D. inornata* has a pair of appendicular diverticula laterally which are not represented in *D. parda.*

The parameres of *D. ornata* and *D. parda* are distally flattened and essentially horizontal (Figs. 2, 3, 16, 19); those of *D. inornata* are distally hooked and essentially vertical (Figs. 9, 12).

Among females, the triangulum is exposed in *D. decorata* but not in *D. inornata* (Figs. 7, 13). The female of *D. parda* is unknown.

Disderia appears to be an old genus that exhibits a remarkable degree of divergence in the genitalia of the 3 species. The few species and the large interspecific differences are consistent with the assumption of generic antiquity. The spiracles on the 8th paratergites and 8th sternite retain the primitive character state. Eversible conjunctiva, as exhibited by *D. inornata* and *D. parda,* occurs infrequently among Pentatomini, but it is characteristic of several groups, e.g. the acanthosomatids, that are generally considered to be less recent phylogenetically than the Pentatomini.

KEY TO SPECIES OF *Disderia*

1. Tibiae asulcate; large white spot in each basal angle and at apex of scutellum, other white markings on body; little of pygophore evident from ventral view (Fig. 1) .... *D. decorata* (Distant)

– Tibiae sulcate; conspicuous pale markings confined to connexiva; pygophore prominent from ventral view (Figs. 8 and 15) 2

2. Dorsum light brown, abdominal punctation nearly concolorous with sternites; length without membrane about 10 to 12 mm; posterolateral angles of pygophore deeply incised laterally, without digitiform process, parameres hook-shaped (Figs. 9, 12) .... *D. inornata* Ruckes

– Dorsum dark brown, abdominal punctation mostly much darker than sternites; length without membrane about 8 mm, posterolateral angles of pygophore not incised, each bearing slender digitiform process directed obliquely mesad; parameres irregularly palmate (Figs. 16, 19) .... *D. parda,* new species

ACKNOWLEDGMENT

The description of *Disderia parda* is based on specimens donated by Dr. George E. Ball of the University of Alberta.

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A STUDY OF WINGED QUEENS OF THE COLORADO HONEY ANT, *MYRMECOCYSTUS MEXICANUS,* IN CAPTIVITY

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Abstract.—Winged queens (24) were captured issuing from a honey ant nest north of Colorado Springs prior to the nuptial flight and placed in Janet-type nests. Six nests housed one queen and six housed three queens each. These nests were fed three different diets to determine their effect on queen longevity and egg production. Maximum longevities occurred in nests given the most complete diet. All nests produced eggs 7–12 days after swarming, but only one larva developed, and it lived only 72 days. Data on egg numbers, locations, durations and clump size are presented. Observations were made on dealation, abdominal distension, mite infestation, and queen behavior and death. Dealation attempts took place over a long period and were successful in only two queens. Queens developed swollen abdomens in every nest except one. However, neither dealation nor a swollen abdomen is essential for egg production. There was no hostility in three-queen nests and they cooperated caring for eggs. Behavior, longevity, and reproductive potential of virgin queens are compared to fertilized queens in captivity.

Although a number of investigators such as McCook (1882), Wheeler (1908, 1910, 1913, 1917), Creighton (1950), Cazier and Statham (1962), Gregg (1963), Cazier and Mortenson (1965), Slocumb (1966), Conway (1975, 1977, 1980a, b, 1981a, b), Hölldobler (1976), Snelling (1976), Kay (1978), Kay and Whitford (1978), Chew (1979), and Hölldobler and Lumsden (1980) have discussed the biology of *Myrmecocystus mexicanus,* there has been no systematic study of winged queens in captivity. This study attempts to remedy that deficiency and had the following objectives:

1. To see if winged, presumably virgin queens, issuing from a nest prior to the nuptial flight, could lay eggs and rear young.
2. To determine longevity of winged queens.
3. To note behavioral differences between winged queens in solitary confinement and those kept in groups of three.
4. To investigate the effect of three diets on winged queens.
5. To see what effect natural and artificial dealation would have on queen behavior and reproduction.
6. To compare behavior and reproductive potential of virgin queens with fertilized queens (Conway, 1981a).

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MATERIALS AND METHODS

Twenty-four winged queens were captured as they left a *M. mexicanus* nest on a mesa north of Colorado Springs on July 28, 1972 prior to the nuptial flight, and placed in plaster Janet-type nests on July 30.

The plaster nests contain two glass-covered chambers, each 10.8 cm long, 8.9 cm wide, and 0.6 cm high, connected by a passageway 1.3 cm long and 1.6 cm wide. The passageway was blocked with foam to form two compartments. Water was added daily to a small sponge or piece of cotton in each chamber.

Three nests, with six compartments, were set up with one winged queen in each compartment. Queens in the first nest received the complete diet of sugar water, protein and fat (see section on sustenance), and water. Queens in the second nest received sugar water and water, and those in the third nest received water only.

Three nests, with six compartments, were set up with three winged queens in each compartment. Queens in the first nest were given the complete diet, those in the second nest received sugar water and water, and those in the third nest drank water only.

Sugar water given to colonies was dyed with blue food coloring so its intake and distribution could be followed.

RESULTS AND DISCUSSION

Queen sustenance—complete-diet nests. Queens in these nests were given the most complete diet which consisted of a variety of foods, such as sugar water, honey solutions, milk, sugar-sweetened milk, peanut butter, cereal, hamburger, live *Drosophila,* mealworms, and water. Queens fed mainly on blue sugar water and their abdomens usually became bluish. The only other foods they ate were honey solutions, *Drosophila,* and one mealworm. There were only two observations of a queen drinking water.

Sugar water and water nests. Queens in these nests received blue sucrose solutions frequently, blue honey water infrequently, and tap water almost daily. Most queens developed swollen blue abdomens, but there were no observations of them drinking tap water.

Water only nests. Queens in these nests received tap water almost daily and periodically were observed drinking it.

Queen longevity. In solitary-queen nests, maximum longevity occurred in a queen receiving the complete diet, who lived 194 days, and minimum life span belonged to a queen receiving water only who survived 88 days (Table 1).

Single queens provided with complete diets lived longest (mean 149 days). Those in water-only nests lived only slightly longer (mean 104.5 days) than those fed sugar water and water (mean 100.5 days) (Table 1).

Table 1. Longevity, wing condition, and method of dealation of solitary and grouped *Myrmecocystus mexicanus* queens supplied with three diets in captivity.

Nest	Longevity (days)			
	1st queen	2nd queen	3rd queen	Mean
A—solitary queen—sugar water, protein, water	194 winged			149
B—solitary queen—sugar water, protein, water	104 winged			
A—solitary queen—sugar water and water	107 winged			100.5
B—solitary queen—sugar water and water	94 wingless—natural			
A—solitary queen—water only	88 wingless—natural			104.5
B—solitary queen—water only	121 winged			
A—3 queens—sugar water, protein, water	275 winged	339 wingless—artificial	419 winged	250
B—3 queens—sugar water, protein, water	5 winged	190 winged	272 winged	
A–3 queens—sugar water and water	85 wingless—artificial	221 winged	249 winged	172.2
B—3 queens—sugar water and water	128 winged	155 winged	195 winged	
A—3 queens—water only	48 wingless—artificial	149 winged	237 winged	165.3
B—3 queens—water only	175 winged	189 winged	194 winged	

In three-queen nests, both maximum and minimum life spans, 419 and 5 days respectively, occurred in colonies receiving complete diets. Nevertheless, these nests still exhibited the longest mean life span (250 days). The queens receiving sugar water and water lived slightly longer (mean 172.2 days) than those given water only (mean 165.3 days) (Table 1).

On the average, solitary queens had shorter life spans (mean 118 days) than queens in groups of three (mean 195.8 days). Perhaps queen cooperation and interaction increase longevity. It is interesting to speculate if this situation is peculiar to virgin queens and whether it would be reversed if fertilized queens were placed together.

In summary, maximum longevities occurred in one- and three-queen nests receiving the complete diet. Individuals in these nests received comparable diets to fertilized queens in another study (Conway, 1981a) who lived even longer (mean 297.6 days). Thus, as might be expected, fertile queens lived much longer than their solitary unfertilized counterparts. What is surprising however, is that when virgin queens were in groups, their mean life span (250 days) approached that of fertile queens (297.6 days).

Data suggest that wingless virgin queens do not live as long (mean 130.8 days) as winged ones (mean 188.4 days). And, among wingless queens, the average life of queens who dealated themselves was shorter (91 days) than among those artificially dealated (157.3 days).

First appearance of eggs. Eggs first appeared in virgin-queen colonies 7 to 12 days after swarming (Table 2). They appeared sooner, 4 or 5 days after the nuptial flight, in fertilized-queen nests (Conway, 1981a).

Eggs were laid in every virgin-queen nest. The number of eggs in the first clump varied from 1 to 8 (Table 2), but was somewhat larger, 5 to 10, in fertilized-queen colonies (Conway, 1981a).

Egg survival. The number of days eggs were present in solitary virgin-queen nests ranged from 66 to 138. There was no correlation with persistence of eggs and completeness of diet except that eggs survived longer, on the average, in complete-diet nests (Table 2).

The number of days eggs were present in three-queen nests varied from 92 to 340. The two nests given water only, contained eggs for the shortest period (mean 94). Both colonies nourished on sugar water had eggs for 145 days, the added carbohydrate seeming to increase egg longevity. Nests provided with the complete diet had eggs for the longest period (mean 257.5) (Table 2).

Eggs persisted longest in one- and three-queen nests which received the complete diet. Eggs also survived much longer in three-queen colonies than in solitary-queen nests, except those receiving only water. In water-only nests, egg durations were not significantly different (Table 2).

The only virgin-queen nests comparable to fertilized-queen colonies in another study (Conway, 1981a) were those fed the complete diet. Fertile queens maintained eggs a couple weeks longer (mean 132.6 days) than solitary virgin queens in those nests (mean 114.5 days), but not nearly as long as nests with three queens (mean 257.5 days) (Table 2).

Disappearance of eggs. In four of six solitary-queen nests, eggs disappeared before the queen expired, but in two water-only nests, the queen passed away while some eggs were still present.

In all three-queen colonies, eggs vanished before the third queen died, and in one water-only nest, eggs perished before the first queen expired. In nests

Table 2. Data on first appearance, duration, maximum number, and disappearance of eggs in solitary and grouped *Myrmecocystus mexicanus* queens supplied with three diets in captivity.

Nest	Appearance of 1st eggs—days after swarming (7/28/72)	Number of 1st eggs	Disappearance of eggs	Egg durations (days)	Mean duration (days)	Egg maxima and dates
A—solitary queen—sugar water, protein, water	9	8	10/20/72– 11/29/72 2/1/73	138	114.5	18 (8/13/72)
B—solitary queen—sugar water, protein, water	11	1	11/7/72	91		17 (9/23/72)
A—solitary queen—sugar water, water	10	4	10/12/72	66	69.5	11 (9/12/72)
B—solitary queen—sugar water, water	10	8	10/19/72	73		28 (9/10/72)
A—solitary queen—water only	9	2	10/25/72	81	96	25–30 (9/7/72)
B—solitary queen—water only	10	5	11/26/72	111		20 (8/22/72)
A—3 queens—sugar water, protein, water	8	2	11/30/72– 2/1/73 9/11/73	340	257.5	60 (8/28/72)
B—3 queens—sugar water, protein, water	12	4–5	10/4/72– 12/11/72 4/14/73	175		40 (8/28/72)
A—3 queens—sugar water, water	8	clump	12/28/72	145	145	60 (8/31/72)
B—3 queens—sugar water, water	10	6	1/1/73	145		60 (9/9/72)
A—3 queens—water only	8	1	11/5/72	92	94	40 (8/22/72)
B—3 queens—water only	7	4	11/8/72	96		44 (9/20/72)

receiving sugar water and water, and the other water-only nest, eggs disappeared before the demise of the second queen. Only in the two complete-diet nests did the third queen continue to lay eggs after the death of the second.

Fluctuation in egg number. Egg numbers fluctuated in all virgin-queen nests, and in some, they dropped to zero for a time before increasing again. This seemed to occur because the queen laid eggs, some deteriorated, and then she deposited more. Queens were not observed consuming eggs.

In three complete-diet nests, eggs vanished for a period and then reappeared (Table 2), but did not reach the maximum number attained originally. One exception was a complete-diet, solitary-queen nest, which achieved the original maximum of 18 eggs during the second period of deposition. In four of seven fertile-queen colonies, eggs also perished before returning again (Conway, 1981a).

It is hypothesized that queens ceased laying eggs when there was a temporary lack of protein. When protein was added, usually in the form of *Drosophila* and mealworms, eggs reappeared, although in one case not until 40–50 days later. In one nest in which eggs did not recur, the solitary queen probably received very little protein.

In both sugar water and water-only nests, ova never reappeared after declining to zero for several days, presumably due to a lack of protein.

Maximum number of eggs. The maximum number of eggs in one-queen nests varied from 11 to approximately 30 (mean 20.3). The largest numbers occurred in a water-only nest (25–30) and sugar water nest (28). The maxima in the two colonies given the complete diet were 17 and 18 (Table 2). Egg maxima in fertilized-queen nests given a comparable diet varied from 5 to 34 (mean 13.6) (Conway, 1981a). It is surprising that the mean maximum (20.3) is higher in virgin, solitary-queen nests than in fertilized-queen nests (13.6).

In three-queen colonies egg maxima varied from 40 to 60. Greatest numbers occurred in nests with the complete diet or receiving sugar water. The one complete-diet colony in which the total was not 60 may be explained by the fact that one queen died almost immediately and hence all eggs were laid by two queens. Two nests receiving water only had egg maxima of 40 and 44 (Table 2).

Evidence is inconsistent with regard to nourishment and egg maxima in virgin-queen nests. In one-queen nests, greatest numbers appeared in nests fed either water only or sugar water. But in three-queen colonies, the greatest numbers were in nests given the complete diet or sugar water.

Egg maxima in three-queen colonies were greater than in solitary-queen nests, suggesting that more than one queen, and probably all three, laid eggs. And since the mean total for solitary queens was 20, and the mean maximum for three-queen colonies was 51, there is the likelihood that each queen lays a total of about 20 eggs. However, since the mean three-queen total, 51, is somewhat below the theoretical 60, there may be some inhibition to egg deposition due to group interaction.

Egg grouping. In five of six solitary-queen nests, eggs were predominantly or only in one clump. In the sixth nest, eggs were scattered most of the time. Maximum number of clumps varied from zero to two. In fertilized-queen colonies eggs were also predominantly in one clump (Conway, 1981a).

Although eggs were mainly in one clump in three-queen colonies, the maximum number of clumps varied from one to four. In one colony there were almost as many observations of scattered ova as of eggs in a clump. Eggs were sometimes in two clumps of different sizes. For example, in one nest there were 40 eggs in one clump and 6 in another.

When total number of eggs is divided by number of clumps, the range is 6½ to 30 eggs per clump (mean 13.7). It is postulated that the mean of 13.7 reflects an optimum clump size which can best be cared for and transported by the queen, and that as egg numbers increase, they are divided into several clumps to preserve optimum size.

Defective eggs. Defective eggs were variously described in my notes as "small, yellow, shriveled, wrinkled, not firm or turgid, containing internal globules, caved in, crushed, dried up, decaying, and amorphous" and began appearing about one week after the first eggs were laid. Actually all ova were non-viable in that none developed into adults, and only one metamorphosed into a larva. Defective eggs were sometimes scattered and sometimes in separate piles from normal eggs. By contrast, there was only one observation of defective eggs in fertilized-queen colonies (Conway, 1981a).

Egg color. It is probable that yellow and white eggs occur in all nests, but white eggs (more viable?) seem more abundant in nests given the complete diet or sugar water whereas yellow eggs seem more numerous in nests receiving water only. White eggs also seemed to predominate in fertilized-queen colonies (Conway, 1981a).

Location of eggs. Most observations from virgin-queen (150) and fertile-queen nests were of eggs close to moisture (damp sponge or piece of cotton). There were 35 sightings of eggs away from moisture in virgin-queen nests.

Care of eggs. Virgin queens were observed tending eggs in every nest except one, just as fertile queens do (Conway, 1981a). Tending consists of standing over, holding, or carrying eggs. Queens seem to tend both healthy and defective eggs.

In three-queen colonies, eggs were most frequently tended by one queen at a time (72 observations), but often (31 observations) all three queens were around an egg cluster or single egg. There were seven observations of two queens tending a group of eggs. Sometimes, different queens watched over separate clumps simultaneously (6 observations). There was only one observation of a queen replacing another over a clump and this occurred when one queen left the eggs and another came over to carry them away.

Queens are protective towards eggs and often picked them up when nests were opened. On one occasion, a queen found an egg mired in honey, plucked it out, and placed it with the others. Despite this attention, queens stepped on eggs from time to time.

Egg deposition. One of the most significant findings of this study was that queens which do not participate in the nuptial flight may nevertheless lay eggs. The question arose as to whether dealation was necessary to trigger egg laying, but clearly it is not, since eggs appeared in nests with only winged queens. Nor does a swollen abdomen seem essential, since one queen laid eggs but was never distended.

Larvae. A larva developed only in one three-queen colony given sugar water. It emerged 32 days after eggs were first observed and survived 72 days. It emerged later and survived for a shorter duration than larvae in fertile-queen colonies. In these nests first larvae appeared 17 to 23 days (mean 20.1) after eggs were laid and were present 171 to 290 days (mean 261.1) (Conway, 1981a).

It seems unusual that the larva developed in a sugar water nest instead of one given a complete diet.

The larva's blue midgut attested to its success in soliciting blue sugar water. Larvae in fertile-queen colonies also fed on eggs, larvae, dead workers and mealworms (Conway, 1981a) and may explain why they completed metamorphosis.

All queens seemed to care for and transport the larva. On one occasion, when it was in water, a queen pulled it out. Despite their solicitude, queens occasionally stepped on the larva.

Queen cooperation. A primary question of the study was how winged queens would behave when put together after the nuptial flight. There was no hostility among queens in the three-queen colonies. In fact, they seemed to share responsibility caring for eggs.

A possible case of altruism occurred when a queen was accidentally tipped onto her back. Another queen went over and tapped the first with her antennae. The upside-down queen then seized the helper and righted herself.

Queen trophallaxis. Trophallaxis occurred in every three-queen colony. The exchange took different forms; either both queens had their mandibles open, both had them closed, or one had hers open while the other kept hers closed. One queen regurgitated a droplet between her open jaws and attempted to pass it to others, but if there were no takers, she would swallow it again. Some queens disgorged fluid on the floor prior to their death.

Movement of gravel. Queens usually scattered the pile of gravel placed in the nests 2 to 15 days after it was added. They also deposited gravel and other debris (dried eggs, wings, etc.) on food and water placed in nests.

Queen abdominal distension. Queens developed distended abdomens in every nest except a solitary-queen one given water only. Queens became swollen 7 to 43 (usually 7–10) days after the nuptial flight. Fertilized queens in four of seven nests became inflated somewhat sooner, 4–6 days after the nuptial flight (Conway, 1981a).

Virgin queens in water-only nests became dilated either by drinking, producing eggs, or both. Since the solitary queen in one nest did not enlarge and yet laid eggs, it follows that a distended abdomen is not an essential accompaniment of egg production.

Queens in sugar water and complete-diet nests developed inflated blue abdomens, hence, at least part, if not all their swelling, could be attributed to drinking the blue sucrose solution. In six fertilized-queen nests, the queen also developed an inflated blue abdomen 1 to 13 days after blue sugar water was first presented.

All wingless virgin queens, whether artificially or naturally dealated, developed enlarged abdomens rapidly. Wingless fertilized queens also became inflated (Conway, 1981a) and thus it was theorized that dealation triggers distension. That this is not the case was demonstrated by the fact that winged virgin queens became distended as well.

It was noted that in almost every three-queen colony, one or two queens were more inflated than others. There were a few observations in both solitary- and three-queen nests which suggest some queens fluctuated in abdominal size. This fluctuation also occurred in some fertilized-queen nests (Conway, 1981a).

Although the majority of queens developed distended gasters, most were not swollen at death, apparently because they disgorged fluid prior to passing away. There were four exceptions, two winged and two wingless queens, which were inflated at death. Some fertilized queens also disgorged fluid and began to deflate prior to death (Conway, 1981a).

Queen dealation. Fertilized queens dealate themselves quickly. In fact, all were wingless when collected shortly after the nuptial flight (Conway, 1981a). By contrast, dealation attempts in virgin-queen colonies were often unsuccessful and took place over a long period of time, beginning as early as August 5, 1972 and continuing, in one instance, until January 27, 1973.

All queens in three-queen colonies retained their wings, except three dealated with forceps. There were a few attempts by queens in two nests to remove their wings but they were not successful. Queens tried to remove their wings in all solitary-queen nests except one, and two individuals succeeded eight days after the nuptial flight.

In conclusion, it appears that solitary virgin queens attempt to dislodge their wings more often and with more success than grouped queens. If fertilized queens remove their wings in the same fashion as virgin queens attempt to, they first spread them, lift their hind legs simultaneously over the tops, and step on them. Sometimes the dealation act was altered or did not go to completion. A queen might lift her hind legs, but not set them on the wings. One queen with a wing spread at a right angle, raised her hind leg over the other wing which was folded straight back. Occasionally, queens placed only one rear leg on top of the abdomen or wings. Another queen was observed simply walking, raising her gaster, and spreading the wings slightly. Infrequently a foreleg was used to dislodge wings, either by hooking it under the wing junction or moving it back and forth over the point of articulation.

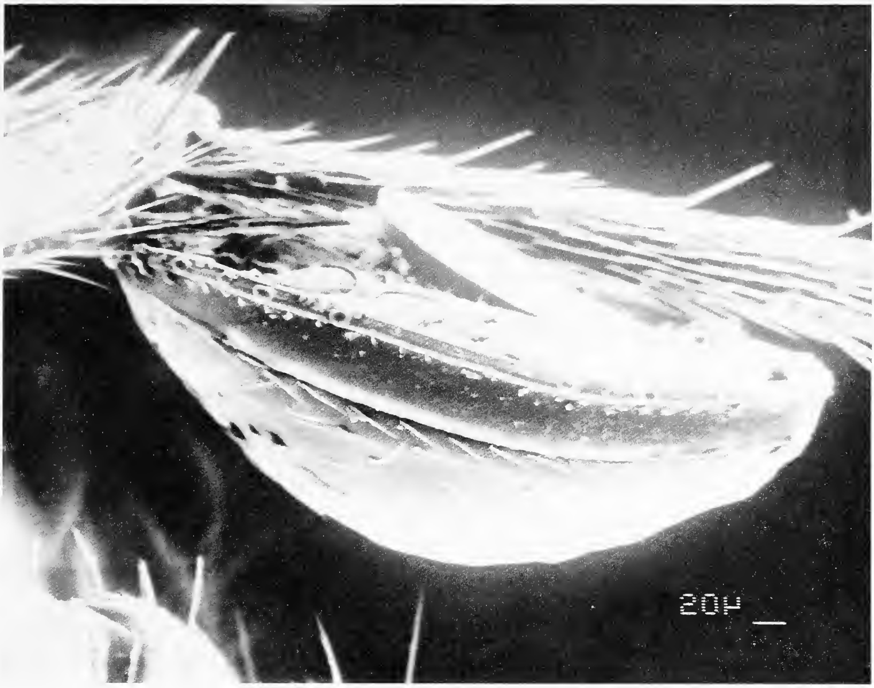

Fig. 1. Uropidine mite on leg of *Myrmecocystus mexicanus* worker.

Queen grooming. Although grooming between virgin queens was not observed, both virgin and fertilized queens groomed themselves. They clean their antennae by pulling them through foreleg spurs and draw their front legs between mouthparts. One queen bent her abdomen forward between her legs to clean the tip.

Mite infestation. Although mites were not observed on solitary queens or fertilized queens, they were in four three-queen colonies. They are probably the same Uropidine mites (Fig. 1) found on honey ant workers. Mites were first noted in two nests seven days after queens were placed in them. Six mites was the maximum number observed in a nest at one time. The greatest number on a queen was five; two on each middle leg and one on a hind leg. The most on a single leg was three on a middle leg. The greatest number on a foreleg or hindleg was two.

Usually mites were on middle legs, less frequently on rear legs, and least frequently on forelegs. An exception occurred in one nest where the only mite was usually on the hind leg. Another unusual location was the dorsal thorax near the meso-metanotal suture.

Mites are mobile and may move about on the queen, wander onto the floor, or transfer to a different queen. On the other hand, they may remain in the same position for some time. A mite was on a hind leg for nine days, and another stayed on a middle leg for ten days. One mite was on the dorsal thorax for seventy days. It could not be determined how long mites live, but in one nest the single mite was present 138 days and in another nest, the mite was there 111 days.

There was no conclusive evidence that any queen perished due to mite infestation, but it may have been a contributing factor. However, it is known that some queens were parasitized more heavily and that two passed away with mites still attached.

Queen death. In many cases there was no forewarning of a queen's death, but in other instances there was some portent, such as the queen moving slowly or disgorging fluid. This behavior was noted 10 to 16 days before demise in virgin queens and 1 to 7 days before in fertilized queens (Conway, 1981a). Sixteen virgin queens died with their abdomens not swollen, or telescoped somewhat. Two had slightly dilated abdomens and four died with enlarged abdomens.

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NESTING BIOLOGY OF THE BEE *SVASTRA SABINENSIS* (HYMENOPTERA, ANTHOPHORIDAE)

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Abstract.—A single nest of *Svastra sabinensis sabinensis* (Cockerell) is described, illustrated, photographed, and compared with the nests of *Svastra obliqua* (Say), the only other member of the genus whose nest has been described. *Svastra sabinensis sabinensis* is ground nesting, with a branched, meandering burrow descending to approximately 80 cm, at which level numerous cells occur. Cells are vertical, elongate, and lined with a non-waxlike waterproof lining. Unlike in any other anthophorid bee, parts of the nest are plugged with sorted pebbles, presumably by the females associated with this nest, and a single specimen of the cuckoo bee *Triepeolus penicilliferus* (Brues) was collected while trying to enter the nest. This is the first association of *T. penicilliferus* with any host.

While searching for nests of various bees at Corona de Tucson, a small development about twenty miles southeast of Tucson, Pima County, Arizona, I discovered and excavated a nest of *Svastra sabinensis sabinensis* (Cockerell) on August 27 and 28, 1982. Dr. Wallace E. LaBerge, who kindly identified two females associated with the nest, suggested that my fragmentary observations would be of interest because so little has been published on the nests of any species in the genus. Only Rau (1922), Custer (1928, 1929) and Rozen (1964) have contributed nesting information heretofore, all authors reporting on *Svastra obliqua* (Say). Like that species, *Svastra sabinensis* belongs to the subgenus *Epimelissodes,* but its range is much more limited, and the nominate subspecies is known only from Arizona and New Mexico (LaBerge, 1956).

The single isolated nest penetrated the nearly horizontal ground (Fig. 1) where there was no shade, although *Cercidium, Echinocactus,* several species of *Opuntia,* and other typical Sonoran desert plants were abundant. The entrance was open, without turret, and not situated near any prominent marker such as a stone, and it was not surrounded by a tumulus. The main shaft (Fig. 3), circular, about 6 mm in diameter, unlined by any secretion,

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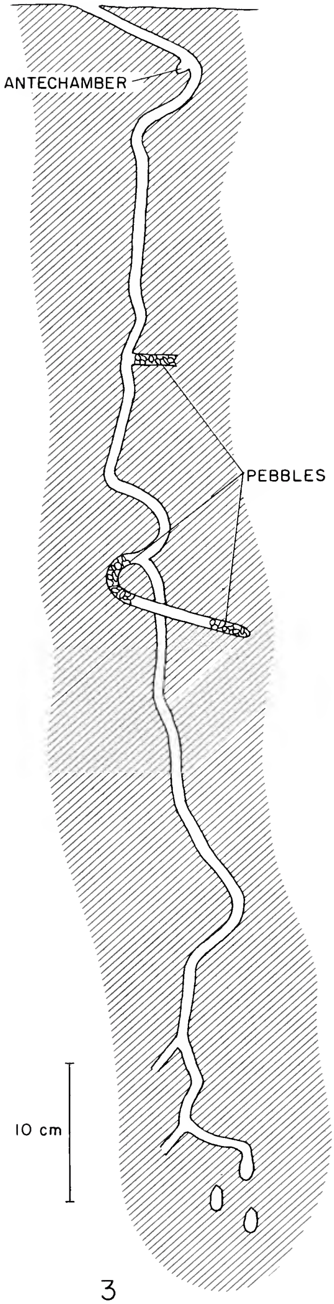
Figs. 1, 2. 1. Nesting locale of *Svastra sabinensis sabinensis* at Corona de Tucson, showing characteristic vegetation. 2. Section of nest of *Svastra sabinensis sabinensis* showing pebbles blocking curved branch, side view. Arrow marks point of attachment of main descending branch with pebble filled one. White material in burrow above is dry, powdered plaster of paris, used by the author to follow burrow during excavation.

and without masoned walls, descended at about a 30° angle from the surface for about 8 cm, at which depth a short branch was attached, presumably an antechamber as described by Custer (1928) and Rozen (1964) for *Svastra obliqua.* Below the antechamber the main tunnel turned downward, with



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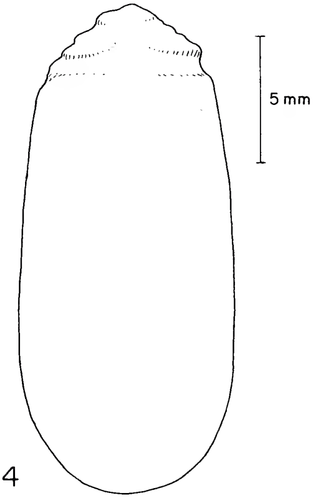

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Figs. 3, 4. 3. Schematic diagram of nest of *Svastra sabinensis sabinensis,* side view. 4. Diagram of cell lumen of same, made from plaster cast using camera lucida to depict exact shape, side view.

some meandering. At about the 25 cm level, a side tunnel branched, which was filled with rather large, sorted pebbles (Fig. 3). The side tunnel was lost and may have been filled with soil beyond the pebbles. Not having seen such a plug of pebbles in any anthophorid nest before, I postulated that a wasp might have constructed the tunnel using the *Svastra* burrow as an access tunnel. The open burrow continued to descend to about the 40 cm level, at which point it branched. One branch curved and was filled for about 4 cm, again with sorted pebbles (Fig. 2); then it was open for about 6 cm and then again plugged with pebbles for 3 cm more, after which it appeared to end blindly. The occurrence of pebble plugs at various places in this nest almost certainly indicated that the female bees occupying the nest had collected and deposited them, but their function, if any, is not clear. The other branch, completely open, descended, still meandering, to the approximate depth of 75 cm, where it branched and then branched again at 80 cm. One of the last branches, extending obliquely downward, ended in a vertical cell without rising before the cell entrance. In this vicinity four other cells were found near one another, all presumably arranged singly. Side tunnels leading to them were filled with soil and not discernible from the nesting substrate. Although I had hoped to find a cell arrangement similar to that diagrammed by Custer (1928) for *Svastra obliqua* or by Rozen (1974) for *Thygater analis* (Lepeletier), no such distinctive patterns could be identified.

The cells (Fig. 4) were elongate, with a broadly rounded bottom and a distinct, deeply concave closure. This closure, a well formed spiral with approximately five coils to the radius, possessed a rather poorly formed inner coil. This coil appeared to be less consolidated than that of the other rows. The plane of two such closures was tilted so that it was not at right angles to the long axis of the cell (not visible in profile drawn in Fig. 4). Unlike that of *Svastra obliqua* (Rozen, 1964), the cell wall did not appear to be plastered, but was slightly harder than the surrounding soil, suggesting that it had been either worked by the female or impregnated by her. It was very smooth and coated with a thin, somewhat shiny, transparent, non-waxlike material that was tan and translucent when viewed against a plaster cast made of the cell lumen. This lining extended to the cell closure, but not beyond, where the wall of the side tunnel was rough, not shiny, and readily absorbed water droplets.

Cells were 8.0 to 8.2 mm in maximum diameter (3 measurements) and the cast of one cell from apex of closure to bottom was 19 mm. The cell diameter at the closure was 6.5 mm (2 measurements).

A number of feeding immature larvae were recovered but none had reached the last instar. The provisions were orange, homogeneously moist but not liquid. As in *Svastra obliqua,* more than one female occupied a single nest. Two badly worn females were recovered from the nest, and a single *Tri-*

epeolus penicilliferus (Brues)[1] was collected while it was trying to enter the nest, although no eggs or larvae of the cuckoo bee were recovered. This is the first host record for *T. penicilliferus.*

Samples of cells, and the two female specimens, as well as the *Triepeolus penicilliferus* pinned with one of the females, are in the collections of the American Museum of Natural History.

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[1] Compared with specimens from the vicinity of Tucson, Arizona, identified by Dr. Paul D. Hurd, Jr.

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RESPONSE OF A GOLDENROD BEETLE TO FOUR SELDOM-ENCOUNTERED GOLDENROD (*SOLIDAGO*) SPECIES

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Abstract.—The goldenrods *Solidago bicolor* and *S. nemoralis* are scarce in the old-field habitat of a goldenrod leaf beetle, *Trirhabda virgata* LeConte, in central New York. Two additional species, *S. caesia* and *S. flexicaulis,* are wholly restricted to woodlands. In the laboratory only *S. bicolor* supported complete development and reproduction by *T. virgata,* but this plant was an inferior host compared to five common meadow goldenrods that had been tested previously. Nine *Solidago* spp. can be ranked in four categories of suitability for *T. virgata.* Host quality is not well correlated with taxonomic affinities of the plants.

More than 15 species of goldenrod (Asteraceae: *Solidago*) occur in central New York (Clausen, 1949). These rhizomatous perennials typically grow in natural openings (e.g., rocky hillsides) and in disturbed areas (e.g., abandoned fields). In a recent paper I described (Messina, 1982a) how five common goldenrods vary in quality for a leaf beetle, *Trirhabda virgata* LeConte (Coleoptera: Chrysomelidae). To provide a broader perspective on the *Trirhabda-Solidago* association, I report here the performance of *T. virgata* when offered four *Solidago* species that the beetle rarely encounters in nature.

Solidago nemoralis and *S. bicolor* are least common among seven goldenrods in old fields of central New York, perhaps because they prefer dry, gravelly soils (Wiegand and Eames, 1925; Sinclear, 1979). Although *S. bicolor* is rare in open meadows where *Trirhabda* occurs, it is common along woodland edges. Two additional goldenrods are restricted to shaded habitats. *Solidago caesia* is characteristic of dry woods, whereas *S. flexicaulis* is common in moist, well-shaded woods (Wiegand and Eames, 1925). Like most chrysomelids, *Trirhabda* beetles fail to disperse into shaded areas. I therefore tested whether *S. caesia, S. flexicaulis,* and possibly *S. bicolor* escaped herbivory by *T. virgata* because of their affinity for woodlands. The life cycle

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Table 1. Comparison of the performance of *T. virgata* larvae and adults on *S. canadensis*[1] and on 4 'novel' goldenrods.

	Solidago host					
	canadensis	*bicolor*	*caesia*	*flexicaulis*	*nemoralis*	N
Larval survivorship[2]	0.45	0.30	0	0	0	40
Developmental endpoint	adult	adult	instar III	instar III	instar I	
Adult longevity[3] ($\bar{x}$ ± SE days)	31 ± 2	20 ± 2	7 ± 1	6 ± 1	5 ± 1	35

[1] Var. *scabra* = *S. altissima* (see Messina, 1982a).
[2] Fraction surviving from egg hatch to adult emergence.
[3] All adults shared *S. canadensis* as the larval host.

of *T. virgata* is described elsewhere (Messina, 1982b). Larvae and adults feed on goldenrod leaves and can reach densities that result in complete defoliation in open fields.

METHODS

Trirhabda larvae were reared from egg hatch to adult emergence on each of the four goldenrods in a room-size growth chamber (24 ± 2°C, 16L:8D). Cohorts of 40 larvae were placed on each host. Every other day I provided fresh-cut goldenrod stems which were placed in florists' water-pics to maintain plant turgor. I measured variation in plant quality for adults by using newly emerged adults that had fed as larvae on *S. canadensis,* an optimal larval host. Thirty-five adults were used in each host treatment, and fresh-cut stems of the appropriate host again were provided every other day. I used plants grown outdoors to ensure that larvae and adults received stems in the proper phenological stage. Further details are found in Messina (1982a).

RESULTS AND DISCUSSION

The performance of beetles fed the 'novel' goldenrods can be compared to the performance of beetles reared simultaneously on *S. canadensis,* the most common old-field host. Of the four test hosts, only *S. bicolor* supported complete larval development; survivorship was similar to that on *S. canadensis* (Table 1). However, larvae fed *S. bicolor* required on average 38.1 d (N = 12) to develop into adults, whereas larvae fed *S. canadensis* required only 31.3 d (N = 18, $P < 0.01$, Mann-Whitney test). *Solidago bicolor* afforded slower growth than did any of the five common old-field hosts (Messina, 1982a).

All first-instar larvae fed *S. nemoralis* died within 5 d; this mortality is

Table 2. Relationship between the field preference of *T. virgata* and the suitability of nine *Solidago* spp.

Solidago sp.	Host use in the field	Host suitability[1]	
		larvae	adults
bicolor	not utilized	+	+
caesia	not utilized	−	−
canadensis	frequent	++	++
flexicaulis	not utilized	−	−
gigantea	frequent	++	++
graminifolia	rare	+	++
juncea	rare	+	++
nemoralis	not utilized	−	−
rugosa	frequent	++	++

[1] ++ = optimal host, + = inferior but adequate for survivorship or reproduction, − = unsuitable.

comparable to that of starved individuals (Messina, 1982b). In contrast, several larvae fed *S. caesia* or *S. flexicaulis* molted to the second stadium, and three larvae in each treatment progressed to the third (last) stadium before dying. One larva fed *S. caesia* lived for 32 d, a period of time that would be sufficient for complete development on a normal goldenrod host.

The four goldenrod species were ranked similarly in food quality for adults. Most of the 105 adult beetles fed *S. caesia, S. flexicaulis,* or *S. nemoralis* died within 10 d (Table 1). No females in these treatments became gravid, even though one female fed *S. caesia* lived for 42 d. As it was for larvae, *S. bicolor* was intermediate in quality for adults. The longevity of beetles fed *S. bicolor* was significantly lower than the longevity of beetles fed *S. canadensis* (Table 1), but several females survived long enough on *S. bicolor* to produce fertile eggs (hatching success = 83%, N = 58).

The rare old-field goldenrods strongly diverged in suitability. *Solidago bicolor* was a suboptimal but adequate host, whereas *S. nemoralis* was the least suitable goldenrod tested. *Solidago nemoralis* produces very little leaf biomass/stem; if the plant were suited to *T. virgata* it would be rapidly defoliated. Observations suggest that *S. nemoralis* leaves may be especially well defended against many goldenrod herbivores.

The relationship between *T. virgata* and nine *Solidago* spp. is presented in Table 2. The plants constitute four categories of suitability. *Solidago canadensis, S. gigantea,* and *S. rugosa* are frequently utilized, optimal hosts. *Solidago graminifolia* and *S. juncea,* which afford slower development of larvae, are rarely used by either larvae or adults, and are colonized only when they are interspersed among preferred hosts (Messina, 1982a). *Solidago* *bicolor* is an inferior food plant for both stages. Finally, the woodland goldenrods and *S. nemoralis* are unsuitable for larvae and adults.

A plant can escape herbivory by growing in sites that are not invaded by insects otherwise adapted to feed on it. For example, the woodland crucifer *Dentaria diphylla* is suitable for many crucifer-feeding insects that restrict host search to open areas (Cromartie, 1975). I did not find an analogous relationship between *T. virgata* and the woodland goldenrods, which are protected by both extrinsic (habitat) and intrinsic (plant quality) barriers to colonization.

Only a subset of *Solidago* species are thus potential hosts for *T. virgata.* Plant quality does not seem to follow taxonomic lines within *Solidago. Solidago graminifolia,* which is occasionally placed in the separate genus *Euthamia* (Cronquist, 1980), is distantly related to all the other goldenrods but is more suitable than any of the four rarely encountered goldenrods. Moreover, *T. virgata* successfully develops and reproduces on certain asters, such as *Aster novae-anglicae* (unpubl. data). It remains to be determined which morphological or chemical characteristics are shared by host goldenrods and asters but are lacking in non-host species in each genus.

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PRECOPULATORY BEHAVIOR OF THE WHIRLIGIG BEETLE *DINEUTES DISCOLOR* (COLEOPTERA:GYRINIDAE)

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Abstract.—The sexual behavior of whirligig beetles is more complex than has previously been described. Precopulatory mounting is a behavior pattern performed by males, and proleg-up is performed by females. These interactions are more in accord with the potential complexities of mate selection and sexual synchronization than earlier accounts of whirligig courtship behavior.

Precopulatory communication is believed to be important in allowing animals to select mates of the appropriate species and of robust phenotype, and in synchronization of sexual behavior. It is of special interest therefore, when the accounts of a species' reproductive behavior seems to preclude any interactions complex enough to facilitate these processes. The only descriptions of whirligig beetle precopulatory behavior speak of males merely leaping on females and inseminating them (Smith, 1926), which in light of current ideas about sexual communication seems unlikely. I undertook this study in order to uncover any behavior interactions in gyrinid precopulatory behavior that might supply a context in which precopulatory communication of a more substantial sort might occur.

These beetles have four compound eyes, have good vision (Bennett, 1967; Carthy and Goodman, 1964) and appear to be very visually oriented (Brown and Hatch, 1929). As surface film dwelling predators, whirligigs have evolved antennal specializations that allow their Johnston's organs to serve as extremely sensitive surface vibration detectors (Wilde, 1941; Rudolph, 1967). Other analogous surface vibration detectors occur in insects found at the air-water interface (Murphey, 1971, 1973; Murphey and Mendenhall, 1973) and in some cases precopulatory signals are transmitted via surface film vibrations (Wilcox, 1972, 1979).

The basic gyrinid body plan consists of streamlined elytra covering the thorax and abdomen, with flat paddle-like mesothoracic and metathoracic legs that are efficient swimming organs (Nachtigall, 1961). The long, slender

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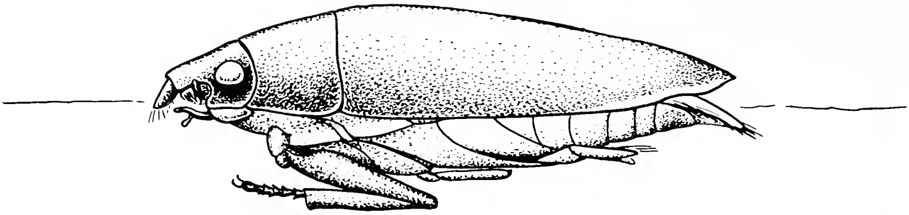

Fig. 1. A view of *Dineutes discolor* swimming. The prothoracic leg is shown lowered somewhat so that its form is apparent.

prothoracic legs are used to seize prey and are held under the beetles' bodies in recessed grooves when unused (Fig. 1 shows these legs lowered somewhat).

MATERIALS AND METHODS

Dineutes discolor were removed from a swarm located on the Wisconsin River near Arena (Iowa Co.), Wisconsin in September 1977 and throughout May and June 1978. The beetles were housed in screen-covered aquaria filled with tap water and fed live flightless *Drosophila.* Approximately 70 beetles individually marked on their elytra with Testor's PLA enamel paints were used in my observations.

The observation tank was a 92.5 × 46.5 × 46.5 cm aquarium containing floating vegetation and live prey. The beetles were therefore free to climb out of the water or feed, rather than being constrained to interacting in a more impoverished environment. Observations were normally for 55 min sessions, occasionally 44 min.

The rates at which every pair of beetles performed different behavior patterns were recorded and Mann-Whitney *U* tests (Siegel, 1956) were used to compare the behavior patterns performed by beetles which mated to the data collected during observation periods during which the beetles did not mate. It is important to note that all data from subjects that were never observed to mate were discarded, so that nonmating data were collected

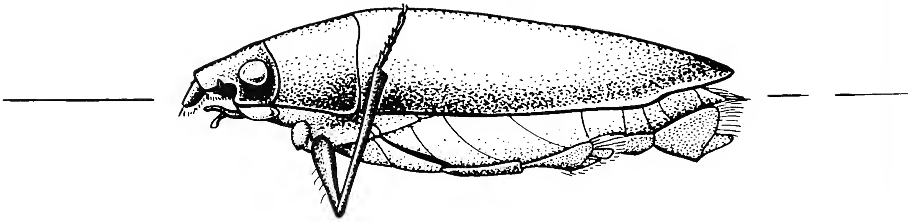

Fig. 2. A proleg-up performed by a female beetle.

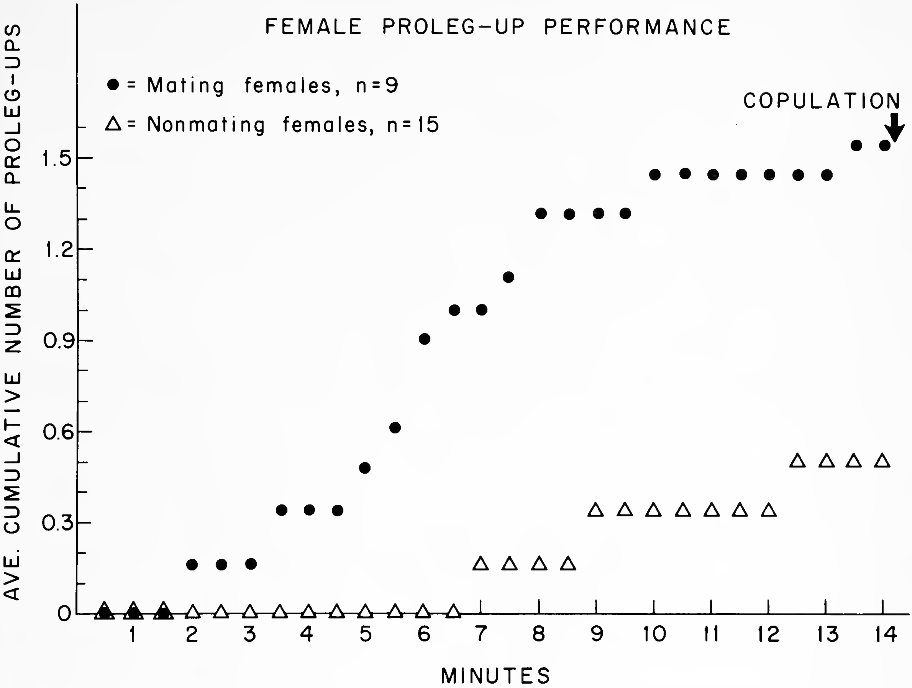

Fig. 3. Performance of the proleg-up behavior by female beetles, in observations with one pair of beetles present. Values for control females are based on the first 14 min of each observation of nonmating pairs (which was the average precopulatory interval in mating pairs).

from animals known to be capable of carrying out successful precopulatory sequences at other times.

RESULTS

I conducted 56 observation periods, during which 24 copulations were observed. Twenty-four observation periods had one pair of beetles present in the experimental apparatus, and 32 of the observations had two pairs present. Data collected in these two situations were consistent with one another in form and in statistical significance, and they are reported together. Data on fifteen behavior patterns were collected. These categories included: different postures of legs and elytra, mouthpart movements, proximity and contacts between beetles, diving, swimming, climbing, general activity level, feeding, and grooming. Of these behavior patterns, only two proved to be statistically related to successful copulation.

Female beetles perform a behavior pattern called *proleg-up* more frequently before they copulate (Mann-Whitney U test, $P < 0.05$). This act

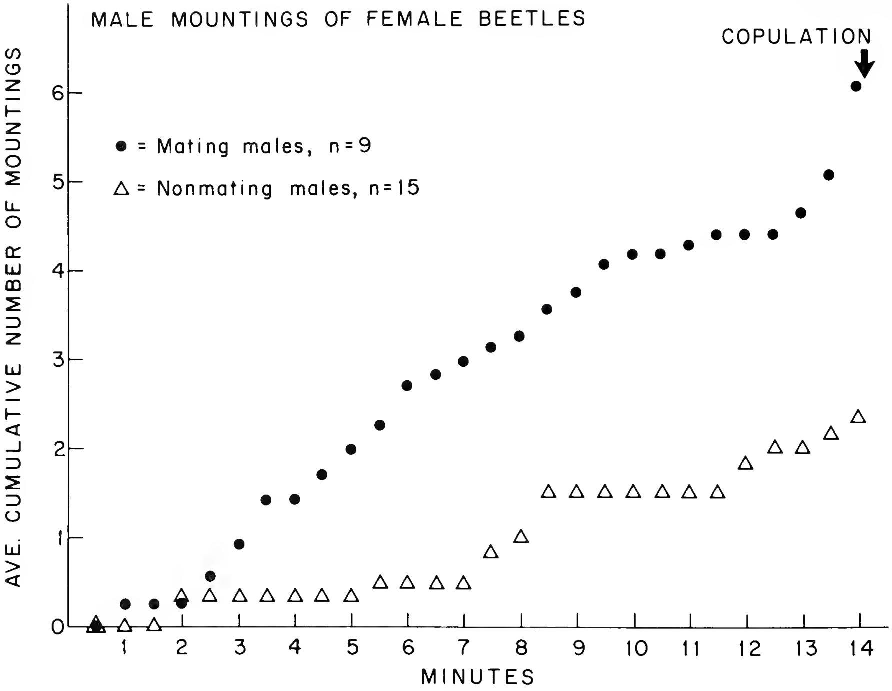

Fig. 4. Male mountings of female beetles, in observations with one pair of beetles present. Values for control males are based on the first 14 min of each observation of nonmating pairs (which was the average precopulatory interval in mating pairs).

consists of the beetle swinging her leg out toward the lateral margin of her body, flexing the leg so that its distal region (tibia and tarsus) extends perpendicularly up from the water, and then rapidly reversing these movements (Fig. 2). Male performance of proleg-up is not statistically related to ensuing copulation.

The data in Figure 3 show the average number of proleg-up performances plotted against time to copulation, for female beetles observed with one male present. The proleg-up behavior has reached almost its final level when copulation is still 5 min away. It appears therefore to be a signal used early in precopulatory communication, rather than in the final stages. No specific distance or direction between male and female during proleg-up performance was noted, but this may have been an artifact of their relatively enforced proximity in the observation aquarium.

Male beetles *mount* female beetles more frequently before they copulate (Mann-Whitney U test, $P < 0.05$), with the males clinging to the dorsal surface of the females for periods ranging from very brief to 10 min. These mounts do not involve insertion of the male genitalia (those were scored

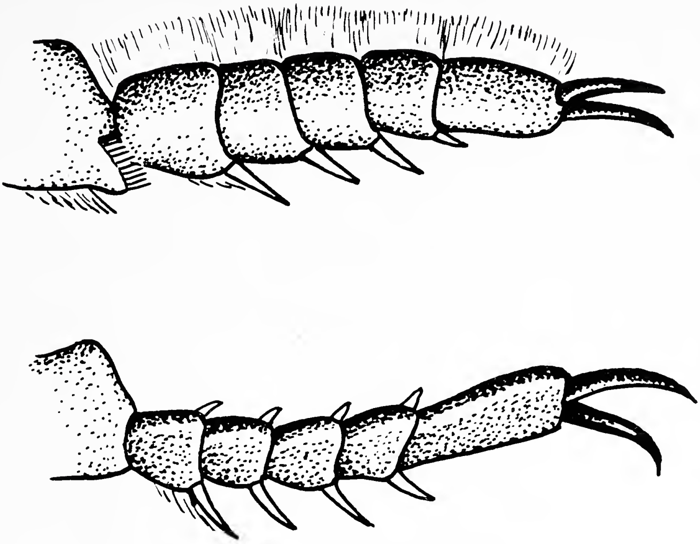

Fig. 5. Male (above) and female (below) tarsal segments of the prothoracic leg.

separately as copulations). Interestingly although male/male, male/female, and female/male mounts were all common, only male/female mounts are especially associated with successful precopulatory sequences.

The data in Figure 4 show the average number of male mountings of females, plotted as in Figure 3. These mountings continue throughout the precopulatory exchange, increasing in rate somewhat in the final 2 min before copulation. Beetles are adjacent to one another immediately before a mounting, but no specific direction of approach by the male relative to the female was apparent.

DISCUSSION

Based on statistical analysis of rates of different precopulatory behavior patterns, mountings of females by males and proleg-up by females may be serving in the precopulatory communication of *Dineutes discolor.*

The proleg-up behavior pattern exposes the distal segment of the prothoracic leg as high above the water line as is possible. This leg region is the animal's one strikingly sexually dimorphic characteristic (Fig. 5) aside from the form of the genitalia themselves. This behavior pattern may therefore serve to demonstrate sexual identity and indicate willingness to copulate.

The occurrence of males mounting females as a precopulatory display is known in a wide variety of animal species. These mountings in *D. discolor* are best viewed as signals rather than as unsuccessful attempts to copulate, especially in light of the facts that (a) females mount males, (b) males mount other males and (c) the male genitalia are not extended during any of these mountings.

The sensory channels that might be involved in the proposed displays of *D. discolor* are diverse, but visual transmission seems likely for the proleg-up and tactile transmission seems likely for male/female mountings. In the latter, ample tactile cues are certainly present—although contact chemoreception cannot be ruled out. In the former, the striking sexual dimorphism of the distal prothoracic leg segments could be easily apparent via visual cues—but again, due to the remarkable sensitivity of the gyrinid surface vibration detector (Rudolph, 1967) a second stimulus channel cannot be ruled out.

The proleg-up performance by female beetles reaches a plateau early in precopulatory exchanges, and is more likely to be involved in initially signalling for female receptivity than in facilitating the final approach of the male for copulation. Male mountings of females occur throughout the precopulatory period, and increase somewhat in frequency during the last 2 min before copulation. This behavior may be involved both in signalling sexual readiness, and in facilitating the final synchronization and orientation of the beetles for copulation.

This type of observational study is inherently limited in its conclusion. In order to further elucidate the signal value of these behavior patterns, either their performance or perception would have to be experimentally manipulated and the results observed. Nonetheless, this study is adequate to strongly indicate that whirligig precopulatory behavior contains interactions that could supply the reciprocal complexity we have come to expect in situations where mate selection or sexual synchronization occur.

ACKNOWLEDGMENTS

I greatly appreciate the aid of Professors Jeffrey R. Baylis and Jack P. Hailman in the course and completion of this study. Among others, Laurence Berg, Clyde Gorsuch, Leigh Hurst, Katherine C. Noonan, and Scott R. Robinson have given me encouragement and advice. Cheryle Hughes produced the excellent illustrations. This work was supported in part by Fellowships from the Graduate School of the University of Wisconsin.

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SEM STUDY OF THE ANTENNAL SENSILLA AND SETAE OF *SOLVA PALLIPES* (LOEW) (DIPTERA: XYLOMYIDAE)

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Abstract.—The antennal sensilla and setae of both sexes of *Solva pallipes* are described using SEM. Sexual dimorphism is evident on the first flagellomere and its functional significance is postulated.

Light microscope observations of antenna of xylomyids were made by Leonard (1930) and Steyskal (1947) with the latter using antennal characteristics to help separate *Solva* from *Xylomya.* Steyskal indicated *Solva pallipes* (Loew) is widely distributed throughout the Nearctic region. However, much of its biology is poorly known and electron microscopic investigations have not been undertaken.

Other investigators have clearly demonstrated the importance of insect antennal sensilla in perceiving a variety of external stimuli (Acree et al., 1968; Kellogg, 1970; McIver, 1974; Chu-Wang et al., 1975; Zacharuk, 1980). It is anticipated that these SEM observations will be utilized to better understand the structural components of the antennal sensilla and to provide some evidence for their functional role in the behavior of this species.

MATERIALS AND METHODS

Dried specimens of both sexes of *Solva pallipes* were mounted on aluminum studs with silver paint and gold coated in Polaron diode sputterer. Rehydrated specimens were similarly treated and showed less distinctly the sensillar pattern. Critical point drying was, therefore, not deemed desirable. Specimens were examined in an ISI Alpha-9 SEM.

RESULTS AND DISCUSSION

The antennae of xylomyid flies consists of a scape attached to the head, followed by a pedicel and a segmented flagellum. Leonard (1930) indicated

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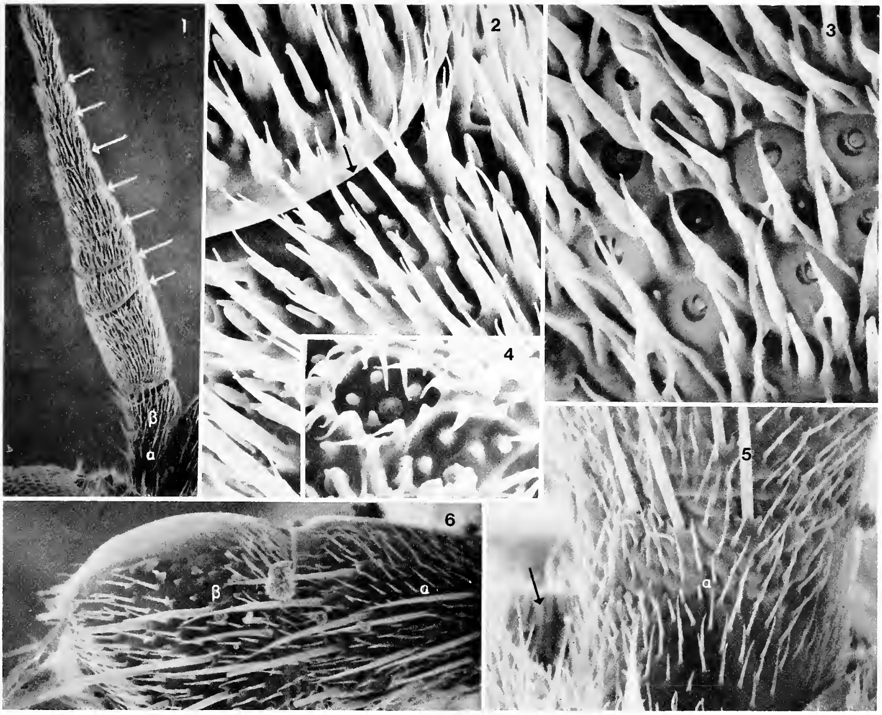

Figs. 1–6. 1. Antenna of female *Solva pallipes* showing scape (α) and pedicel (β). Arrows indicate flagellar annuli. 100×. 2. Flagellar segments demonstrating typical fluted tricoid sensilla. Arrow indicates pattern of depressions near flagellar junction. 100×. 3. Basal segment of male flagellum with typical coeloconicoid sensilla. 2,000×. 4. Depressions of flagellar segments showing two types of sensilla and cuticular wall surrounding each wall. 1,000×. 5. Scape (α) of antenna showing antennal socket (arrow) and pattern of tricoid sensilla. 700×. 6. Lateral view of scape (α) and pedicel (β) showing absence of sensilla on dorsum. 400×.

seven flagellar segments while Steyskal (1947) reported eight for both sexes. The latter number is supported by our studies (Fig. 1).

The flagellum contains a variety of trichoid sensilla and setae having the same pattern of distribution on all segments and being the most frequently encountered type in both sexes. These have evident fluting and are not socketed (Fig. 2). In males, the basal segment bears a large number of coeloconic sensilla which are surrounded by fluted setae (Fig. 3) not found on the female antennae. The basal region of the female antennae bears a uniform pattern of basiconic sensilla. Moreover, the basiconic sensilla are found in both sexes from annulus two through seven, and are always located in "well-like" depressions surrounded by the fluted setae which appear to be elevated on a cuticular wall around the well (Figs. 2, 4). Figure 4 shows the distinct arrangement of five to six basiconicoid sensilla characteristic for a given well, and four to five unfluted basiconicoid sensilla surrounding a shorter fluted sensillum. The "well-like" areas decrease in number as one proceeds distally and were not found on the eighth flagellomere.

The scape arises from an antennal socket and bears large, fluted setae which arise from sockets on the ventral and lateral surfaces. These setae do not occur on the lower one-third of the scape (Fig. 5). This pattern is seen on both sexes. Smaller, non-socketed setae cover the entire scape except for the dorsal surface (Fig. 6). The setal pattern of the upper portion of the scape continues on to the pedicel.

Although specific evidence is not available from this study, Zacharuk (1980) has indicated that coeloconic and basiconic sensilla are generally chemosensory. It is entirely possible, then, that the different sensilla pattern observed on the first flagellomere of the male might be functional in mating.

ACKNOWLEDGMENT

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BOOK REVIEWS

The Growth of Biological Thought. Diversity, Evolution, and Inheritance.—Ernst Mayr. 1982. Belknap/Harvard University Press, Cambridge, Massachusetts, xiii + 974 pp. $30.00.

This is a big book, containing close to a thousand pages of densely packed facts, interpretations and opinions. It is not light reading, but in general it is clearly written and unambiguous. After a first reading through, I think many biologists will find it valuable above all as a reference work, albeit one often as strongly colored by the author's personal viewpoints as was Dr. Johnson's dictionary.

Major themes of the work are the long struggles, now all but completely won, of biological-evolutionary science against the retarding forces of essentialism, natural theology, and reductionism, and the rise at last of population thinking and natural selection theory. These themes are driven home relentlessly throughout the book, occasionally through repetition that exceeds the bounds of didactic advantage. Examples of some other less conventional but welcome lines of thought are Mayr's espousal of the philosophy of emergence, and his vigorous correction of the common misconception that Lamarck was a failed evolutionist.

The range of literature in philosophy and science that is covered (and referenced) in this history is truly impressive, and the reader learns again and again of important contributions by scholars whose names have been barely familiar to most.

Like many histories that reach into present times, this one tends to fall off into spotty and idiosyncratic, often perfunctory discussion of evolutionary issues currently in controversy—for example, group selection. I doubt whether there really is a "general consensus" that most ostensible group selection cases "can be interpreted in terms of individual selection, except perhaps in social animals . . . ."

Some other interesting topics, probably even less to Mayr's taste, are barely or never mentioned. The revolt against the concept of race (subspecies), so widely flaring in the fifties, was grudgingly recognized by him in 1963, but by 1982, the gate has clanged tight against this and other heretical uprisings. Mayrian peripatric speciation, proposed as a theory of incipient macroevolution in 1954, has become the firm dogma of 1982, although interesting models exist that offer attractive alternatives to some of its main assertions. In contrast to his silence on these ideas, Mayr introduces some contributions of his own, or of his students, that do not seem as cardinally important to evolutionary theory.

It is difficult indeed to exaggerate the importance of this man in distilling and in teaching to my generation the systematics and evolutionary theory of the mid-twentieth century, especially through his influential classic of 1942. Yet in a curious way Mayr does himself succeed in producing this exaggeration because, despite disclaimers to the contrary, this history gives the impression that the growth of biological thought has reached a sort of culmination for Mayr in his personal perceptions and opinions (fulsomely but incompletely indexed on p. 968) of its state as of about 1960. But as the facts related in this great volume suggest, every contributor and his contribution, no matter how fundamentally correct and triumphant they may appear contemporaneously, are liable to suffer some revision as the surprises of time and discovery emerge.

It seems likely to me that the evolutionary understandings of a half century from now will view many of our current concepts as quaint. But looking back a full century from then, to 1933 and earlier, they may well find their agreement with Mayr's history becoming more substantially complete. Let us then celebrate and learn from the earlier periods of coverage by this book, and be cautious about its account of modern times.—*William L. Brown, Jr., Department of Entomology, Cornell University, Ithaca, New York 14853.*

Vicariance Biogeography: A Critique.—Gareth Nelson and Donn E. Rosen (eds.). 1981. Columbia University Press, New York, xvi + 593 pp. $35.00.

Vicariance Biogeography is a historical approach to biogeography which searches for general patterns of relationship among areas of endemism. These patterns are discovered through congruence among taxa cladograms—congruence which can presumably be attributed to the vicariance of a widespread ancestral biota, but not to the combined effect of chance dispersal events. Vicariance biogeography has also been called the "Platnick, Nelson, and Rosen method" (Patterson, this volume, p. 466) due to the method's formalization by Platnick and Nelson (1978) and application by Rosen (1978). A more lengthy explication of the method may be found in Nelson and Platnick (1981).

Among the more salient factors which have contributed to the formalization of vicariance biogeography are: (1) the growing evidence in support of continental drift (cf. Darlington, 1957, 1965; Tarling and Runcorn, 1973); (2) the introduction of Hennigian phylogenetics into the English language (Hennig, 1965, 1966); (3) the union of continental drift theory and Hennigian phylogenetics (Brundin, 1966); (4) the introduction of Popperian philosophy into phylogenetic systematics (Bock, 1973; Ball, 1975; Wiley, 1975); and (5) the incorporation of various aspects of Croizat's "Panbiogeography" (Croizat et al., 1974; Rosen, 1975). Application of drift theory to biogeography had already been attempted in Jeannel's *La Genése des Faunes Terrestres* (1942). Unfortunately, this antedated the vindication of continental drift and the development of an explicit means of inferring the relative recency of common ancestry among taxa.

MacArthur and Wilson (1967:5) have criticized historical biogeography, stating that: "The conventional issues relate to specific places and specific groups of plants and animals" and, therefore, the "major issues are *ad hoc* and historically oriented; for example: What was the ultimate origin of the Antillean vertebrate fauna?"; "Did Central America develop a discrete insular fauna during the Tertiary?"; "How can we account for the phylogenetic similarities of the biotas of southern South America and New Zealand?"; "Why is Hawaii rich in species of *Nesoprosopis* but lacking in other native bee genera?". These are exactly the kinds of biogeographic questions which systematists—neontologists and paleontologists—are most interested in. All questions concerning the distribution of organisms properly fall under the heading of biogeography; however, it should be obvious that when one is asking different questions one might need to employ different methods. Vicariance biogeography presumably obviates MacArthur and Wilson's criticism of historical biogeography in that it (1) searches for general patterns and (2) produces biogeographic hypotheses which are predictive and testable (Nelson and Platnick, 1981).

Vicariance biogeography has indirectly benefited from a de-emphasis on speciation via founder events (Mayr, 1942, 1963), a mode of speciation perfectly amenable to dispersalist biogeography. Templeton (1981), based upon a review of the population genetics literature, concludes that among divergence types of speciation (adaptive, clinal, and habitat) adaptive divergence (the erection of an extrinsic isolating barrier followed by independent microevolution) "is probably the dominant mode in both plants and animals" (p. 39). Among transilience modes, Templeton concludes that hybrid maintenance and hybrid recombination are important, particularly in plants, and that genetic transilience (speciation via a founders event) can be important for certain groups and situations. Speciation by chromosomal transilience is judged to be relatively rare. Among all the speciation modes discussed by Templeton, adaptive divergence (speciation following vicariance) is painted as the most general. Bush (1975:357) suggested that "the number of animals that may be speciating sympatrically or parapatrically (i.e., rodents, parasites, flightless insects, etc.) might exceed or at least equal the number of those speciating allopatrically." This is a ridiculous statement which implies that rodents, parasites, and flightless insects do not speciate allopatrically.

The present volume, *Vicariance Biogeography: A Critique*, is the product of a three day symposium (May 2–4, 1979) organized by the Systematic Discussion Group of the American Museum of Natural History. The purpose of the symposium according to Rosen (Introduction, p. 4) was to provide a forum to discuss whether vicariance theory and method as recently discussed by various authors, was useful, useless, or irrelevant for dealing with problems of historical biogeography. According to Rosen (Introduction, p. 3): "It was the decision of the altered committee that the symposium should include speakers who, except for Croizat, had never before written on vicariance theory and who represented recognizably different points of view in biogeography." Although I found the entire text interesting and enjoyable reading, I question whether the volume as a whole constitutes a thorough critique of vicariance biogeography. This may be due in part to the choice of speakers and in part to the speakers' choice of topics.

Rosen (Introduction, p. 1) refers to Croizat as a vicariance biogeographer, and yet Croizat (1982) flatly denies being a Hennigian. One can only conclude from Croizat (1982) that Croizat is not a vicariance biogeographer. Vicariance biogeography is apparently a hybridization between Brundin's phylogenetic biogeography and Croizat's "Panbiogeography," and it presumably incorporates the best aspects of each. "Panbiogeography" offers to vicariance biogeography the concept of generalized tracts (congruent distribution patterns) against a background of allopatric speciation by vicariance which sidesteps the Neodarwinistic and largely dispersalistic approaches of Darlington (1957) and Simpson (1965). Croizat's (1982) falling out with vicariance biogeography may be due to its piece meal incorporation of various aspects of "Panbiogeography" and the unsolicited editorial notes interjected within his contribution to the present volume.

Vicariance biogeography, as mentioned previously, searches for congruence between area cladograms (generalized tracks, *sensu* Platnick, Nelson, and Rosen). A critique of vicariance biogeography should, therefore, be a critique of generalized tracks. Other pertinent issues would include phylogenetic methods, Popperian philosophy, and models of speciation. Continental drift is not really an issue.

Six of the twelve invited papers are largely ancillary as critiques of vicariance biogeography. These include: Erwin's discussion of "taxon pulses"; Solem's discussion of land-snail biogeography; Hallam's review of plate movements, eustasy, and climate since the early Mesozoic; two papers discussing evidence for a lost Pacific continent, one by Melville and one by Nur and Ben-Avraham; and the paper by Haffer on Neotropical bird speciation. It is interesting, and perhaps no coincidence, that these six papers are buried centrally and consecutively within the text. Not surprisingly, discussions of these six papers are equally ancillary as critiques of vicariance biogeography. This is due to no fault of the discussants.

Of the remaining six formal papers, only the paper by Simberloff et al. really constitutes a serious critique of vicariance biogeography by directly questioning the statistical significance of congruent cladograms. Udvardy's paper is a useful interpretation of the possible position of vicariance biogeography within biogeography as a whole. The contributions by Brundin and by Patterson are recommended reading for an understanding of the difference between "phylogenetic biogeography" and "vicariance biogeography," a division which in some respects parallels the divisions referred to as "process" and "pattern" cladism (Platnick, 1979). Wolfe's paper on "Vicariance biogeography of angiosperms in relation to paleobotanical data" should be noted for the interesting discussion which it elicited. The final invited paper in the volume by Croizat is equally as entertaining as his 1982 paper in *Systematic Zoology.*

Nelson's summary of the symposium is clearly partisan and his manipulations of what the participants actually said are unwarranted. His reference to participants' reservations and criticisms of vicariance biogeography as "stumbling blocks" casts an air of naiveté upon the participants—a display of arrogance which will be more of a disservice than a shot in the arm for vicariance biogeography.

The format chosen for the symposium and this volume—contributed paper followed by discussants' comments and a final response—is excellent. I detected very few typographical errors in the text. I have reservations about symposium volumes in general; however, given the excellent format, good physical production, and the relatively low cost of this volume, I would recommend it to anyone with more than a passing interest in biogeography.—*Stephen W. Nichols, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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REVISION OF THE *PHILANTHUS ZEBRATUS* GROUP (HYMENOPTERA: PHILANTHIDAE)[1]

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Abstract.—Philanthus basilaris Cresson is removed from synonymy with *Philanthus zebratus* Cresson. A key to the six species of the *Philanthus zebratus* group is presented and their relationships, distribution and intraspecific variation discussed.

The *Philanthus zebratus* group, as defined by Bohart and Grissell (1975), is characterized by a narrow vertex and by the inner eye margins diverging below the eye emarginations. *Philanthus basilaris* Cresson has been found to be a good species and is removed from synonymy with *Philanthus zebratus* Cresson. The six species in the group are characterized and discussed, and a key for their separation is presented.

During the past few years I have received for identification a large number of philanthid wasps collected by Dr. F. D. Parker and colleagues at the USDA Bee Biology and Systematics Laboratory, Utah State University, Logan. Most of the collections have been from areas in and around the San Rafael Desert, Emery County, Utah. Among the 12 species of *Philanthus* collected is a long series of *P. basilaris* Cresson previously synonymized under *P. zebratus* Cresson. The studies reported here were undertaken to clarify the relationships and distribution of *P. basilaris* and its closely related congeners. Over 1,500 specimens have been examined in the course of the work.

The following abbreviations are used in the text and in the key:

LOD—Least distance from lateral ocellus to eye margin measured in lateral ocellus diameters.
MOD—Least distance from midocellus to eye margin measured in midocellus diameters.
V/MO—Least width of vertex divided by diameter of midocellus.
H/F Ratio—Maximum width of head divided by width of face between apices of eye emarginations.

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[1] Oregon Agricultural Experiment Station Technical Paper No. 6551.

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F/V Ratio—Width of face between apices of eye emarginations divided by least width of vertex.

C/F Ratio—Maximum width of clypeus divided by width of face at apices of eye emarginations.

Measurements in the ocellocular area were made at 40–70× magnification, and those of the head, face and clypeus at 10–30× depending on the size of the specimen. Variation in the vertex and ocellocular ratios is given in the diagnosis of each species. The H/F and C/F ratios were remarkably constant within species. Only those ocellocular ratios which show a substantial difference are used in the key.

Abbreviations of institutional repositories are given under Acknowledgments.

A progressive narrowing of the vertex occurs within the group such that three subgroups may be recognized. In the *gloriosus* subgroup, composed of *Philanthus gloriosus* Cresson and *Philanthus bicinctus* (Mickel), the LOD is 0.7 to 1.5 in males and 2.0 to 2.5 in females; the F/V ratio is 1.8 to 2.3 in males and about 1.5 in females. In the *zebratus* subgroup, composed of *Philanthus basilaris* Cresson, *Philanthus ventralis* (Mickel) and *Philanthus zebratus* Cresson, the LOD is less than 0.5 in males and about 1.0 in females; the F/V ratio is about 3 in males and about 2 in females. In the intermediate *sanbornii* subgroup, composed only of *Philanthus sanbornii* Cresson, the males have the vertex and ocellar characteristics of the *zebratus* subgroup, and the females have those of the *gloriosus* subgroup.

Strandtmann (1946) recognized four species within the *zebratus* subgroup, *P. basilaris, P. nitens* (Banks), *P. ventralis* and *P. zebratus.* Bohart and Grissell (1975) recognized two species: *P. ventralis* and *P. zebratus,* synonymizing *P. basilaris* and *P. nitens* under *P. zebratus.* They suggested that, if subspecies of *zebratus* were recognized, the name to be used for the whitish phase east of California would be *P. basilaris* with *P. nitens* as a synonym. However, both *P. basilaris* and *P. zebratus* occur in a whitish phase. As interpreted here *P. basilaris* is resurrected as a good species and *P. nitens* remains a junior synonym of *P. zebratus.*

The following key is adapted and modified from that given by Bohart and Grissell (1975).

KEY TO *Philanthus zebratus* GROUP

1. Males 2
– Females 7
2. MOD at least 1.0; LOD at least 0.7 3
– MOD less than 1.0; LOD less than 0.5 4
3. MOD about 1.5; LOD about 1.2; clypeal brush mostly yellowish .... *gloriosus* Cresson
– MOD about 1.0; LOD about 0.75; clypeal brush mostly or entirely blackish .... *bicinctus* (Mickel)

4. Scutal punctures dense, mostly separated by about 1 puncture diameter, more or less uniformly distributed; tergum III with punctures about same size as on scutum; pubescence of head and thorax brown to fuscous; tergum I all dark (black or red) or with widely separated pale spots .... *sanbornii* Cresson
– Scutal punctures, at least medially, unevenly separated by many smooth interspaces of several puncture diameters; tergum III with at least a few smooth-rimmed punctures distinctly larger than scutal punctures; pubescence of head and thorax pale yellow to white; tergum I with a pale band which may be incised medially or narrowly divided 5
5. Antennal flagellum pale below to tip; pale bands of terga I and/or II interrupted medially .... *ventralis* (Mickel)
– Antennal flagellum with apical 1 to 5 flagellomeres black or infuscated below; pale bands of terga I and II continuous (rarely interrupted in northern Rocky Mountain forms) 6
6. H/F ratio 1.8; propodeal enclosure usually shagreened; tergum I and/or sternum I usually marked with red .... *basilaris* Cresson
– H/F ratio 1.7; propodeal enclosure polished between punctures; tergum I and sternum I rarely marked with red .... *zebratus* Cresson
7. MOD 2.4 to 3.1; LOD 2.0 to 2.5; V/MO 6 to 7 8
– MOD 1.2 to 1.5; LOD 0.8 to 1.1; V/MO 3.2 to 4.0 10
8. Scutal punctures sparse, unevenly distributed, almost impunctate across middle third; terga III–V black; about 20 mm long .... *bicinctus* (Mickel)
– Scutal punctures dense and more or less evenly distributed, at least on lateral third; one or more of terga III–V maculated; length 18 mm or less 9
9. Punctures of tergum III rather dense and uniformly distributed; tergum I about twice as wide as long, distinctly transverse; about ¾ of surface of lateral lobe of clypeus finely and densely punctate; pale band on tergum II interrupted medially .... *sanbornii* Cresson
– Punctures of tergum III sparse and irregularly spaced; tergum I about 1.5 times as wide as long, somewhat bell-shaped; about ⅔ of surface of lateral clypeal lobe polished, impunctate; pale band on tergum II complete or anteriorly emarginate, not completely interrupted .... *gloriosus* Cresson
10. Scutal punctures sparse, separated by many large, polished areas; pale facial mark truncate or crown-shaped above, separated from midocellus by much more than ocellus diameter .... *zebratus* Cresson
– Scutal punctures dense laterally, at least along parapsidal lines; pale facial mark narrowed above, reaching to midocellus or nearly so 11
11. Pale bands of terga I/II continuous; H/F ratio 1.7; tergum I and/or sternum I usually marked with red .... *basilaris* Cresson
– Pale bands on terga I and II usually interrupted or deeply incised medially; H/F ratio 1.6; terga and sterna never marked with red .... *ventralis* (Mickel)

Philanthus gloriosus Cresson

Philanthus gloriosus Cresson, 1865:86. [Female lectotype, Colorado; ANSP]; Strandtmann, 1946:31 and prior literature; Burks, 1951:1001; Bohart and Grissell, 1975:11; Bohart and Menke, 1976:565; Krombein, 1979:1723.

Philanthus insignatus Banks, 1913:421. [Female holotype, Alpine, Texas; AMNH]; Synonymy by Strandtmann 1946:31.

Diagnosis. Male 14–16 mm; LOD 1.2 (1.0–1.5); MOD 1.6 (1.3–1.8); V/MO 4.2 (3.8–4.5); H/F 1.6; F/V 1.8; C/F 1.1; clypeal brush pale. Female 16–18 mm; LOD 2.5 (2.4–2.8); MOD 3.1 (2.8–3.3); V/MO 7.0 (6.5–7.5); H/F 1.6; F/V 1.4; C/F 1.2; scutal punctures dense except medially. *P. gloriosus* is assumed to be the most generalized member of the group since the vertex is wider relative to the width of the face than in any other species within the group.

Variation. Color pattern is quite constant in the populations east of the Rocky Mountains, eastern Arizona and in Mexico. Females have a deep tongue-shaped anterior emargination in the pale band of tergum II, and males have a triangular posterior emargination on tergum II completely interrupting the pale band. The background color is usually bright red, especially in females, in the desert areas in and around southeastern Arizona. Both northward and southward the red gradually changes to black such that the specimens from Canada and Mexico D.F. have identical coloration with a black and yellow pattern and few, if any, red markings. A similar double cline also occurs in *Cerceris sexta* Say which has a similar distribution.

In northern Arizona (Coconino and Mohave Counties), Utah and California the emargination on tergum II has been lost in both sexes, the specimens being broadly banded with bright yellow. Dorsally the background color is largely black. Morphologically this form differs from the eastern form only in having the terga somewhat more sparsely punctate. An anomaly is the fact that males collected at Government Holes, 5,000 ft., San Bernadino County, California, IX-12-76 [USU] are identical in color pattern to the populations east of the Rocky Mountains. Specimens of the "yellow" form are in the collections of ALB, AZS, UCD, CDA, OSU, USNM, and USU.

Flight period. Dates of capture are July–August in the northern plains; August–September in southern Arizona, New Mexico, Texas and Chihuahua; and September–October in the remaining states of Mexico. The species is apparently univoltine in the above areas.

California records are in June–July and September–October leading Bohart and Grissell (1975) to suggest that there were two broods per year. Collection dates in northern Arizona and Utah are in May–June and August–September, indicating that the species is bivoltine in that area as well.

Distribution. West of the 100th meridian in the United States and Canada from Alberta (Medicine Hat) and Saskatchewan (near Empress, Alberta) south through the high plains and eastern slope of the Rocky Mountains to Culberson and Brewster Counties, Texas; Hidalgo County, New Mexico; and west through eastern and northern Arizona and Utah to southeastern California. In Mexico it occurs in the states of Chihuahua, Coahuila, Durango, San Luis Potosí, Hidalgo, Mexico D.F., and Puebla.

Specimens examined. 134 males, 96 females.

Philanthus bicinctus (Mickel)

Ococletes [sic] *bicinctus* Mickel, 1916:407. [Female holotype, Ute Creek, Sage Flats, Colorado; NEB]; 1918:326.
Ococletes [sic] *hirticulus* Mickel, 1918:326. [Male holotype, Ute Creek, Sage Flats, Colorado; NEB].
Philanthus bicinctus, Strandtmann, 1946:35; Burks, 1951:1001; Evans, 1964: 275 (larva); Krombein, 1967:413; 1979:1721; Bohart and Grissell, 1975: 5, 7 (in key); Bohart and Menke, 1976:564.
Philanthus hirticulus, Strandtmann, 1946:40; Burks 1951:1001; Synonymy by Krombein 1967:413.

Diagnosis. Male 17–19 mm; LOD 0.7 (0.6–0.8); MOD 1.1; V/MO 3.2 (3.1–3.3); H/F 1.6; F/V 2.3; C/F 1.2; clypeal brush blackish, sometimes pale at tip. Female 20–22 mm; LOD 2.1 (2.0–2.2); MOD 2.7 (2.6–2.7); V/MO 6.4 (6.1–6.6); H/F 1.6; F/V 1.5; C/F 1.2; scutal punctures sparse, mostly impunctate over middle third. In males the eyes are somewhat more diverging at the clypeus with a C/F ratio of 1.2 compared to 1.1 for the remaining species of the group.

P. bicinctus is our largest species. The males are yellow banded and resemble males of the western form of *P. gloriosus,* but the larger size and characters given in the key easily separate them. The female is a strikingly beautiful insect with a red tergum I, yellow tergum II, and the remaining terga black.

Biology. Digging, feeding, provisioning, nesting and hunting activities of females as well as male behavior suggesting territoriality were described by Armitage (1965). Nests were found in aggregations in a silty clay soil. Prey consisted of eight species of worker and male *Bombus* with Megachilidae (*Megachile* sp.) and Anthophoridae (*Anthophora* sp., *Melissodes* sp.) also taken. Gwynne (1978) and Gwynne and O'Neill (1980) described and discussed male territorial behavior. Gwynne (1980, 1981) described female behavior and nesting activities. Prey records included ten species of *Bombus* plus one species of *Psithyrus* and *Apis mellifera* in the Apidae; five species of Megachilidae in two genera; two species of Anthophoridae in two genera; and one species of Sphecidae (*Podalonia communis*). Bumblebees constituted about 99% of the prey in 1976, 1977, but only 39% of the prey in 1978.

Flight period. July to September.

Distribution. Rocky Mountains from Montana to southern Colorado at recorded elevations of 6,900 to 8,000 ft.

Specimens examined. 6 males, 4 females.

Philanthus sanbornii Cresson

Philanthus sanbornii Cresson, 1865:89. [Female lectotype, Massachusetts; ANSP]; Strandtmann, 1946:37 and prior literature; Burks, 1951:1002; Krombein, 1958:197; 1979:1725; Bohart and Grissell, 1975:5, 7 (in key); Bohart and Menke, 1976:566.

Philanthus scutellaris Cresson, 1879:xxxiv. [Male holotype, Kansas; ANSP]; Synonymy by Strandtmann, 1946:37.

Philanthus eurynome Fox, 1890:107. [Female lectotype, Florida; ANSP]; Strandtmann, 1946:34; Burks, 1951:1001; Krombein, 1967:413; Synonymy by Bohart in Bohart and Menke, 1976:566.

Philanthus trumani Dunning, 1897:70. [Male, not female, holotype, Brookings County, South Dakota; location of type unknown]; Synonymy by Dunning, 1898:152.

Philanthus magdalenae Strandtmann, 1946:39. Name created in synonymy, authorship (p. 37) incorrectly attributed to Viereck.

Diagnosis. Male 12–14 mm; LOD 0.3 (0.3–0.5); MOD 0.7 (0.6–0.7); V/MO 2.4 (2.3–2.5); H/F 1.7; F/V 3.1; C/F 1.1; pubescence brown to fuscous on head and thorax. Female 14–17 mm; LOD 2.0 (1.8–2.3); MOD 2.4 (2.0–3.0); V/MO 6.0 (53.–7.2); H/F 1.6; F/V 1.6; C/F 1.2; scutum, scutellum and terga rather densely and uniformly punctate. *P. sanbornii* exhibits an intermediate condition in the evolution of the ocellocular area. The vertex of the male is narrowed markedly compared to the *gloriosus* subgroup, whereas the female vertex is not. The eyes of the male have slightly enlarged to a H/F ratio of 1.7 compared to 1.6 in both *P. gloriosus* and *P. bicinctus.*

Variation. The geographical variation in color pattern is a common one in philanthid wasps. The Florida specimens are usually heavily marked with red on the anterior terga, and the western specimens are more highly maculated with yellow.

Biology. Evans (1955) and Evans and Lin (1959, as *P. eurynome*) reported honeybees used as prey with Halictidae also taken. Nesting was in sandy areas but not in dense aggregations. *Megachile inermis* Provancher (det. W. P. Stephen) is also used as prey based on a specimen of *P. sanbornii* pinned with this bee from Aweme, Manitoba, VI-28-78 [MTB].

Flight period. Dates of capture are March–April in Florida; June in Georgia; and June 15 to August 30 elsewhere. It is apparently univoltine.

Distribution. United States and southern Canada east of the 100th meridian with occasional captures in the high plains. Peripheral records west of the 100th meridian are: ALBERTA (Writing-On-Stone) [ALB]; NORTH DAKOTA (Dunn County) [NDS]; NEBRASKA (Thomas County) [OSU]; and NEW MEXICO (Socorro County), the latter record from Strandtmann (1946).

Specimens examined. 48 males, 62 females.

Philanthus ventralis (Mickel)

Ococletes [sic] *ventralis* Mickel, 1918:329. [Female holotype, Sacramento, California; NEB].

Philanthus ventralis, Strandtmann, 1946:43; Bohart and Grissell, 1975:18; Bohart and Menke, 1976:566; Krombein, 1979:1726.

Philanthus strandtmanni Burks, 1951:1002. Unnecessary new name for *Philanthus ventralis* (Mickel).

Diagnosis. Male 12–14 mm; LOD 0.3 (0.3–0.4); MOD 0.7 (0.6–0.8); V/MO 2.5 (2.4–2.7); H/F 1.7; F/V 2.9 (2.6–3.2); C/F 1.1. Female 13–15 mm; LOD 1.1 (0.9–1.2); MOD 1.5 (1.3–1.7); V/MO 3.9 (3.5–4.4); H/F 1.6; F/V 2.1 (2.0–2.2); C/F 1.2. See Table 1 for additional characters separating this species from *P. basilaris* and *P. zebratus.*

Variation. There is little variation in morphology or color pattern over most of the range of this species. However, some males from southern California (San Diego County, Kitchen Creek, Laguna Mountains, IX-31-78 [LAM], and Kern County, Walker Pass, IX-26/27-57 [UCD]) have the apical two or three flagellomeres infuscated below. Over the balance of the range of the species the flagellum is pale below to the apex. This may indicate some introgression of either *P. basilaris* or *P. zebratus* genes.

Flight period. This is a late summer and early fall species with most captures in August–September. Bohart and Grissell (1975) provide a frequency distribution showing a peak flight period in September. Oregon and Washington specimens have been collected between August 9 and September 8 with a peak in late August. The earliest collection date is July 6 in Siskiyou County, California, and the latest date is October 21 in Contra Costa County, California.

Distribution. California and western Nevada to British Columbia. Bohart and Grissell (1975) presented a distribution map and detailed locality records for California. In Oregon I have seen specimens from Baker, Harney, Klamath, Union and Wheeler Counties, all east of the Cascade range. The Inyo County, California, specimens listed by Bohart and Grissell (1975) are discussed under *P. basilaris.*

Specimens examined. 159 males, 67 females.

Philanthus basilaris Cresson (Revised Status)

Philanthus basilaris Cresson, 1879:xxxiii. [Female lectotype, Colorado; ANSP]; Strandtmann, 1946:48 and prior literature; Burks, 1951:1001.

Philanthus zebratus, in part, Bohart and Grissell, 1975:18; Bohart and Menke, 1976:567; Krombein, 1979:1726.

Diagnosis. Male 12–14 mm; LOD 0.3 (0.2–0.4); MOD 0.8 (0.7–0.9); V/MO 2.5 (2.3–3.0); H/F 1.8; F/V 2.8 (2.6–3.2); C/F 1.1. Female 13–15 mm;

LOD 0.8 (0.7–0.9); MOD 1.3 (1.1–1.6); V/MO 3.4 (3.1–3.7); H/F 1.7; F/V 2.0 (1.9–2.1); C/F 1.2. See Table 1 for additional diagnostic characters.

P. basilaris resembles *P. ventralis* in having denser scutal punctation compared to *P. zebratus,* and in its late-season flight period compared to a midsummer flight period in *P. zebratus.* The swollen eyes of *P. basilaris,* indicated by a H/F ratio of 1.8 in males and 1.7 in females, separate it from both *P. ventralis* and *P. zebratus.* In the latter two species the H/F ratio is 1.7 in males and 1.6 in females. Another distinctive feature is that the tergal bands of *P. basilaris* are broad and continuous in both sexes, whereas in *P. ventralis* they are interrupted, at least on the anterior terga, in both sexes, and in *P. zebratus* the bands are continuous in the males and interrupted in the females.

Variation. Coloration is rather constant over most of the range of this species. The broad tergal bands vary from lemon yellow to pale yellowish white, and tergum I as well as sterna I–II are conspicuously marked with red. Nevada specimens are whiter, and the red marks are reduced or absent. The pale markings of a male from Humboldt County, Nevada, are entirely white. California specimens are more of a bright yellow, and red marks are absent. Three of four males from Mono County, California [UCD], and one of eight females from Inyo County, California [UCD] have the pale band of tergum I narrowly interrupted, indicating a possible introgression of *P. ventralis* or *P. zebratus* genes.

Biology. Prey consists of diverse adult Hymenoptera, as O'Neill and Evans (1981) reported that the contents of an excavated nest of *P. basilaris* consisted of two conspecific males and a male of *P. bicinctus* "intermingled with other bees and wasps serving as food for the larvae." Evans and O'Neill (1978) and Gwynne and O'Neill (1980) described male territoriality in populations from Weld and Alamosa Counties, Colorado. At that time these populations were considered to belong to *P. zebratus,* but later (O'Neill and Evans, 1981) they were recognized as *P. basilaris.* These populations were compared to a population of *P. zebratus* from Jackson Hole, Wyoming, that did not exhibit territoriality. Nests were not concentrated into dense aggregations in the Colorado populations of *basilaris* as they were in the case of the Wyoming population of *zebratus.*

Flight period. P. basilaris, like *P. ventralis,* is a late-summer and early-fall species. Dates of capture are mostly in August–September with an early record of July 17 in Alamosa County, Colorado (Great Sand Dunes), and a late record of October 12 in Mono County, California. It is apparently univoltine.

Distribution. From Alberta and Saskatchewan south through the high plains and eastern slope of the Rocky Mountains to McKinley County, Texas, and west through northern New Mexico and northern Arizona to Utah, Nevada, and Mono and Inyo Counties, California. Records and collection dates are summarized as follows: ALBERTA (8 km W of Buffalo, VIII-27) [ALB]; SASKATCHEWAN (Tp. 5, Rge 25, W.3 Mer., VIII-17) [ALB]; NORTH DAKOTA (Billings and Golden Valley Counties, VIII-30) [AMNH, MCZ, USNM]; WYOMING (Carbon, Converse, Laramie, Platte and Sweetwater Counties, VIII-4 to IX-27) [AMNH, UCD, COR, OSU, USNM, USU, UWY]; NEBRASKA (Dawes County, VIII-27) [NEB]; COLORADO (Alamosa, Grand, Larimer and Weld Counties, VIII-4 to IX-5) [UCD, CSU, MCZ, OSU, USU]; TEXAS (McKinley County, IX-21) [USU]; NEW MEXICO (Catron and San Miguel Counties, VIII-16 to VIII-19) [ANSP, UCD, OSU]; ARIZONA (Coconino and Navajo Counties, VIII-30 to IX-23) [ALB, UCD, OSU]; UTAH (Emery, Kane and Washington Counties, VIII-19 to IX-20) [UCD, UCR, KAN, OSU, USNM, USU]; NEVADA (Churchill, Douglas and Humboldt Counties, VIII-17 to IX-9) [UCD, OSU]; CALIFORNIA (Inyo and Mono Counties, VIII-23 to X-12) [UCD, MIN, UMO, OSU]. Distribution is essentially sympatric with *P. gloriosus* over the northern portion of the range of the latter.

Specimens examined. Female lectotype, 163 males, 76 females.

Philanthus zebratus Cresson

Philanthus zebratus Cresson, 1879:xxxiii. [Male holotype, Nevada; ANSP]; Strandtmann, 1946:46 and prior literature; Burks, 1951:1003; Bohart and Grissell, 1975:18; Bohart and Menke, 1976:567; Krombein, 1979:1726.

Oclocletes nitens Banks, 1913:423. [Female, not male, holotype, Princeton, British Columbia; MCZ].

Ococletes [sic] *illustris* Mickel, 1918:326. [Female holotype, American River, Placer County, California; NEB]; Synonymy by Strandtmann, 1946:46.

Philanthus nitens Strandtmann, 1946:42; Burks, 1951:1002; Synonymy by Bohart and Grissell, 1975:19.

Diagnosis. Male 12–14 mm; LOD 0.3 (0.2–0.3); MOD 0.6 (0.5–0.7); V/MO 2.3 (2.1–2.4); H/F 1.7; F/V 3.1 (2.8–3.2); C/F 1.1. Female 14–16 mm; LOD 0.9 (0.7–1.1); MOD 1.3 (1.1–1.6); V/MO 3.8 (3.3–4.1); H/F 1.6; F/V 2.0 (1.9–2.2); C/F 1.2. See Table 1 for additional diagnostic characters.

Variation. P. zebratus falls into three distinguishable populations. The Rocky Mountain population is characterized by the females having red tibiae and a tendency for the pale maculations to be white in a majority of the specimens. About one-fourth to one-third of the specimens have yellow maculations. The tendency for pale markings to change from yellow to white in a south to north cline is common in western philanthid wasps.

The Siskiyou population is characterized by a reduced amount of black on the underside of the male flagellum. Commonly only the apical flagellomere is infuscated below, which may represent an influence from adjacent *P. ventralis* populations in which the flagellum is entirely pale below. The allochronicity would not be sufficient to prevent early-emerging *ventralis* males from mating with late-emerging *zebratus* females, if such cross-breeding can, in fact, occur. Females of the Siskiyou population usually have the hind tibiae blotched with red, representing a condition intermediate between the Rocky Mountain and Sierra Nevada populations—the latter having yellow tibiae with only occasional traces of red.

The Sierra Nevada population is characterized by a continued reduction in density of scutal punctures with the posterior two-thirds of the scutum being virtually impunctate (see Bohart and Grissell, 1975, Fig. 23). The transverse band of fine punctures on the posterior margin of the scutum is 4 to 8 punctures wide in the Rocky Mountain and Siskiyou populations, whereas this band of punctures is only 2 or 3 punctures wide, or virtually absent, in the Sierra Nevada population.

Occasional males in the Rocky Mountain population have an interrupted pale band on tergum I and greyish pubescence on the head and thorax. The band on tergum I is usually continuous and the pubescence usually pale, as in other populations. The sternal hair brushes of the male are often fuscous in the Rocky Mountain population and usually amber in the Sierra Nevada population, but these hair brushes in the Siskiyou population are intermediate, being brown to occasionally fuscous. The sterna of males of the Rocky Mountain population are usually immaculate, but almost always maculated in other populations.

A series of 9 males and 5 females collected in Wyoming, Sublette County, 3 mi. N Pinedale, VII-15-71 (R. M. Bohart, E. E. Grissell) [UCD] shows evidence of hybridization with *P. basilaris.* The head/face ratio of the males varies from 1.7 to 1.8. The scutal punctures of the females are very sparse in one specimen, almost as dense as in *basilaris* in one specimen, and intermediate in three specimens. The outer face of the hind tibia is yellow in four females and red in one. The pale band of tergum I is interrupted in three females and continuous in two. The pale band of tergum II is either interrupted or deeply incised in all five females. The anterior terga and sterna have an all black background color in four males and two females with the remainder showing variable amounts of red. The pale facial mark of the females is crown-shaped above and well separated from the midocellus. The pale markings are white in females and white on terga III–VI in males. Typical *basilaris* is known from Sweetwater County, the adjoining county on the south, and typical *zebratus* is found in Teton County, the adjoining county on the north and west.

The three populations of *P. zebratus* might be treated as subspecies, but I have elected not to do so. The ranges of the populations are contiguous and the differences tend to be clinal in nature. The possibility that Pleistocene and Recent ash falls and lava flows from volcanic activity have tended to temporarily isolate these populations cannot be overlooked. The Sierra Nevada and Siskiyou populations of *P. zebratus* abut in Lassen County, California, the site of very recent volcanic activity. The Siskiyou and Rocky Mountain populations adjoin in northern Klamath County, Oregon, an area of extensive volcanic activity only a few thousand years ago.

Biology. Males are non-territorial, but rather form aerial swarms over the densely aggregated nesting sites during the mating period according to Evans and O'Neill (1978). Evans (1966, 1970) recorded 25 species of wasps and 20 species of bees used as prey by *P. zebratus* in the vicinity of Jackson Hole, Teton County, Wyoming. The number of prey specimens was about equally divided between 75 wasps and 74 bees. Families represented were Ichneumonidae, Eumenidae, Masaridae, Sphecidae, Colletidae, Andrenidae, Halictidae, Megachilidae, and Anthophoridae.

A series of 35 female *zebratus* collected on the same day, VII-18-48, at Hope Valley, Alpine County, California, (A. Bartel, J. W. Adams, P. D. Hurd, J. W. MacSwain) [UCB] is each pinned with one or more prey specimens and labelled "taken as prey." The bees were determined by Dr. A. Moldenke and the wasps by the author. One *P. zebratus* is pinned with two small bees, i.e., *Dufourea* sp. (male) and *Osmia* sp. (female). It is implied that the single *zebratus* female was carrying both specimens at the time of capture. The remaining 34 female *zebratus* are each pinned with a single prey specimen as follows:

VESPOIDEA
- *Ancistrocerus* sp. (1 male, 1 female)

SPHECOIDEA
- *Ammophila stangei* Menke (1 male)
- *Aphilanthops subfrigidus* Dunning (3 males)
- *Podalonia luctuosa* (F. Smith) (1 male)
- *Tachysphex* sp. (1 female)

APOIDEA
- *Andrena* (*Andrena*) sp. (3 females)
- *Andrena* (*Euandrena*) sp. (1 female)
- *Andrena* (*Thysandrena*) sp. (1 female)
- *Andrena* (*Trachandrena*) spp. (2 females of 2 species)
- *Andrena* (subgenus ?) sp. (2 females)
- *Hoplitis fulgida platyura* (Cockerell) (1 female)
- *Hoplitis albifrons argentifrons* (Cresson) (1 male)
- *Lasioglossum trizonatum* (Cresson) (2 females)
- *Osmia* (*Chenosmia*) sp. (3 females)
- *Osmia* spp. (8 females, 2 males of 4 species)

Total. Eight wasps in 5 genera and 5 species; 28 bees in 5 genera and 16 species.

Since all captures were on the same day, the record probably reflects local

Table 1. Comparison of species of the *zebratus* subgroup.

Character state	*basilaris*	*ventralis*	*zebratus*
Female scutal punctation	Dense to contiguous on lateral third	Dense to contiguous on lateral third	Sparse to well separated
Male (female) H/F ratio	1.8 (1.7)	1.7 (1.6)	1.7 (1.6)
Propodeal enclosure	Shagreened	Pollished between punctures	Polished between punctures
Propodeal furrow	Not strongly widened posteriorly	Strongly widened posteriorly	Strongly widened posteriorly
Punctures of tergum II—females	Numerous smooth-rimmed large punctures	Few, scattered smooth-rimmed large punctures	Few, scattered smooth-rimmed large punctures
V/MO—males	2.5 (2.3–3.0)	2.5 (2.4–2.7)	2.3 (2.0–2.4)
Male flagellum	Apical 2–5 flagellomeres black below	Pale below to apex	Apical 1–5 flagellomeres black below
Pale facial mark—females	Narrowed above	Narrowed above	Trucated above
Terga I/II pale bands	Continuous in both sexes	Interrupted in both sexes	Continuous in males, interrupted in females
Sterna I/II	Usually red	Black	Black
Flight period	August, September	August, September	July, August
Life zone	Upper Sonoran	Upper Sonoran, transition	Canadian

abundance of prey rather than any difference in prey preference or diversity when compared with Evans' records above. Insofar as I can ascertain, these are the first published prey records west of the Rocky Mountains and simply confirm that *P. zebratus* uses a diverse assortment of Hymenoptera as prey.

Flight period. Rocky Mountain population: Most collection dates are in July with an early record of May 27 in Valley County, Idaho, and a late record of August 25 in Teton County, Wyoming. Siskiyou population: Dates of capture are in July–August with an early date of June 20 in Trinity County, California, and a late date of August 14 in Siskiyou County, California. Sierra Nevada population: Collection dates are mostly in July–August with an early date of June 12 in Plumas County, California, and a late date of September 9 in Sierra County, California. Bohart and Grissell (1975) provide a frequency distribution showing a pronounced peak in July. The species appears to be univoltine throughout its range.

Distribution. Rocky Mountain population: BRITISH COLUMBIA (Chilcotin, Nicola, Okanagan Falls and Osoyoos); MONTANA (Missoula County); WYOMING (Sublette, Teton Counties and Yellowstone National Park); IDAHO: (Owyhee and Valley Counties); WASHINGTON: (Douglas and Kittitas Counties); OREGON: (Klamath and Lake Counties). Siskiyou population: CALIFORNIA: (Humboldt, Lassen, Siskiyou and Trinity Counties); OREGON: (Klamath County). Sierra Nevada population: CALIFORNIA: (all alpine counties from Tulare County to Lassen County); NEVADA: (Douglas and Ormsby Counties).

Specimens Examined. Male holotype of *Philanthus zebratus* Cresson, female holotype of *Oclocletes nitens* Banks, and 423 males, 291 females. Of the three populations discussed under Variation: Rocky Mountain population 41 males, 50 females; Siskiyou population 94 males, 32 females; Sierra Nevada population 288 males, 209 females.

SUMMARY

Certain evolutionary trends are exhibited within the *zebratus* group. The most obvious is the progressive narrowing of the vertex from an F/V ratio of 1.8 in the males of *P. gloriosus* to 2.8 to 3.0 in the *sanbornii* and *zebratus* subgroups, and from 1.4 in the females of *P. gloriosus* to about 2.0 in the *zebratus* subgroup. The size of the eyes in relation to the width of the face increases from a H/F ratio of 1.6 in males of the *gloriosus* subgroup to 1.7 in *sanbornii, ventralis* and *zebratus,* and to 1.8 in *basilaris.* In females the H/F ratio is 1.6 in all species except *basilaris* in which it is 1.7. There has been a reduction in the density of scutal punctures with *P. bicinctus* and *P. zebratus* showing the sparsest punctation.

Within the three closely related species of the *zebratus* subgroup the degree of interspecific variation is less than that between it and the remaining species of the group; however, the differences shown in Table 1 are sufficient to

justify specific recognition of the three taxa in spite of the evidence of occasional gene flow or hybridization. Noteworthy also is the fact that nesting is in dense aggregations in the case of *P. zebratus* but not in *P. basilaris,* and males of *basilaris* exhibit territoriality whereas males of *zebratus* form aerial swarms over the nesting site.

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ESTABLISHMENT OF *HYLES EUPHORBIAE* (L.) (LEPIDOPTERA: SPHINGIDAE) IN THE UNITED STATES FOR CONTROL OF THE WEEDY SPURGES *EUPHORBIA ESULA* L. AND *E. CYPARISSIAS* L.

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Abstract.—The European spurge hawkmoth, *Hyles euphorbiae* (L.) was introduced for control of leafy spurge (*E. esula* L.) and cypress spurge (*E. cyparissias* L.). It was initially established in the United States at Chestertown, New York, on tetraploid cypress spurge and the hybrid *E.* × *pseudo-esula* Schur. The population increased from 180 to about 1 million insects within 5 years, with total defoliation of spurge in some areas.

Cypress spurge (*Euphorbia cyparissias* L.), also known as yellowweed or graveyard weed, was introduced into North America from central and southern Europe by the mid-nineteenth century (Moore and Lindsay, 1953). In North America and Europe, this plant occurs in two forms—a fertile tetraploid (2n = 40) and a male-sterile diploid (2n = 20); a third form in France is a fertile diploid (Pritchard, 1961). The seed-producing tetraploid is an invasive weed that may occupy large areas, but it is relatively rare in North America; the less weedy sterile diploid is often cultivated as an ornamental (Moore and Lindsay, 1953). In the United States, stands of the fertile tetraploid form in New Hampshire, Massachusetts, and four counties (Franklin, St. Lawrence, Herkimer, and Orange) in New York were reported by Muenscher (1936).

Fertile tetraploid cypress spurge has been reported to hybridize with leafy spurge, *E. esula* L. (*sensu lato,* 2n = 60), in Europe and Canada; these morphologically variable hybrids (*E.* × *pseudo-esula* Schur, 2n = 50), produce scant seed (Moore, 1958; Moore and Frankton, 1969).

Leafy spurge (*s.l.*) is a variable, invasive, fertile weed. It originated in central and northern Eurasia, and was first recorded in North America in 1827 (Croizat, 1945; Best et al., 1980). Subsequently, it has spread through-

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out most of the northern half of the United States and southern Canada, with greatest impact in the upper Great Plains region (Hanson and Rudd, 1933; Selleck et al., 1962; Dunn, 1979; Best et al., 1980). Leafy spurge infests 1.2 million ha of pasture and rangeland (Sun, 1981). In New York, leafy spurge has been recorded in 15 counties (Muenscher, 1930; Dunn, 1979), including Orange, St. Lawrence, and Herkimer. It is possible that leafy spurge in these latter three counties may hybridize with the tetraploid cypress spurge known to occur there. These hybrids are known at three sites in Canada (Moore and Frankton, 1969).

Leafy and cypress spurges possess a milky latex that may cause dermatitis in humans and animals; the ingested fresh plants may cause illness in livestock (Moore and Lindsay, 1953; Best et al., 1980). Sheep graze limited amounts of leafy spurge without distress (Johnston and Peake, 1959). The latex contains esters of cocarcinogenic diterpene irritants (Upadhyay et al., 1978) as well as a related antileukemic diterpenoid diester (Kupchan et al., 1976). Control of these vigorous perennial weeds is difficult due to shoot regeneration from deeply buried roots or root fragments, competitiveness with desirable vegetation, and lack of natural enemies in North America.

Efforts to limit the spread and impact of leafy spurge, and to a lesser extent cypress spurge, by biological control were initiated in Canada. After several years of investigation, including host-specificity testing (as summarized in Batra, 1982), the Eurasian spurge hawkmoth *Hyles* (=*Celerio*) *euphorbiae* (L.) was first imported in 1965 and released in Canada. This population did not survive; of numerous subsequent North American releases, only one established population (released in 1966–1967 on tetraploid cypress spurge at Braeside, Ontario) is reported (Harris and Alex, 1971). Mortality is attributed to predation by several genera of ants, deer mice (*Peromyscus leucopus* (Raf.)), *Xyticus* spiders, *Polistes* wasps, pentatomid bugs (*Apateticus* sp.), and four genera of carabid beetles (Harris and Alex, 1971; Forwood and McCarty, 1980a). Due to the poor survival of released *H. euphorbiae,* several other Eurasian host-specific natural enemies of leafy spurge are being investigated.

In southern and south-central Europe, *Hyles euphorbiae* has two generations annually on *Euphorbia* spp., with *E. cyparissias* its preferred larval host. Adults (Fig. 1) lay about 100 eggs in small clusters (Fig. 2) on terminal leaves where the growing larvae feed gregariously (Fig. 3). Pupation occurs 2–15 cm below the soil surface, and the crepuscular adults visit *Saponaria officinalis* L. or other flowers for nectar (Moscardini, 1947). In laboratory tests, each larva is capable of consuming 130 linear cm of fresh cypress spurge stem and foliage (2.7 g dry weight) according to New (1971), or 17.05 g fresh weight (3.37 g dry weight) of leafy spurge (Forwood and McCarty, 1980b).

Figs. 1–4. *Hyles euphorbiae.* 1. Adult; forewings are olive-green and tan tinged with pink, hind wings are salmon-pink and black. 2. Bright-green eggs. 3. Gregariously feeding young larvae; first instar larvae are greenish-black, older instars develop green, yellow and black markings. 4. Mature larva; the aposematic markings of this conspicuous toxic-plant feeder include orange-red on the head, horn, dorsal stripe, lateral stripes and legs, with numerous pale yellow to white speckles and spots on a black integument.

HOSTS AND ESTABLISHMENT IN NEW YORK

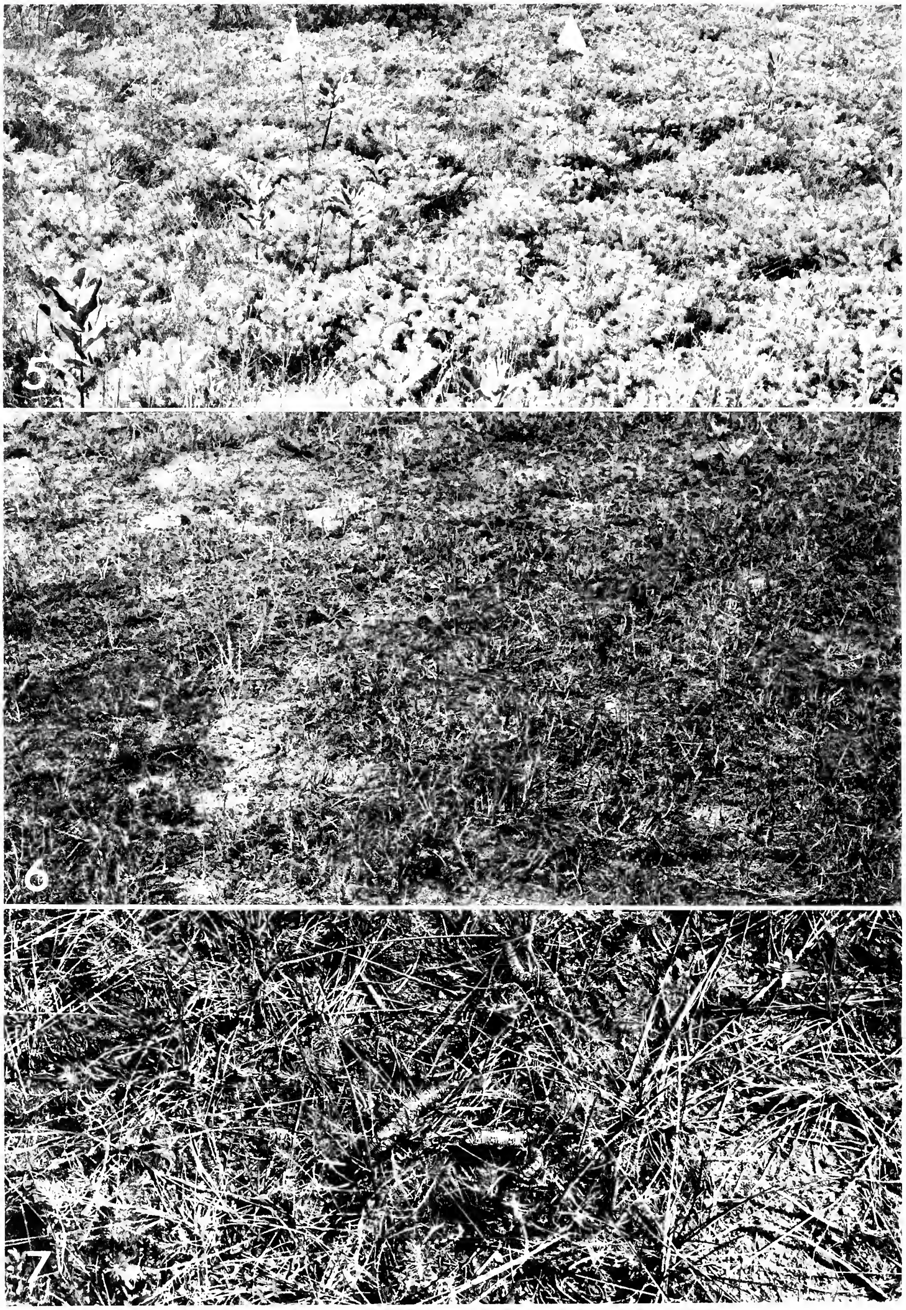
In July 1977, 180 third and fourth instar larvae collected at Braeside, Ontario were released within one day at Chestertown (Warren Co.), New York. The larvae were placed by hand in scattered groups of 3–5 on dense clusters of *E. cyparissias* plants, at two release points 1.6 km apart. Most larvae began feeding immediately. When the 1977 release site near Chestertown was revisited for the first time in July 1982, a thriving population of *H. euphorbiae* was encountered.

The stand of fertile tetraploid *E. cyparissias* (Fig. 5) extends along highways and adjacent nonforested areas for at least 14.4 km east–west and 28.8 km north–south, on fine-textured sand. Growing among the cypress spurge were grasses, *Asclepias syriaca* L., *Saponaria officinalis, Centaurea maculosa* Lam., and *Spiraea tomentosa* L. as well as roadside patches of spurge that morphologically resembled the hybrid, *E.* × *pseudo-esula,* previously not reported to occur in the United States (see Moore and Frankton, 1969). These probable hybrid clones varied considerably in size and fertility. The male parent, leafy spurge, is not recorded from Warren County, and the nearest recorded stands are over 160 km to the south (Albany Co.). Its sticky pollen requires insect transport (Selleck et al., 1962).

A survey of 20 random 1 m^2 plots indicated that the population of *H. euphorbiae* had expanded from the original 180 released to an estimated 10^6 in five years. (Assuming no premature mortality, a 1:1 sex ratio, and 1 generation annually, the population could have increased to 1.13×10^9 in this time.) At an average density of 1 larva/m^2, the insects had spread from the two release points to a distance of 0.48 km to the east (at 1 larva/m^2), 3.2 km to the west (at 0.5 larva/m^2) and 1.6 km to the north (0.1 larva/m^2); the total area occupied was about 4 km^2, with some 25 percent of this area infested by cypress spurge (70–700 stalks/m^2) bearing 1 larva/m^2. The maximum average larval density encountered (12–21 larvae/m^2) occurred in a small area at one of the original release points, where the larvae were effectively defoliating several 50–100 m^2 patches (Fig. 6). The larvae migrated toward, and gregariously fed at, the edges of defoliated areas (Fig. 7), reaching a maximum density of 32 3–4 instar larvae/m^2. According to calculations based on laboratory feeding studies, 14 larvae/m^2 are required to defoliate and weaken a vigorous stand of cypress spurge (New, 1971).

Larvae of all instars were found at Chestertown between July 13 and 27, indicating a long oviposition period. In Ontario, there is one generation annually (New, 1971). Some (3%) of the 150 larvae collected at Chestertown and kept in cages at Beltsville at about 25°C produced second generation female adults within 4 weeks.

The reasons for the excellent reproduction of *H. euphorbiae* at Chestertown and the lack of survival elsewhere in the United States remain to be ascer-



Figs. 5–7. Defoliation by *H. euphorbiae* at Chestertown. 5. Vigorous tetraploid cypress spurge (flags are 1 m apart). 6. Completely defoliated cypress spurge patch. 7. Detail showing 7 larvae stripping remaining leaves from nearly defoliated stems.

tained. Some factors favoring survival may be the presence of soft, fine, well drained sand easily entered by larvae for pupation, and the availability of flowers such as *A. syriaca, S. officinalis* and *Silene cucubalis* Wibel. supplying nectar for adults. Ants are considered to be major predators limiting survival of *H. euphorbiae* (Harris and Alex, 1971); however, nests of ants at Chestertown among the spurge were not noticeably less abundant than at other New York release sites. Myers and Campbell (1976) observed sudden mass attacks on *Tyria jacobaeae* L. larvae by *Camponotus* ants attracted to sap oozing from feeding sites. Spurge flowers are visited by ants for nectar (Selleck et al., 1962); and such foraging ants may attack young *H. euphorbiae* larvae, but no ant predation was observed. *Camponotus pennsylvanicus* (DeGeer) was foraging on spurge flowers and *Formica* sp. also was present at the Chestertown site.

Other causes of mortality among larvae brought from Ontario and cultured at Beltsville between 1977 and 1980 were: (1) 161 pupae buried in a field plot were all dug out and eaten within 2 days by a raccoon (*Procyon lotor* L.); (2) first instar larvae were ingested by large larvae as they ate leaves; (3) death of caged larvae of all instars, which showed symptoms of polyhedrosis virus infection; (4) unidentified tachinid flies were reared from larvae; (5) *Formica* sp. were found feeding on a mutilated dead larva; however, when live larvae were placed on the ants' nest, they dislodged attacking ants by violently squirming, regurgitating, and quickly crawling away and onto spurge plants.

OTHER RELEASES OF *Hyles euphorbiae* IN THE EASTERN UNITED STATES

In July 1976, third and fourth instar larvae of *H. euphorbiae* on cypress spurge were collected from Braeside, Ontario. The actively feeding, apparently healthy larvae were released by the author within 1–5 days of collection as follows:

> 480 larvae on a large area of cypress spurge in hilltop pasture on shaly soil near Bland (Bland Co.), Virginia; no recovery through 1982.
>
> 1,284 larvae on leafy spurge at two uncultivated brushy lots on loam near Watertown (Jefferson Co.), New York; no recovery through 1982.
>
> 70 larvae on leafy spurge in grass along a roadside near Waddington (St. Lawrence Co.), New York; no recovery in 1978.
>
> 100 larvae on leafy spurge in mixed weeds on loam along a railway embankment at Calcium (Jefferson Co.), New York; no recovery through 1982.

In 1978, 70 laboratory-reared pupae were buried in sand with diploid cypress spurge under a cage at Beltsville (Prince George's Co.), Maryland, but there was no recovery in 1979.

Additional releases of *H. euphorbiae* in New York were at New Milford (Orange Co., by R. R. Hahn, 221 larvae, 1978), and by me at Keene Valley (Essex Co., 20 larvae, 1982), Newburgh (Orange Co., 50 larvae, 1982), and Pitcairn (St. Lawrence Co., 52 larvae, 1982).

CONCLUSION

Hyles euphorbiae may be a useful agent for the biological control of cypress and leafy spurge at some locations; however, additional natural enemies of these weeds are needed. Fifty years ago, this insect was considered to be an important pest of *Euphorbia lathyris* L., grown as an oilseed crop in the USSR (Malyuta, 1934). As a result of recently increased costs of petroleum, *E. lathyris* is now being reinvestigated as a commercial source of petroleum substitutes for fuel and chemical feedstocks, yielding over 1 T of oil per 2.5 ha per 7 months (Nielsen et al., 1977; Buchanan et al., 1978). The potential benefit of *H. euphorbiae* for spurge control currently appears to outweigh possible harm to spurges grown as oil crops; however, this is expected to be influenced by changing socioeconomic conditions.

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PATTERNS OF DISTRIBUTION AND ABUNDANCE IN SMALL SAMPLES OF LITTER-INHABITING ORTHOPTERA IN SOME COSTA RICAN CACAO PLANTATIONS

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Abstract.—Collections of Orthoptera and Dictyoptera associated with rotting organic litter in cacao plantations at three localities in Costa Rica are described. These collections, in which the Blattodea were the most represented, were taken from experimental, replicated treatments of rotting discs of banana tree trunks placed on the ground, piles of natural leaf litter on the ground, and arboreal leaf litter contained in large plastic cups suspended from the lower branches of cacao trees. For two localities, there was one collection each for the lengthy rainy season and the short, erratic dry season; only one rainy season collection was taken at the third locality. The most abundant cockroach was *Latiblatta* sp., occupying arboreal litter samples at all three localities followed by *Eurycotis* sp. which occupied both arboreal and ground litter microhabitats at one locality only. Most of the other taxa were represented by one individual at one locality only, suggesting very patchy distributions, assuming an adequate sample size. At one locality (La Lola), the tettigoniid *Idiarthron hamuliferum* Beier was found in arboreal litter, as was a leaf-rolling cricket, *Camptonotus* sp. prob. *affinis.* Most orthopterans were found in litter associated with sunny areas of cacao during the dry season, a probable response to seeking refuge in the few available moist patches, whereas numbers and densities were always lower in the well-shaded areas in both rainy and dry periods. The arboreal leaf litter microhabitat in tropical forests deserves particular attention for understanding the vertical stratification of cockroach faunas.

This paper summarizes some preliminary field data on the association of Orthoptera (Tettigoniidae and Gryllacrididae) and Dictyoptera (Blattodea) with several kinds of rotting organic litter substrates, "microhabitats," in cacao plantations at three localities in Costa Rica. The information gathered in this study was adjunct to an investigation of the occurrence of immature stages of cacao-pollinating Diptera in these litter substrates (Young, 1982, 1983). Orthoptera and Dictyoptera are commonly associated with the cacao plantation habitat overall, although seldom are they of any economic importance (e.g., Leston, 1970). The major group discussed in this paper, the Blattodea or cockroaches, represent only about 10 percent of the total cockroach fauna described for Costa Rica (see the review of Fisk, 1971). Nevertheless, the data are new in terms of both describing cacao plantations in

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the Neotropical Region as Orthoptera and Dictyoptera habitats, and the observed patterns of specificity for some of the forms collected.

METHODS

Between 1978 and 1980, replicated series of field "treatments" consisting of increased abundance of three kinds of natural litter substrates, were distributed in cacao (*Theobroma cacao* L.) plantations at three localities or collecting sites in Costa Rica (see Young, 1982, 1983 for descriptions of these sites and studies). The localities are: (1) "Fincas La Tigra and El Uno," near La Virgen (10°23′N, 84°07′W), Heredia Province, (2) "Finca Experimental La Lola," near Siquirres (10°06′N, 83°30′W), Limon Province, and (3) "Turrialba or CATIE," Turrialba (9°54′N, 83°41′W), Cartago Province. These localities are within Lower Montane Tropical Wet Forest (Turrialba), Premontane Tropical Wet Forest (La Tigra and El Uno), and Lowland Tropical Wet Forest (La Lola) regions (Holdridge, 1967). Each locality experiences a short, irregular dry season each year (Fig. 1), during which the ground leaf litter in sunny areas of cacao plantations (areas with a broken or poor canopy cover of shade trees) becomes dry and crunchy underfoot.

The La Tigra and El Uno cacao is about 10–15 years old, with the La Tigra plantation having a broken canopy of natural tree species from regenerating trees establishing very shaded conditions. The La Lola cacao plantation area studied consists of the UF-29 variety (La Tigra and El Uno is mixed varieties) shaded primarily by *Erythrina* and other Leguminosae, and with one area (A) with heavy shade (shaded habitat) and another (B) with less shade (sunny habitat) throughout the year. The La Lola cacao trees are 20–30 years old. The Turrialba plantation area studied consists of "Catongo" variety trees with a highly variegated canopy establishing both shaded and sunny areas. Cacao trees here are 20–30 years old.

The three kinds of organic litter substrates studied are: 2 × 2-meter ground plots of piled leaf litter (mostly cacao leaves), 22-meter ground plots of discs of banana tree trunks, and 200-cm^2-leaf-litter-filled plastic cups suspended in cacao trees. In addition, observations on Orthoptera, Dictyoptera, and other insects inhabiting piles of rotting cacao pods were also made.

For La Tigra and El Uno cacao plantations each, there are eight replicates of the "ground leaf litter" treatment, employing sturdy wooden frames to hold the litter in place beneath the cacao trees. There are also eight replicates of the rotting discs of banana tree trunks in each of the two areas, as well as twenty plastic cups, the "arboreal leaf litter" treatment in each area. The same distribution of treatments is also used for Areas A and B at La Lola (Figs. 2–4). The rotting discs of banana tree trunks treatment consists of 20–30 discs per replicate renewed approximately every 3–4 months. The plastic cups used for the "arboreal leaf litter" studies (Fig. 3) have perforated bot-

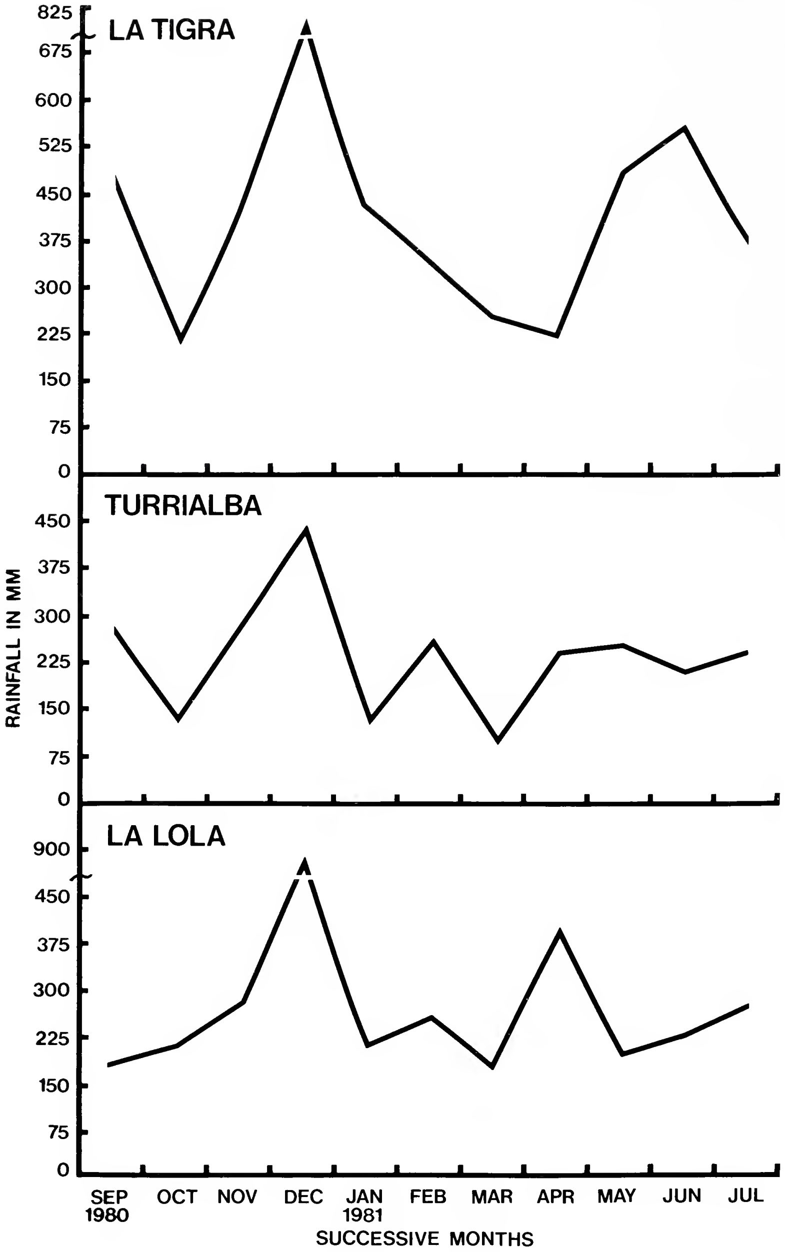

Fig. 1. Monthly patterns of rainfall at three cacao-growing localities in Costa Rica during 1980 and 1981. There is a depression in rainfall during the January–February period at these localities, most evident at the La Lola and Turrialba localities. All three regions, however, are classified as relatively non-seasonal compared to other tropical regions with a very pronounced dry season each year.

Fig. 2. The La Lola cacao plantation, near Siquirres, in Limon Province, Costa Rica. Top: general view of the "sunny habitat" (Area B). Below: ground litter in the shaded habitat (Area A). Note wooden frame filled with leaf litter in the left foreground.

Fig. 3. Ground leaf litter treatment used to assess litter-inhabiting Orthoptera. Top: typical positioning of one replicate beneath a cacao tree. Below: typical distribution of cacao leaf litter in wooden frame. Photographs taken at La Lola during the "dry" season. Note great abundance of leaves in the wooden frame at this time.

toms to allow drainage of rainwater. The cups are suspended by sturdy wires from lower branches of individual cacao trees. A pattern of randomization was used to position treatment replicates in La Lola and Turrialba. For La Tigra and El Uno, a different system was used, one in which replicates were placed in distinctive-appearing sub-areas. Whenever the litter substrates were collected for sampling of insects (see Young, 1982, 1983), fresh litter was added from the same general areas of the plantations to continue the treatments. Further details and descriptions of the treatments are given elsewhere (Young, 1982, 1983).

For the rotting discs of banana tree trunks (Fig. 2), prepared by slicing freshly fallen banana trees with a machete and allowing the discs to rot for several months, field notes were taken on the approximate numbers of insects seen scurrying off when discs were collected in plastic bags for sorting of insect material in the laboratory. Additional notes were taken only on an opportunistic basis for orthopterans that scurried off in the laboratory. For the ground and arboreal leaf litter treatments, however, virtually all of the orthopterans that were found in the individual substrates were collected. It is emphasized that the samples were taken during the daylight hours, a period when many orthopterans were concealed in the litter substrates being studied.

Collected orthopterans were preserved in 70 percent ethanol for subsequent determinations. The litter samples were always collected by placing the contents of a substrate container (wooden frame or cup) into a plastic bag and tying the bag shut. Orthopterans less than 5 mm long were either missed or not collected. For La Tigra and El Uno, there was one major collecting period or sample, August 1980, the mid-rainy season. For La Lola and Turrialba, however, samples were taken in both the late rainy season (November 1980) and mid-dry season (February 1981). In addition to these collections of Orthoptera and Dictyoptera, field observations on the occurrence of these insects in these substrates were made at several other times, although systematic collections were not made.

There is a lapse of at least four months from the time any of the substrates were initially disturbed after being set up. The substrates were sampled several times within the time period of the present study, since they were used to estimate the abundance of cacao-pollinating Diptera (Young, 1982, 1983, and unpubl. data). Interest in the Orthoptera focused upon the comparison of ground and arboreal leaf litter as microhabitats, and relative changes in the estimated abundance of these insects in the rotting discs of banana tree trunks between rainy and dry periods (for La Lola in particular).

RESULTS

For all three collecting sites combined, more than three times the number of orthopteran individuals were collected from arboreal leaf litter than from ground leaf litter in cacao plantations, although number of species in each

Fig. 4. Top: arboreal leaf litter replicate, with forceps for scale. Below: rotting disc of banana tree trunk which forms a suitable microhabitat for roaches throughout the year, particularly during the dry season. Even though such substrates represent a combined area far less than the

kind of microhabitat was similar (Table 1). By far, the most abundant group, in terms of species and numbers of individuals in samples, were members of the Blattaria or cockroaches (Dictyoptera, Blattelidae) (Table 1). Most of the blattids represented in the limited samples from arboreal and ground leaf litter were nymphs, and one genus, *Latiblatta,* dominated the arboreal samples (Table 1). In some instances, individual roaches jumped from the cups when the litter samples were being collected, although this error is estimated at less than 10 percent for all samples.

Of particular interest was the discovery of several individuals of a leaf-rolling cricket, *Camptonotus* sp. prob. *affinis* Rehn, in a few of the arboreal litter samples from Area B (sunny habitat) at La Lola (Fig. 5). This species, along with the tettigoniid *Idiarthron hamuliferum* Beier (Fig. 5), were the only two orthopteran species encountered in the study. For both species, adults were found hiding beneath the dry leaves in the cups. *Camptonotus* specimens formed tubular nests from dead, dry cacao leaves within the cups. In addition, a single individual of *I. hamuliferum* was collected from its hiding place in thick moss in the trunk of a cacao tree at El Uno during the rainy season (July 1981). Both orthopterans were conspicuously absent, however, from cups and ground leaf litter collections at both La Tigra and El Uno throughout the study. Furthermore, both *Camptonotus* and *I. hamuliferum* were absent from all arboreal and ground leaf litter samples in Area A (shaded habitat) at La Lola for the entire study period. Thus, these forms were most abundant, albeit small samples, from the sunny habitat at La Lola and the mixed shade and sunny habitats in the cacao at Turrialba (the latter for *Camptonotus* only).

During both rainy and dry season samples at La Lola, roaches were very low in abundance in the arboreal leaf litter samples from Area A, the shaded habitat. Usually only 1–2 cockroaches were seen scurrying out of individual cups at both times, and with 60–100 percent of the cups without roaches at all. The leaf litter in these cups, as compared to that of the more exposed cups in Area B (sunny habitat), was always very damp and water-logged. In the arboreal samples from the sunny habitat, however, the cups with most individuals of cockroaches had dense layers of dry cacao leaves. During the dry season in Area B, between 80–100 percent of the cups had 1–5 roaches in each, whereas during the rainy season sample, only about 50 percent of the cups had cockroaches and occupied ones with 1–2 cockroaches each. A similar pattern was also found at Turrialba between dry and rainy season samples.

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leaf litter treatments used, densities of insects such as roaches are generally far higher in discs than other treatments, with this effect most noticeable in the dry season in sunny cacao habitats (La Lola).

Table 1. The daytime distribution and abundance of Orthoptera in arboreal ground leaf litter in Costa Rican cacao plantations.[1]

Species	No. localities represented	No. individuals in arboreal litter	No. individuals in ground litter	Totals
Dictyoptera, Blattellidae				
Latiblatta sp.	3	26 (12A, 14N)[2]	0	26
Eurycotis sp.	1	7 (N)	5 (N)	12
Ischnoptera panamae Hebard	1	1 (A)	0	1
Blattella germanica (L.)	1	0	1 (A)	1
Anaplecta domestica Saussure & Zehntner	1	0	1 (A)	1
"Undetermined Blattidae"	1	1 (N)	5 (N) (2 spp.)	6
Tettigoniidae, Pseudophyllinae				
Idiarthron hamuliferum Beier	2	2 (A)	0	2
Gryllacrididae, Gryllacridinae				
Camptonotus sp. prob. *affinis* Rehn	2	5 (A)	1 (A)	6
Total orthopterans by "micro-habitat"		42	13	57
% nymphal Blattidae in samples		52.4%	76.9%	56.1%
No. of "species"		7	6	10

[1] Data are combined for three cacao plantation collecting sites or localities and "no. localities represented" column indicates the localities at which specimens were collected. The three localities are: "Fincas La Tigra & El Uno" (considered as one site); "Finca Experimental La Lola"; "Turrialba or CATIE." See text for descriptions of these sites. For "La Tigra & El Uno" site, only one rainy season collection was made; for other sites, one rainy season and one dry season collection was taken for each one.

[2] Data are broken down in parentheses for numbers of adults (A) and nymphs (N) in samples.

Most of the orthopterans collected in this study were found exclusively in the arboreal leaf litter samples, and most of these were found in the rainy season for all three localities combined (Table 2). The most geographically widespread form is a species of *Latiblatta* occurring at all three localities, even though it is an arboreal leaf litter "specialist." The terms "specialist" and "generalist" species are used in this paper to refer to distributional

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Fig. 5. Top: the leaf-rolling cricket *Captonotus* sp. prob. *affinis* Rehn. Below: the tettigoniid *Idiarthron hamuliferon* after being dislodged from the leaf litter of an "artificial bromeliad" (plastic cup) used as a replicate of arboreal leaf litter treatment. Both of these orthopterans were

encountered occupying arboreal leaf litter replicates in the sunny cacao habitat (Area B) at La Lola.

Table 2. Locality, season, and "microhabitat" specialists and generalists[1] among Orthoptera found in arboreal and/or ground leaf litter in Costa Rican cacao plantations.

Species	Exclusively arboreal	Exclusively ground	Generalist in both	No. of localities	Active season(s)
Latiblatta sp.	X	0	0	3	rainy
Eurycotis sp.	0	0	X	1 (La Lola)	rainy & dry
I. panamae	X	0	0	1 (La Lola)	rainy
B. germanica	0	X	0	1 (La Lola)	dry
A. domestica	0	X	0	1 (Turrialba)	rainy
"Undetermined Blattidae"	0 (?)	0 (?)	X	3	rainy
I. hamuliferum	X	0	0	1 (La Lola)	rainy & dry
C. sp. prob. *affinis*	X	0	0	2 (La Lola & Turrialba)	rainy & dry

No. arboreal specialist species: 4
No. ground specialist species: 2
No. leaf litter generalist species: 2
No. geographically restricted species[2]: 5
No. geographically widespread species: 3
No. dry season specialist species: 1
No. rainy season specialist species: 4
No. of tropical season generalist species: 3

[1] The terms "specialist" and "generalist" are used in this paper to define probable patterns of ecological distribution within the very limited samples obtained in this study. Similar patterns may, or may not, exist in whole populations.

[2] A geographically (regionally) restricted species is operationally defined in this paper as one found in samples obtained for only one collecting site or locality, while widespread species are those found in two or more such localities.

patterns within the very limited samples, and it may be difficult to extrapolate to whole populations due to severe limitations of the samples. The data (Table 2), while limited, suggest that there is considerable ecological diversification within the Blattidae of the Neotropical Region in terms of microhabitat, geographical distribution, and active season.

The La Lola cacao plantation contained the greatest number of "species" of litter-associated Orthoptera, with 4–7 species, depending upon the maximal number of "undetermined Blattidae" in the samples. In contrast, only one species was found at La Tigra and El Uno, an obvious underestimate generated in part by the very limited sampling, while 2–4 species were found at Turrialba. In all cases, however, the data are taken as pronounced underestimates of the actual orthopteran faunas of cacao.

The fact that the cockroaches collected in this study may have different ecological roles in cacao plantations is reflected in part by the morphological differences used in noting them under field conditions. Thus *Latiblatta* sp. was a "large tan roach" with nymphs either 18–22 mm long (La Tigra and

El Uno, and Turrialba) or 7–22 mm long for La Lola. *Eurycotis* sp. was recognized as a "chocolate-brown fat cockroach" with nymphs 15–22 mm long (La Lola), while *I. panamae* is a "medium size dark brown cockroach" with adults about 13 mm long (La Lola). *Blattella germanica* is a "large brown cockroach" with body size of 25 mm for the adult (La Lola), and *Anaplecta domestica* is a "small dark brown cockroach" of 6-mm-long adults (Turrialba). There are also three forms of "undetermined Blattidae" recognized in the field samples: "small dark brown" nymphs (5–8 mm long) (Turrialba); "small sooty brown" nymphs (6 mm long) (all three localities); "small rusty brown" nymphs (7 mm long) (Turrialba). The two orthopteran forms are readily distinguishable in the field (Fig. 5).

Field counts of cockroaches scurrying from the rotting discs of banana tree trunks (Fig. 4) indicate some interesting patterns of distribution: (1) general numbers of cockroach individuals found in discs are very similar among the three localities or collecting sites; (2) during the dry season (La Lola and Turrialba samples), 2–3 species are found in individual discs, mostly nymphs within size range 4–20 mm, with 1–5 individuals per disc and about 80% of the discs with one or more roaches; (3) during the rainy season (all three localities), there are 1–2 species present in discs at each locality, with 1–2 individuals (mostly nymphs) per disc, and about 30–50 percent occupancy rate of discs; (4) during the dry season in a sunny cacao habitat (Area B at La Lola), there are many more cockroaches (1–3 species, and 1–10 individuals per disc) in discs, with an occupancy rate of 80–100 percent, than in the nearby shaded habitat (Area A). Cockroaches are least abundant in all disc samples during the rainy season at all localities.

During the dry season in a sunny cacao habitat (Area B at La Lola), similar numbers of cockroaches are found in the discs and arboreal leaf litter samples, while far fewer are found in the ground leaf litter at this time. Such differences are far less pronounced in the nearby shaded cacao, with an overall depression of roach numbers during both dry and rainy seasons. During the lengthy rainy season at all three cacao-growing localities, there is a profusion of ant colonies (Young, in manuscript) associated with the three kinds of litter microhabitats, while ant colonies are far less abundant in these places during the dry season. Orthopterans such as *Camptonotus* and *I. hamuliferum* are not found in rotting discs of banana tree trunks and ground leaf litter throughout most of all of the year. Orthoptera in general are far less abundant in piles of rotting cacao pod husks than they are in ground litter throughout the year at the three localities.

The dry season impacts upon the sunny cacao habitat by a marked decline in all arthropods on a per unit basis of ground leaf litter, while other substrates, such as arboreal leaf litter and rotting discs of banana tree trunks, may exhibit marked increases in arthropod densities.

DISCUSSION

During the tropical rainy season, optimal conditions for activity in litter-inhabiting insects may be more evenly distributed over the cacao habitat than during the dry season, and such an effect is most pronounced in sunny areas of cacao (see also Young, 1983, for a discussion of these effects). A partial or broken canopy over cacao during the dry season permits the ground litter to dry out more thoroughly and faster than in more shaded areas of cacao. The result is an increased period of environmental thermal or moisture stress to small organisms inhabiting the litter. The data in the present paper indicate that cockroaches and large-bodied Orthoptera that occupy leaf litter and other litter substrates (rotting discs of banana tree trunks) during the daylight hours in cacao plantations may become more abundant in arboreal litter microhabitats characterized by dense layers of dead leaves. Rotting discs of banana tree trunks become ecological "refuges" for small-bodied insects (less than 5 mm long) during the dry season, even in sunny cacao habitats (Young, 1983). Even though cockroaches in the tropics may be active nocturnally for feeding and courtship (e.g., Schal, 1982; Schal and Bell, 1982), the availability of moisture-holding microhabitats in cacao habitats provides a daylight shelter for hiding from thermally stressful conditions and deleterious biological factors such as predators. Given the large diversity of the Costa Rican cockroach fauna (Fisk, 1971), the observed patterns of different distributions in the small number of species studied here indicate that the group as a whole has undergone considerable ecological diversification in the Neotropical Region.

Assuming that the sample data are adequate to explain patterns of distribution in populations, it appears that most of the cacao cockroach fauna is arboreal in terms of litter microhabitat. Tropical cockroaches are considered as major converters of decaying litter to other nutrients (e.g., Irmler and Furch, 1979). Some species, such as *Anaplecta domestica* Saussure and Zehntuer, may be ecologically flexible in occupying both arboreal and ground litter. In the present study, this species was found in ground litter, although the related *A. mexicana* Saussure occurs in epiphytes in Costa Rica (Fisk, 1971). Such species, and the very common *Lattiblatta* sp. may be adapted to exploit litter and other litter-inhabiting organisms as food in natural epiphytes such as tank bromeliads as well as in the "artificial bromeliads" of arboreal leaf litter used in the present study. In a previous study of the daytime-foraging of insects at experimentally-placed food baits in the lower understory layer (at heights of 1–2 m) in lowland tropical rain forest ("Finca La Tirimbina," adjacent to "Finca La Tigra") and semi-deciduous wet forest ("Barranca Site, near Miramar, Puntarenas Prov.") in Costa Rica during the 1975 dry season (January–February 1975 collections), a total of 5 cockroaches (2 species) were collected from three bait-types (pineapple, orange, and grape jelly) at Barranca at 0900 hours, one on pineapple at 1300, none at 1500, and a total of four on three bait-types (pineapple, jelly and ground beef) at 1700 hours (A. M. Young, unpubl. data). Only one cockroach foraged at one bait from 0900 to 1300 hours at La Tirimbina (Young, unpubl. data). Such data, involving replicated series of food baits along transects in forest understory, and in which large quantities of other insects were captured at baits, indicate the low activity level of roaches during these periods and times of the day.

The layers of dead leaves in the plastic cups most likely provide a suitable hiding site for *Camptonotus* and *I. hamuliferum* during the daytime, and feeding presumably occurs elsewhere, such as in the cacao canopy. *Camptonotus carolinensis* (Gerstaecker) is known to feed on scale insects in North American forests, and this species constructs rolled-leaf nests anchored with silk, using fresh, attached leaves of the tree (Blatchley, 1920). The use of dead cacao leaves by *Camptonotus* in the present study as a rolled-leaf nesting site represents a departure from the usual habit of using leaves on the host plant. The absence of *Camptonotus* sp. from the La Tigra and El Uno arboreal litter may reflect a difference in food preferences. The occurrence of bromeliad-festooned shade trees in both cacao habitats may provide a suitable dry-season refuge for these orthopterans, whereas at La Lola, at least *Camptonotus* sp. requires the artificial bromeliads as a refuge. Whether or not these orthopterans move each evening into the canopy trees for feeding remains to be studied.

The marked difference in abundance of orthopterans in the small samples between dry and rainy seasons, with most occurring in the rainy season samples for all localities, may reflect the complex fluctuations in the abundance of roaches and other foliage-dwelling insects in response to seasonal conditions in Central America (Wolda, 1978; Wolda and Fisk, 1981). Nymphal stages of roaches in particular exhibit marked cycles of abundance (Wolda and Fisk, 1981).

The lower densities of Orthoptera and other litter-inhabiting arthropods observed for cacao habitats with heavy shade and year-around moist conditions (see also Young, 1983) may be due in part to the more uniformly moist conditions of such areas and also to a greater abundance of predatory forms such as ants under these conditions. Shaded cacao habitats tend to accumulate a high number of ant species (Bigger, 1981). Orthoptera are more abundant in sunny cacao habitats (Bigger, 1981), as also observed for the Area B habitat at La Lola in the present study. Rotting discs of banana tree trunks may exhibit less of a water-loss response to the tropical dry season than less dense substrates such as dead cacao leaves. Under such conditions, insects inhabiting discs, both in sunny and shaded cacao habitats, may exhibit less of a response, in terms of density or shifts in numbers of species, than insects in leaf litter. Young (1983) found that such discs provided a suitable refuge for the immature stages of cacao-pollinating Diptera (Ceratopogonidae) to pass the dry season at La Lola, particularly in the sunny habitat. Cacao leaf litter may represent a relatively more ephemeral microhabitat for many small-bodied insects, including the early instars of cockroach nymphs, in sunny cacao habitats, and particularly during the drier months of the year. Large-bodied insects such as bigger roach nymphs, adult cockroaches of some species, and other orthopterans (such as *Camptonotus* sp. and *I. hamuliferum*), may have little difficulty in occupying the semimoist to dry arboreal leaf litter provided by the plastic cups in cacao trees. But during such periods, small-bodied insects, including ants, are virtually absent from such microhabitats. For those orthopterans that actually feed on the leaves of cacao trees, seasonal cycles in the availability of young leaves may greatly influence the abundance of these insects in cacao plantations (Majer, 1975). Tettigoniidae, for example, increase in abundance with the onset of flushes of cacao leaves in Ghana plantations (Majer, 1975). Cockroaches, being opportunistic feeders on a variety of food-types, may exhibit less regular fluctuations in abundance.

The foregoing discussion considers what might be the overall trends in relative abundance patterns, seasonal distributions, and daytime-resting places for a relatively small portion of the Costa Rican orthopteran fauna associated with cacao plantations. Given the type of sampling performed and the number of collection dates, the data are large underestimates of the probable fauna resident in such habitats. Had larger samples been obtained for longer periods of time, it might very well have been shown that individual taxa of Blattodea exhibit very flexible behavior in terms of daytime-resting sites. Thus, it would not be surprising to discover that most or all of the cockroach taxa discussed in this paper are "generalist" forms in terms of hiding in both arboreal and ground leaf litter. Yet given the tremendous vertical complexity of tropical rain forests (e.g., Richards, 1964), it would also not be surprising to discover that some of the taxa are, in fact, canopy or sub-canopy "specialists," occupying large epiphytes accumulating organic litter. Such effects must be taken into account when considering the relatively low vertical complexity of the cacao habitat, a condition that may alter the distribution of cockroaches that would otherwise be found in undisturbed tropical rain forests.

ACKNOWLEDGMENTS

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COORDINATED PREY CAPTURE BY *NOVOMESSOR COCKERELLI* (HYMENOPTERA: FORMICIDAE)

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Abstract.—*Novomessor cockerelli* uses coordinated behavior to subdue large orthopteran prey. When a partially disabled grasshopper is encountered, the first worker finding it mounts the dorsum of the grasshopper and clamps its mandibles over the wings, thus preventing escape by flight. Workers which arrive subsequently systematically remove or subjugate additional appendages. Behavioral coordination allows *N. cockerelli* to efficiently exploit large orthopteran prey which would otherwise escape if workers attempted to capture these individually.

The genus *Novomessor* comprises three species. Of these, the species *N. cockerelli* (Andre) is encountered commonly in the intermountain plains of the deserts of southern North America (Wheeler and Creighton, 1934). Although the generic name suggests that *N. cockerelli* is a harvester ant, it is in fact omnivorous (Creighton, 1950; Chew, 1977; Whitford, 1978), and insects comprise about one-half of its normal forage (Whitford et al., 1980).

N. cockerelli normally employs an individual foraging strategy (Whitford, 1976; Davidson, 1977) but is also capable of recruiting and cooperatively carrying large food items (Hölldobler et al., 1978). Both chemical (Hölldobler et al., 1978) and vibrational (Markl and Hölldobler, 1978) signals are used during recruitment. Here we report on cooperative and coordinated prey capture by *N. cockerelli* under field conditions, paying particular attention to the adaptive sequences of behaviors by individual foragers.

METHODS AND MATERIALS

Studies were conducted at the Jornada Experimental Range, 60 km NNE of Las Cruces, New Mexico, from May to July, 1979. The site has been described in detail elsewhere (Whitford et al., 1980). All studies were performed from 0800–1100 hr (MDT) during weekly visits to the site to collect long-term data on related projects.

Two separate observational series were performed. In the first, grasshoppers were hand collected and placed in an active entrance to a *N. cockerelli* nest. The sequence of attack by workers of *N. cockerelli* on the body parts

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of the grasshopper were recorded, as well as the ability of the workers to subjugate and capture the grasshopper. The body parts sequenced were the wings, antennae, pro-, meso-, and metathoracic legs, the cervix of the head, and the abdomen. All of the latter six body regions were combined and compared with the sequence of attack on the wings, using the binomial test (Siegel, 1956). Likewise, the ability of the workers to capture the grasshopper was dichotomized: capture or escape.

In the second series of observations, grasshoppers were captured and tethered with a fine copper wire which was passed through the body from the pronotum to the mesosternum. The copper wire was then anchored by a stone. The length of the copper wire from grasshopper to anchor was approximately 10 cm, allowing the grasshopper to move but not to take flight. For each of five distances from the nest entrance (0.5, 1.0, 2.0, 4.0 and 6.0 m), 16 separate grasshoppers were tethered. The number of grasshoppers found at each distance upwind from the nest entrance per distance class, and the maximum number of *N. cockerelli* workers present at the grasshopper during the 30 min. period were recorded. The sequence of attack by workers on tethered grasshoppers was recorded as described previously. Only 45 of the 80 grasshoppers offered were attacked, and only data from these successful attacks are presented. The sequences of attack on the body parts were recorded in inverse order, i.e., 7 = attacked first, 1 = attacked last. The number of occurrences of attack observed for each sequence was multiplied by the rank for that sequence. By dividing this weighted sum by 315, or the expected weighted score if that body part was always attacked first, a relative preference for attack on each of the 7 body regions was obtained.

RESULTS AND DISCUSSION

A total of 53 grasshoppers were captured and placed at the nest entrances of active *N. cockerelli* nests. Of these 53, 39 (74%) escaped. Of the 36 grasshoppers offered by this technique which were attacked, the first worker attacking the grasshopper mounted the dorsum and clamped its mandibles over the wings in 28 (78%) of the observations, indicating a highly significant preference for attacking the wings (binomial test, $P < 0.001$, Siegel, 1956). Moreover, all 14 grasshoppers which were captured by *N. cockerelli* workers were first attacked by this method, as well as 14 of the 36 grasshoppers attacked which escaped. It should be noted that only about one-quarter (14/53) of grasshoppers presented at the entrances of active nests were captured.

The conditional probability of encounter and the maximum number of workers present at the immobilized grasshoppers declined slightly with increasing distance from the nest (Table 1). However, this reduction was not dramatic until a distance of 6.0 m was reached (Table 1). Hölldobler et al. (1978) have demonstrated that recruitment is mediated by poison gland

Table 1. The conditional probability of encounter and the maximum number of workers arriving at tethered grasshoppers at various distances from the entrance of *Novomessor cockerelli* nests.

Distance (m) from nest entrance	Conditional probability of encounter[1]	Number of workers arriving (mean ± 1 standard deviation)[2]
0.5	0.6875	24.6 ± 16.5
1.0	0.5000	22.6 ± 12.3
2.0	0.6250	19.8 ± 10.6
4.0	0.5625	15.2 ± 8.5
6.0	0.4375	6.0 ± 3.7

[1] The number of grasshoppers encountered within 30 min./16, the total number of grasshoppers offered at each distance.

[2] Calculated only for those grasshoppers which were encountered within 30 minutes.

secretions deposited by individual ants from the food source to the nest. The decline in the number of workers present at the food source (grasshoppers) was similar to the pattern reported by Hölldobler et al. (1978) to artificial food sources.

As in the first series of experiments, the first worker which attacked a tethered grasshopper mounted the dorsum and clamped its mandibles over the wings in 34 of the 45 attacks observed. Likewise, a significant preference for attacking the wings first was found (binomial test, $P < 0.0001$, Siegel, 1956). The metathoracic legs and the antennae were the body parts of the grasshopper attacked most frequently sooner than the other body parts after the wings (Table 2).

The sequence of prey capture employed by *N. cockerelli* is thus coordinated. Moreover, the sequence of attack is apparently very adaptive. By pinning the wings of orthopteran prey first, the prey is thus deprived of flight as an escape mechanism. Subsequent subjugation of the jumping legs and/or antennae then deprives the grasshopper of saltatorial escape, or flight, directed by the antennae, if the ant subjugating the wings is dislodged.

Given our results, it is uncertain how frequently *N. cockerelli* may employ this adaptive sequence of prey capture. Grasshoppers placed in the entrances of active nests were only captured about one-quarter of the times tested. It is unlikely that many grasshoppers would land at an active nest entrance. More likely, *N. cockerelli* probably employs the sequence described in capturing injured or weakened grasshoppers. Grasshoppers escaping bird strikes, or the attacks of lizards, scorpions or other desert predators may be injured to the extent that rapid escape is not possible. Under such conditions, *N. cockerelli,* employing the adaptive sequences of behavior described, may be able to capture these individuals.

Coordinated prey capture of orthopteran prey, organized around adaptive

Table 2. Observed frequency distribution of the order of attack on the body parts of immobilized grasshoppers by workers of *Novomessor cockerelli.*

Behavior/ body part	Observed order of attack							Totals	Score*
	1	2	3	4	5	6	7		
Pin wings	34	5	1	1	4	0	0	45	0.917
Grab/clip									
Antenna	2	10	11	5	16	0	1	45	0.679
Prothoracic leg	3	6	9	8	11	7	1	45	0.578
Mesothoracic leg	1	5	14	8	7	8	2	45	0.565
Metathoracic leg	4	14	8	15	3	1	0	45	0.708
Head (cervix)	0	0	2	5	3	16	19	45	0.286
Abdomen	1	5	0	3	1	13	22	45	0.282
Totals	45	45	45	45	45	45	45	315	

* Obtained by weighting each frequency (rank 1 = 7, rank 2 = 6, etc.) by multiplying the frequency by its rank and then dividing by the maximum possible score, 315 (i.e., all 45 observations given rank of 1, or 45 × 7).

sequences of behavior, and the consequential cooperative removal of captured prey to the nest (Hölldobler et al., 1978), is an efficient strategy of resource procurement, as well as a means of counteracting interference competition by mass-recruiting ant species. With the exception of army ants, termite predator specialists of the genus *Leptogenys,* and some of the slave-making formicines, we know of no instance of pack-like hunting behavior being recorded for ants. Indeed, the constancy of the attack sequences reported here is similar to that observed in pack-hunting felines and canines (Wilson, 1975).

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HABITAT PREFERENCES OF CARRION BEETLES IN THE GREAT SWAMP NATIONAL WILDLIFE REFUGE, NEW JERSEY (COLEOPTERA: SILPHIDAE, DERMESTIDAE, NITIDULIDAE, HISTERIDAE, SCARABAEIDAE)

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Abstract.—A total of 2,397 individuals representing 8 species of carrion beetles (Silphidae) and 2,336 individuals representing 4 species of "carrion beetles" from 4 other families were collected on carrion in the Great Swamp National Wildlife Refuge during June, July and August in 1980 and during April and May in 1981. Beetles were trapped in 3 habitats—forest, field, and marsh. Of the 8 silphid species, 5 manifested a *strong preference* for a given habitat. These species were *Oiceoptoma noveboracense* (forest), *Necrophila americana* (field), *Nicrophorus orbicollis* (forest), *Nicrophorus pustulatus* (forest), and *Necrodes surinamensis* (forest). Two silphid species manifested a *slight preference* for a given habitat: *Oiceoptoma inaequale* (field), and *Nicrophorus tomentosus* (field). One species, *Nicrophorus marginatus,* manifested a *probable preference* for the field. Insofar as other "carrion beetles" are concerned, 1 species, *Onthophagus hecate* (Scarabaeidae) showed a *strong preference* for the field. Three species manifested *slight preferences* for given habitats: *Omosita colon* (Nitidulidae) and *Dermestes caninus* (Dermestidae) for the forest, and *Euspilotus assimilis* (Histeridae) for the field.

A search of the literature on carrion beetles indicates that there has been increased interest and research on this group of beetles during the past quarter century. Many of the papers that have appeared have dealt with the ecology and behavior of species of the taxon. Conspicuous, however, has been the lack of information on the habitat preferences of these beetles. In the 2 papers that have mentioned habitat preferences, Walker (1957) tabulated arthropod species that were attracted to carrion-baited pitfall traps in 4 habitats—mesic forest, bottom forest, ridge forest and old field and Anderson (1982) studied Silphidae that were collected in carrion-baited pitfall traps in 4 very distinct habitats—deciduous forest, coniferous forest, field/meadow, and marsh.

In a recent study to determine the species composition and seasonal abundance of carrion beetles in an oak-beech forest in the Great Swamp National Wildlife Refuge (GSNWR), Basking Ridge, New Jersey, 7 species of Silphidae were present (Shubeck et al., 1981). Over 98% of these silphids were taken from early April through August. *Oiceoptoma noveboracense* was very

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abundant from April through July with a peak in May. *Necrophila americana* was most active from May through August with a pronounced peak in July. *Oiceoptoma inaequale* was an early season silphid, being most active from April through June, with a peak of activity in April. *Nicrophorus orbicollis* was active from May through September and peaked in August. Although *Necrodes surinamensis* was active from June through September over ⅔ of the individuals were taken in August. *Nicrophorus pustulatus* was collected in May and into September with over ½ of the season's catch taken in June. *Nicrophorus tomentosus* was taken from June through October but almost ½ of these individuals were collected in August. Among the 55 additional taxa also present were 4 very abundant species from other beetle families (Nitidulidae, Histeridae, Dermestidae, Scarabaeidae).

For this study it was decided that additional information about the carrion beetles of GSNWR might be obtained by collecting and comparing the numbers of carrion beetles in the 3 distinct habitats found in this refuge—forest (deciduous), field, marsh. The species of carrion beetles included in this study were: *all* species of Silphidae, *Dermestes caninus* (Dermestidae), *Omosita colon* (Nitidulidae), *Euspilotus assimilis* (Histeridae), and *Onthophagus hecate* (Scarabaeidae).

MATERIALS AND METHODS

Carrion beetles were trapped in 6 No. 10 food cans (3.78 liter), each of which was concealed in a wooden box having 1.27 cm wire mesh at the top and a rain cover 5 cm above the opening. These traps have been described elsewhere (Shubeck, 1976). Two traps, 10 meters apart, were placed on the ground in a red oak forest about 2 km northeast of the former refuge headquarters building. Two traps, also 10 meters apart, were placed on the ground in an old field adjacent to the forest. This field collecting station was about ½ km northeast of the forest collecting station and about 100 meters from the edge of the forest. Two traps, 10 meters apart, were individually mounted on stakes that had been driven into the mud of a marsh adjacent to the field. The marsh collecting station was about 400 meters east of the field collecting station but only 5 meters into the marsh. I would have preferred to situate the traps farther into the marsh but this was not possible because of the very soft ooze (mud) and about 20 cm of water covering the mud from April through July. The difference in distance (field traps situated 100 meters from edge of forest and marsh traps situated 5 meters from the edge of field) was not considered a problem because a previous study had shown that the return to baited traps by carrion beetles released at 5 to 75 meters was a result of random wandering (Shubeck, 1968). The same study showed that the periphery of odor perception seems to be about 1 meter from carrion. Given this information it seemed improbable that baited traps would attract beetles from adjacent habitats.

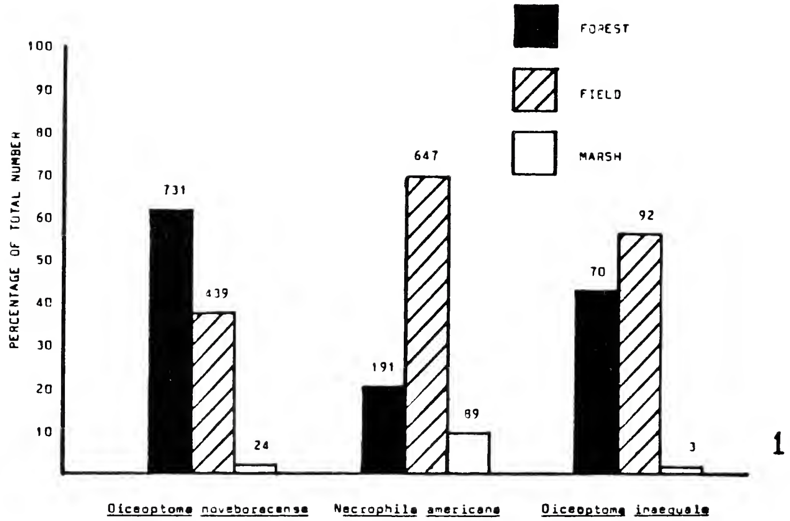
Each of these 3 habitats is located in the management area which is off-limits to visitors. The forest is dominated by red oak (*Quercus rubrum*), but American beech (*Fagus grandifolia*) occurs on its moist fringes. This woodland stand is about 5 hectares in size. The field is about 2 hectares in size and is covered by grasses about 1 meter tall. *Solidago* spp., *Daucus carota,* and *Aster* sp. are also present. The marsh, about 100 hectares in size, contains a variety of hydrophytes including *Pontederia cordata, Typha latifolia, Peltandra virginica,* and *Sagittaria latifolia.*

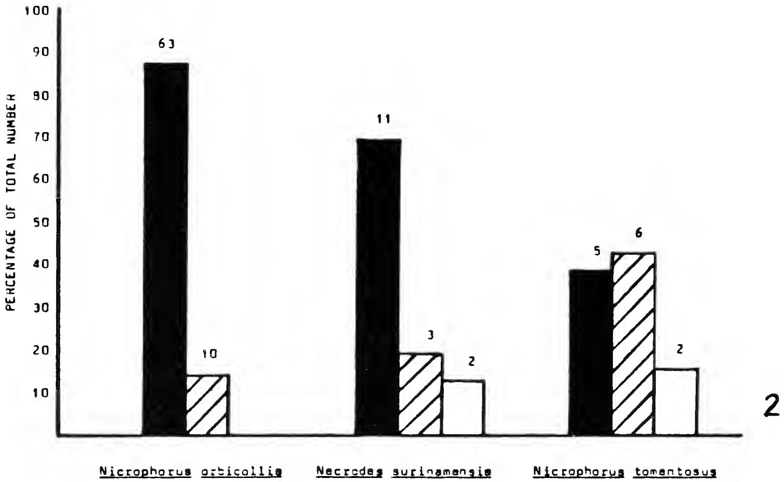
One of the pair of traps situated in each habitat was baited with fish (smelt), and the second was baited with chicken legs (drumsticks). Carrion bait in each trap consisted of 3 "fresh" fish (about 90 g total weight) and 3 "stale" fish (about 90 g), or 1 "fresh" chicken leg (about 90 g) and one "stale" chicken leg (about 90 g). The fresh and stale components were individually placed into a styrofoam cup (0.258 liter) so that each trap had a cup of fresh carrion and one of stale carrion. These traps were initially baited with "fresh" carrion 1 week before the season's collecting began and on the Saturday that collecting was begun "fresh" carrion was added to the "stale" carrion. Each trap was serviced once per week, throughout the season, at which time the oldest carrion (and cup) was replaced with fresh carrion (and cup), and all beetles were collected and preserved in jars containing 70% alcohol. At all times, therefore, each habitat had one trap baited with fish 1–7 days old (fresh) and fish 8–14 days old (stale), and a second trap baited with a chicken leg 1–7 days old (fresh) and a chicken leg 8–14 days old (stale). This technique (Pirone, 1974) resulted in the presence of fairly uniform "attractive" carrion continuously.

Weekly collections were made from 7 June to 25 August in 1980 and from 3 April to 30 May in 1981. A previous study in GSNWR had shown that carrion beetles were most abundant during the months of April through August (Shubeck et al., 1981).

RESULTS AND DISCUSSION

The catch for both seasons was totaled, by species for each habitat, and the bar graphs in Figures 1 to 4 show the numbers of individuals, and the percentage of the total for the habitat. In order to compare these results with Anderson's results (1982) I had to revise his percentages [Figs. 15–18] after removing his data for the coniferous forest habitat. By doing this I was able to compare results for deciduous forest, field, and marsh habitats in New Jersey and Canada (Table 1). In preparing Walker's data (1957) for comparison it was necessary to average his figures for the 3 deciduous forest habitats [Fig. 7] (mesic forest, bottom forest, ridge forest), and to then work out the percentages for species for deciduous forest versus field for a partial comparison (Table 1).





Figs. 1, 2. Habitat association. 1. *Oiceoptoma noveboracense* (Forster), *Necrophila americana* (L.), *Oiceoptoma inaequale* (F.)—[Silphidae]. 2. *Nicrophorus orbicollis* Say, *Necrodes surinamensis* (F.), *Nicrophorus tomentosus* Weber—[Silphidae].

Oiceoptoma noveboracense was the most abundant species collected (1,149 individuals) and it was common in the forest and in the field but the species preferred the forest habitat (Fig. 1). It was rarely collected in the marsh (2% of total). Anderson (1982) also found this species most common in the

Table 1. A comparison, by percentage, of carrion beetles and their habitat associations in Tennessee, Toronto, Canada, and New Jersey. Percentages rounded off to whole numbers.

	Tennessee		Canada			New Jersey		
	Forest	Field	Forest	Field	Marsh	Forest	Field	Marsh
Oiceoptoma noveboracense (Forster)	—		45	29	26	61	37	2
Necrophila americana (L.)	100	0	21	7	72	20	70	10
Oiceoptoma inaequale (F.)	—		94	0	6	42	56	2
Nicrophorus orbicollis Say	95	5	63	12	25	86	14	0
Necrodes surinamensis (F.)	100	0	0	100	0	69	19	12
Nicrophorus tomentosus Weber	100	0	34	45	21	39	46	15
Nicrophorus pustulatus Herschel	100	0	76	24	0	100	0	0
Nicrophorus marginatus (F.)	—		0	80	20	0	100	0
Dermestes caninus Germ.	9	91	—			44	37	19
Omosita colon (L.)	70	30				57	33	10
Euspilotus assimilis (Payk.)	94	6				43	56	1
Onthophagus hecate Panz.	100	0				9	79	12

deciduous forest and least common in the marsh. Although least common in the marsh 26% of the individuals taken were, in fact, collected in this habitat. It should be noted that Anderson's description of his marsh indicated that it ". . . underwent seasonal inundation, with water accumulating in the spring or after heavy rainfall." It seems clear, therefore, that it was relatively dry part of the time and may have superficially resembled an old field. Walker did not collect this species in his Tennessee study (1957).

Necrophila americana, the second most abundant species (927) collected in GSNWR strongly preferred (70%) the field habitat yet it was somewhat common (20%) in the forest and less common (10%) in the marsh (Fig. 1). Anderson's results were virtually identical for his deciduous forest habitat but he collected 72% of this species in his marsh and 7% in his field (Table 1). If one compares the New Jersey and Canadian data for this species in terms of forest versus field *and* marsh (combined) the results are virtually identical. The Tennessee data are completely different—all of the 162 individuals were collected in the 3 forests and none was taken in the field (Table 1).

Oiceoptoma inaequale, with 165 individuals collected, was the third most abundant silphid species in Great Swamp. Although it slightly preferred the field it was, in fact, common in both forest and field but rarely taken in the marsh (Fig. 1). Anderson found that the bulk (94%) of the individuals collected were taken in the forest, none in the field and 6% in the marsh (Table 1). Walker did not find this species in his study.

The fourth most abundant species in this study was *Nicrophorus orbicollis* and it showed a strong preference for the forest (86%) over the field (14%)

(Fig. 2). Results of the studies in Tennessee and Canada were somewhat similar since Walker collected 95% of his individuals in the forest and 5% in the field, and Anderson took 63% of his individuals in the forest, 12% in the field, and 25% in the marsh (Table 1).

The fifth most abundant silphid species, *Necrodes surinamensis,* was in fact not abundant (Fig. 2). Of the 16 individuals taken, ⅔ were collected in the forest and the remaining ⅓ about equally divided between the field and marsh. Although Walker did not take a single individual in his field, he collected 543 individuals in his deciduous forests (Table 1). Anderson took 7 individuals in his field (Table 1) (plus 4 others in his coniferous forest).

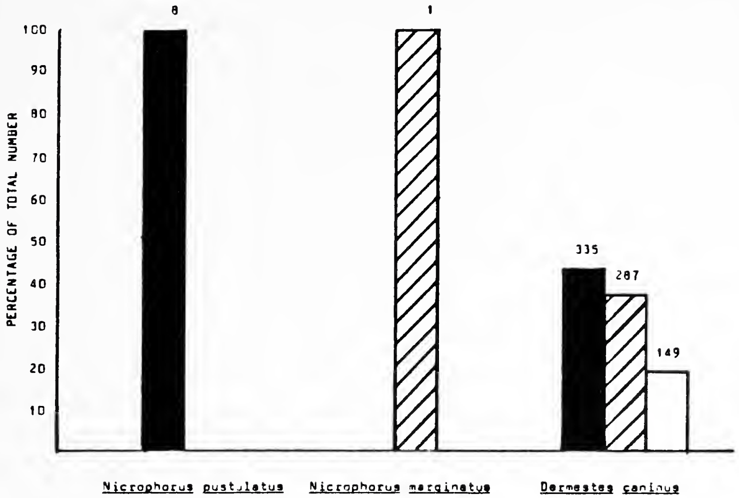
In spite of the fact that only 13 individuals of *Nicrophorus tomentosus* were taken in New Jersey but 1,488 were collected in Anderson's study (1982), a remarkable similarity in the forest : field : marsh percentages was evident (39:46:15 in New Jersey and 34:45:21 in Canada) (Table 1). On the other hand, *all* 51 individuals taken by Walker were collected in the 3 forests. Over 20 years of carrion beetle field studies have made it quite obvious to me that this is the *most active Nicrophorus* species of the 4 I have observed. It is the one that I would expect to have the widest range in its random flight (Shubeck, 1968) as it searches for carrion. This was supported by the data from both the New Jersey and Canadian studies.

Nicrophorus pustulatus, the seventh silphid species in order of abundance numbered but 8 individuals (Fig. 3), all from the forest. Walker's data were also limited to a few individuals (13) and they were all taken in the forest habitats (Table 1). Anderson's data too, were based on a small sample (17) and it indicated a preference of 3:1, forest : field (Table 1). In spite of the small sample in each case the preference of this species for the forest habitat is consistently clear.

The least abundant silphid in GSNWR was *Nicrophorus marginatus* which was limited to 1 individual (Fig. 3). However, it was taken in the open field like Anderson's sample of 125 individuals which showed a preference for the field over the marsh by a 4:1 ratio (Table 1). Although this species was not taken in the Tenneessee study, 1 individual was taken in a field but in no other habitat in Maryland (Shubeck, unpublished data, 1981).

The remaining 4 species are not members of the family Silphidae but they are members of 4 other families which contain species associated with silphid species on carrion. None of these species was included in Anderson's study but they were included in the Tennessee study.

Dermestes caninus (Dermestidae) was the most abundant (771 individuals) non-silphid species collected (Fig. 3). It was common in all 3 habitats but slightly preferred the forest (44%) over the field (37%). A substantial percentage (19%) of individuals was also taken in the marsh. This species is a good flyer and apparently ranges widely in search of dry carrion. The majority of individuals (91%) in Walker's study was collected in the field (Table 1).



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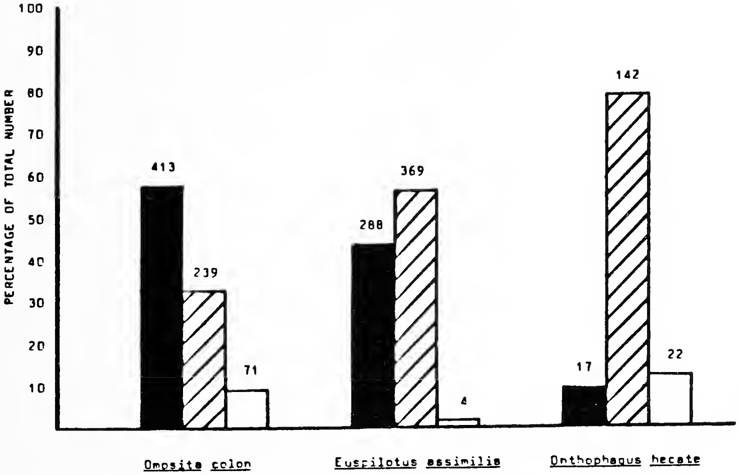

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Figs. 3, 4. Habitat association. 3. *Nicrophorus pustulatus* Herschel, *Nicrophorus marginatus* (F.)—[Silphidae], and *Dermestes caninus* Germ.—[Dermestidae]. 4. *Omosita colon* (L.)—[Nitidulidae], *Euspilotus assimilis* (Payk.)—[Histeridae], *Onthophagus hecate* Panz.—[Scarabaeidae].

Omosita colon (Nitidulidae) was also taken in large numbers (723). Although this species was present in the marsh (10%) and common in the field (33%), it showed a slight preference for the forest (57%) (Fig. 4). Walker also found in his study that the species preferred the forest to the field in a 7:3 ratio (Table 1).

A total of 661 individuals of the species *Euspilotus assimilis* (Histeridae) was collected in GSNWR. The species was rarely taken in the marsh (less than 1%) and it was common in the forest and field but slightly preferred the latter (Fig. 4). The overwhelming majority (94%) of Walker's specimens in Tennessee was taken in the forest (Table 1).

The last species included in this study is *Onthophagus hecate* (Scarabaeidae). Although it is called a "dung" beetle, it is, in fact, found on dung *and* carrion (Arnett et al., 1980). About $\frac{1}{10}$ of the 181 individuals collected were taken in the forest and a comparable number in the marsh, but the majority (79%) was taken in the field (Fig. 4). All of the individuals of this species collected in Tennessee by Walker were taken in the forest (Table 1).

CONCLUSIONS

Of the 8 silphid species collected in 3 habitats in GSNWR, 5 had a *strong preference* for 1 habitat over the other 2 (more than 60% of the species' representatives were taken in the preferred habitat). These were *Oiceoptoma noveboracense, Necrophila americana, Nicrophorus orbicollis, Nicrophorus pustulatus,* and *Necrodes surinamensis.*

Two silphid species had a *slight preference* for 1 habitat over the other 2 (56% or 46% of the species' representatives were taken in the preferred habitat). These species were *Oiceoptoma inaequale* and *Nicrophorus tomentosus.*

One silphid species manifested a *probable preference* for 1 habitat. *Nicrophorus marginatus,* although limited to 1 specimen was taken in the same habitat (field) in this and 2 other studies.

Insofar as the carrion beetles from other families are concerned 1 species, *Onthophagus hecate* (Scarabaeidae), showed a *strong preference* for 1 habitat (79% of the species' representatives were taken in the preferred habitat). Three species showed a *slight preference* for 1 habitat over the other 2 (44%, 56%, or 57% of the species' representatives were taken in the preferred habitat). These species were *Dermestes caninus* (Dermestidae), *Euspilotus assimilis* (Histeridae), and *Omosita colon* (Nitidulidae).

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MICROCLIMATE OBSERVATIONS AND DIEL ACTIVITIES OF CERTAIN CARRION ARTHROPODS IN THE CHIHUAHUAN DESERT

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Abstract.—Diel activity cycles of carrion arthropods and microclimate in and around carcasses were recorded using a bait trap and electronic telethermometer apparatus, respectively. Arthropod collections and temperature data were gathered for 24 hours each on 2 collection dates in 12 consecutive 2-hr intervals. Ants, histerid and dermestid beetles were active throughout the 24 hr period. Temporal segregation was observed between diurnal muscoid flies and nocturnal trogid beetles. Small numbers of maggots emerged from carcasses between 1 AM and 9 AM MDT. In the microclimate experiments, highest temperatures were noted on the soil surface (50°C), whereas the carcass surface (47°C), carcass interior (42°C), and surrounding air temperatures (36°C) were notably lower. Highest mean temperatures were recorded in the carcass interior and were probably attributable to internal heat generation by bacteria and maggots.

Most previous studies on carrion arthropods have addressed aspects of insect phenology and succession, trophic relationships and stages of decomposition. Other studies have examined the influence of environmental factors on rate of decomposition (Nabaglio, 1973), arthropod succession (Payne, 1965), flight activities of carrion beetles (Shubeck, 1975), and carcass microclimate (Reed, 1958; Payne, 1965). However, diel activities among carrion arthropods relative to microclimates in and around carcasses have received only casual attention. Diel variations in the carrion fauna (Reed, 1958; Payne, 1965; Shubeck, 1971) indicate that some arthropods (histerids, ants, silphids, phalangids, and dipterous larvae) that are active on carcasses by day also are nocturnal; whereas other taxa are almost exclusively diurnal (adult dipterans) or nocturnal (trogid beetles).

This paper supplements an earlier study (Schoenly and Reid, 1983) on the community structure of carrion arthropods in the northern Chihuahuan desert. Here I describe microclimate and diel activity patterns of arthropods on rabbit carrion during peak periods of arthropod diversity and carcass decomposition.

MATERIALS AND METHODS

The study area was located in a desert shrub community adjacent to the Franklin Mnts in El Paso County, Texas. In this region of the Chihuahuan

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desert, mean annual precipitation is 211 mm, temperatures range from −21° to 43°C, and the growing season averages 238 days (Norquest, 1941).

Observations of diel activity and carcass microclimate were made using a bait trap and telethermometer apparatus. The trap consisted of a square wooden box and was designed to collect arthropods immigrating to and emerging from carcasses (Schoenly, 1981). Arthropods were collected from the trap with a system of eight killing jars charged with an ethylene glycol mixture (Morrill, 1975). Adult blacktailed jackrabbits (*Lepus californicus* Gray) with an average mass of 2,250 gm were used for bait and placed in the trap. Sampling was begun when maximum arthropod diversity was reached; a period of 4–6 days after carcass placement (Schoenly and Reid, 1983). Arthropod collections and temperature data were gathered for a 24 hr period during 12 consecutive 2-hr intervals. Two experiments, using one rabbit carcass each, were conducted on July 26–27, and August 25–26, 1980. Penetration and contact thermocouples were attached to the carcass to monitor internal and surface temperatures. Ambient air and soil surface temperatures were monitored by securing thermocouples to the top and bottom of a 1-meter vertical post (Fig. 1). A Yellow Springs Instruments telethermometer was used to measure temperature. To maximize sampling efficiency, collecting jars were changed with fresh preserving fluid during each visit.

Patterns of temporal utilization among carrion arthropod taxa were compared using Levins (1968) measure of niche breadth:

$$B_i = 1/\sum_j p_{ij}^2$$

where p_{ij} is the importance value (proportion of individuals) of the ith species found on j resource units. The resource units in this study refer to time of carcass visitation by arthropods; thus, there were 12 2-hr resource units. Niche breadth values range from 0 to 1. A value of 1 indicates carrion utilization on all 12 resource units, whereas a value approaching 0 indicates very restricted use of carrion. Correlation statistics were used to test for significant differences between variables.

RESULTS AND DISCUSSION

Activity distributions of 5 arthropod taxa and temperature records pooled from the 2 collection dates are summarized in Figure 2. Although a brief summer shower temporarily interrupted arthropod activity on July 26, species composition overlapped considerably in both trials. Arthropods collected from the July and August experiments included: dipterans (97 and 268), hister beetles (18 and 109), ants (36 and 30), trogid beetles (4 and 10) and dermestids (3 and 17). The only other notable difference between the 2 experiments was the absence of maggots in the July trial.

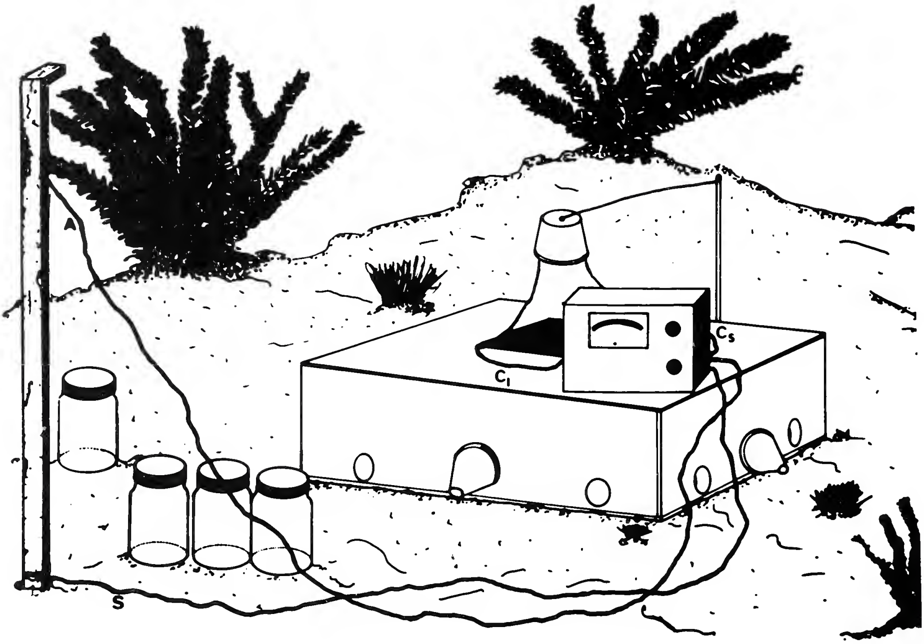

Fig. 1. Diagrammatic representation of the bait trap and telethermometer apparatus used for recording microclimate data and diel activity patterns of arthropods frequenting rabbit carrion. The height of the vertical post is 1 meter. A = ambient air, S = soil surface, C_s = carcass surface, and C_i = carcass interior thermocouples.

Adult dipterans were collected from the trap from 9 AM to 9 PM, and no activity occurred after 9 PM (Fig. 2A). A relatively high niche breadth value (0.754) corresponded to a uniform pattern of diurnal activity (1–7 PM) and a large density of individual flies, particularly from 9 to 11 AM. The relationship between diurnal activity of adult flies and air temperature was significant and negative ($r = -0.62$, $P < 0.05$). The calliphorid, *Cochliomyia macellaria* (Fabricius) was the most abundant species observed (N = 329), followed by *Musca domestica* L. (Muscidae) (24) and the sarcophagid, *Blaesoxipha plinthopyga* (Wiedemann) (12). In addition, small numbers of

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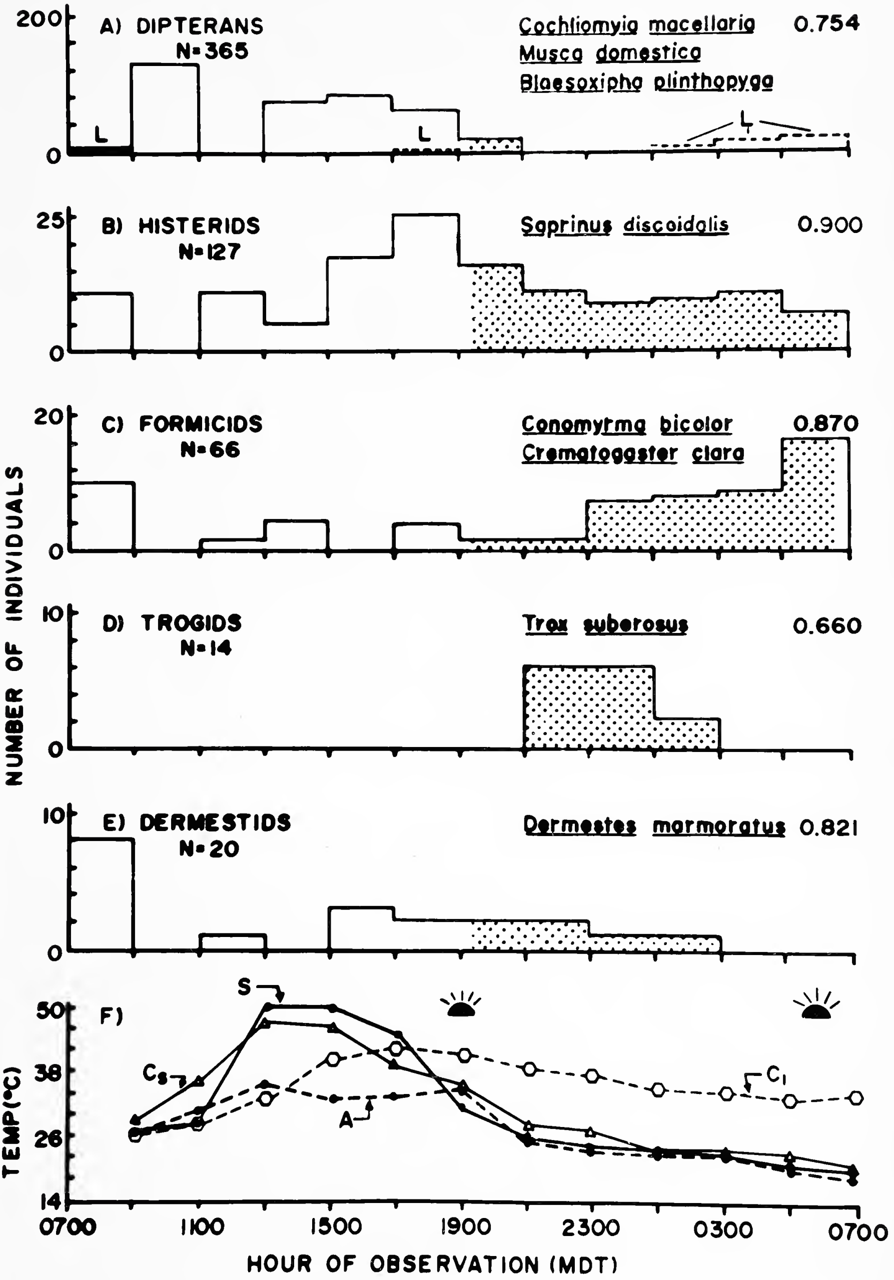
Fig. 2. (A–E) Number of arthropods collected from jackrabbit carrion during periods of active decomposition (days 4–6 after placement) in summer, 1980. Numbers in the right margin of each graph refer to values of temporal niche breadth (see text). Shaded portions indicate nocturnal periods. L = fly larvae. (F) Microclimate temperatures taken on the carcass and near the trap; S = soil surface, A = ambient air, C_s = carcass surface and C_i = carcass interior temperatures. Partial sun symbols indicate approximate periods of sunset and sunrise (MDT).


A) DIPTERANS
N=365
Cochliomyia macellaria 0.754
Musca domestica
Blaesoxipha plinthopyga
L
L
L
200
0
B) HISTERIDS
N=127
Saprinus discoidalis 0.900
25
0
C) FORMICIDS
N=66
Conomyrma bicolor 0.870
Crematogaster clara
20
0
D) TROGIDS
N=14
Trox suberosus 0.660
10
0
E) DERMESTIDS
N=20
Dermestes marmoratus 0.821
10
0
NUMBER OF INDIVIDUALS
F)
S
Cs
A
Cl
50
38
26
14
TEMP(°C)
0700
1100
1500
1900
2300
0300
0700
HOUR OF OBSERVATION (MDT)

dipteran larvae (N = 22) emerged from carcasses at night between 1 and 7 AM and continued into late morning (Fig. 2A).

The histerid beetle, *Saprinus discoidalis* LeConte, was second in abundance (N = 127) and had the highest niche value of all the taxa considered (0.900). This species was active throughout the day and night, but had a distinct peak of activity 2 hr before sunset (Fig. 2B).

Of the ants observed, *Crematogaster clara* Mayr and *Conomyrma bicolor* (Wheeler) were the most frequent visitors to carrion. Ants were least active during daylight hours, whereas nocturnal observations showed a rapid increase in numbers beginning at 11 PM with a prominent peak 1 hr before sunrise (Fig. 2C). Ant activity was negatively correlated with increasing air ($r = -0.63$, $P < 0.02$) and soil temperatures ($r = -0.56$, $P < 0.05$). A significant positive relationship was observed between nocturnal ant activity and dipteran larvae emergence from carrion ($r = 0.93$, $P < 0.01$) suggesting that ants were preying on the larvae. Predation by ants on larvae in carrion has been reported previously from the Chihuahuan desert (McKinnerney, 1978; Schoenly and Reid, 1983) and elsewhere.

Trogid beetles (*Trox suberosus* Fabricius) were collected in small numbers (N = 14) during nocturnal periods only from 9 PM to 3 AM (Fig. 2D), and had the lowest value of temporal niche breadth (0.660). During the heat of the day, trogids remained inside or under carcasses where subdued light conditions prevailed.

A total of 20 dermestid beetles (*Dermestes marmoratus* Say) were collected between 7 AM and 3 AM. Eight or 40% of the individuals collected were captured in the 2 hr between 7 AM and 9 AM (Fig. 2E).

Smaller numbers of other arthropods (not shown in Fig. 2) also were collected including 3 solpugids (*Eremobates marathoni* Muma), 2 arachnids (*Syspira longipes* [Simon]), and a staphylinid beetle (*Creophilis maxillosus* [Linné]).

Highest temperatures were recorded on the soil (50°C) and carcass surfaces (47°C) between 1–3 PM, whereas carcass interior and ambient air temperatures peaked later at lower temperature (42° and 36°C, respectively). However, the mean temperature of the interior of carcasses (35°C) was much higher than the mean temperature of the carcass surface (31°C) and the surrounding soil surface temperatures (30.6°C) (Fig. 2F). Payne (1965) stated that rising temperatures in the carcass during active and advanced decay stages are attributable to the actions of bacteria and maggots. My data would seem to support this hypothesis.

My results indicated that diel variations in the desert carrion fauna are similar to those reported by Reed (1958) and Payne (1965) in temperate forest ecosystems. Higher environmental temperatures do not appear to restrict arthropod activity in or around carrion, at least in those taxa studied here. Temporal segregation was noted in 2 taxa (flies, trogids) and densities of all 5 taxa peaked at different times. Analysis of feeding habits revealed that even among ecologically similar carrion taxa patterns of diel activity differed. Among the necrophagous taxa, trogid beetles were exclusively nocturnal, whereas dipterans and dermestids were both active after sunrise but displayed distinct peaks of activity at different times (9–11 AM and 7–9 AM, respectively). Of the predaceous arthropods, hister beetles and ants both are known to prey on maggots (Schoenly and Reid, in press and references therein), however, peak densities occurred at dusk for beetles and dawn for ants. Members of the carrion community in other regions may show similar patterns in carcass utilization.

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SEASONAL DYNAMICS OF FLEAS ASSOCIATED WITH THE GRAY-TAILED VOLE, *MICROTUS CANICAUDUS* MILLER, IN WESTERN OREGON[1]

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Abstract.—A study of the population dynamics of fleas associated with the gray-tailed vole, *Microtus canicaudus* Miller, was conducted on three sites surrounding the city of Corvallis, in Oregon's Willamette Valley. Over a period of 12 months, 22,641 adult and larval fleas representing eight species were recovered from 377 comparable voles and 256 nests. On all sites, adult and larval flea populations experienced spring and early winter peaks followed by drastic summer and midwinter declines. These fluctuations are consistent with the thesis that humidity and temperature are the chief factors influencing flea populations.

This is the third in a series of papers on the fleas that parasitize the gray-tailed vole, *Microtus canicaudus* Miller, the principal species of field mouse inhabiting grassy lowlands between the Cascade and Coast Ranges of western Oregon and Washington. Earlier, the fleas of this vole served to illustrate the use of statistics for measuring interspecific associations of vertebrate ectoparasites (Faulkenberry and Robbins, 1980) and for modeling parasite populations (Robbins and Faulkenberry, 1982). By contrast, this and succeeding papers will be confined to an analysis of flea populations specific to the gray-tailed vole and its immediate mammalian associates.

DESCRIPTION OF THE STUDY SITES

The three sites selected for this study lie north, south, and west of the city of Corvallis, Oregon, which itself is situated west-centrally in the Willamette Valley, a rich agricultural region characterized by warm, dry summers and cool, wet winters. Since the sites are ecologically and physiographically similar to one another, data obtained from any one site were compared with data from the other two which, in effect, served as controls. Additional criteria used in site selection were accessibility, relative freedom from human interference, and the presence of significant populations of Norway rats (*Rattus norvegicus* (Erxleben)) and house mice (*Mus musculus* Linnaeus).

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Each site is bounded by larger areas of similar terrain permitting free movement of animal populations. In addition to the gray-tailed vole, Norway rat and house mouse, mammals found on all three sites include the vagrant shrew (*Sorex vagrans* Baird), Townsend mole (*Scapanus townsendii* (Bachman)), deer mouse (*Peromyscus maniculatus* (Wagner)), Townsend vole (*Microtus townsendii* (Bachman)), and the introduced Eastern cottontail rabbit (*Sylvilagus floridanus* (Allen)). While various species of grasses account for most of the vegetative cover, larger plants common to all sites are sweetbriar rose (*Rosa eglanteria* Linnaeus), Himalaya berry (*Rubus procerus* Mueller), Northwest nettle (*Urtica lyallii* Watson), Queen Anne's lace (*Daucus carota* Linnaeus), and Douglas' hawthorn (*Crataegus douglasii* Lindley).

The north Corvallis collecting site, hereafter referred to as the North Site, occupies approximately 1.3 hectares of land within the apex of the inverted isosceles triangle formed by the tracks of the Southern Pacific Railroad at the Corvallis Junction. During winter, standing water may persist for long periods in ditches that parallel the tracks. Tall oat-grass (*Arrhenatherum elatius* (Linnaeus) Mertens) is the dominant grass species, covering most of the site and broken only occasionally by clumps of orchard-grass (*Dactylis glomerata* Linnaeus). Because part of this area is used as a public dumping ground, Norway rats and house mice are most abundant here. Being moist, the North Site also supports the largest population of Townsend voles.

Extensive real estate development along the southern edge of Corvallis necessitated several minor shifts in the location of the South Site and effectively curtailed collecting during two months of this study (May–June 1973). However, all southern sites were located immediately east or west of U.S. Route 99W between Millrace Creek and Wake Robin Avenue, and no site exceeded 0.8 hectares in area. Again, tall oat-grass is the dominant grass species, but orchard-grass and a variety of weeds are also abundant. The South Site is only slightly drier than the North Site.

The West Site embraces 0.6 hectares of land along the north side of Philomath Boulevard 1.3 kilometers west of its junction with 53rd Street. Both tall oat-grass and orchard-grass are absent here, their place being taken principally by colonial bent-grass (*Agrostis tenuis* Sibthorp), followed by velvet-grass (*Holcus lanatus* Linnaeus), bristly dog's-tail grass (*Cynosurus echinatus* Linnaeus), meadow fescue (*Festuca elatior* Linnaeus), and small, scattered clumps of tufted hair-grass (*Deschampsia caespitosa* (Linnaeus) Palisot de Beauvois). On this relatively dry site, the Eastern cottontail and Townsend mole are conspicuously abundant.

SAMPLING TECHNIQUES

Between December 1972 and January 1974, gray-tailed voles and their nests were collected at regular monthly intervals on all three sites. Initially, voles were taken by placing Sherman all-metal live traps (H. B. Sherman,

Table 1. Composition of the adult flea population of the gray-tailed vole.

Flea species	Nests No.	Nests Percent	Hosts No.	Hosts Percent
Atyphloceras multidentatus (C. Fox) 1909	2,550	41	100	20
Catallagia charlottensis (Baker) 1898	3,291	53	252	49
Corrodopsylla curvata (Rothschild) 1915	32	0.5	11	2
Hystrichopsylla occidentalis Holland 1949	212	3	25	5
Monopsyllus wagneri (Baker) 1904	36	0.5	44	8.5
Nosopsyllus fasciatus (Bosc) 1800	71	1	14	3
Peromyscopsylla selesis (Rothschild) 1906	57	1	62	12
Rhadinopsylla sp.	1	0	3	0.5
Totals	6,250	100	511	100

De Land, Florida) in their runways; however, the winter of 1972–1973 was so cold that most animals captured in this manner died before they could be retrieved. Persistent vandalism, which must be expected when working in a suburban environment, also discouraged this approach. In place of traps, a variety of old boards and panels were scattered at random over each site. Voles seeking shelter under these objects were easily caught by hand. Each vole was then immediately transferred to a large, labeled plastic jar containing fresh grass clippings and pieces of fruit. All jars were fitted with wire mesh lids. Because some voles died or injured themselves in transit or were found naturally injured in the field, not all of them could be used in this study.

Ordinarily, the gray-tailed vole constructs its nest in a chamber located 15–30 centimeters below the surface of the ground (Pearson, 1972); however, should objects be present at the surface the vole will also build under these. Only surface nests were routinely collected for this study, though during the summer of 1973 five subterranean nests were successfully exhumed for comparative purposes. As most fleas require about one month to develop, an effort was made to collect only those nests that had been occupied for at least this time. Each nest and the loose soil below it was swiftly transferred to a labeled, half-gallon Freezette-Flat plastic container (Cole-Parmer Instrument and Equipment Company, Chicago, Illinois) sealed with an airtight lid. If a litter was found, it was removed and notes were taken on the age and number of the young.

In the laboratory, all voles were killed by quickly wrapping them in cotton blankets saturated with chloroform. This technique prevented the escape of any ectoparasites and preserved them in the positions they occupied on their host's body while it was alive. Once dispatched, each vole was placed in a labeled plastic bag and stored at −16°C. The nest fauna was extracted with

Berlese funnels set for 72 hours and equipped with 60-watt Ken-Rad light bulbs. All fleas and their larvae were preserved in labeled vials of 75% ethyl alcohol.

At irregular intervals, groups of 12 voles were removed from cold storage, thawed, and examined for fleas. Though a number of washing and dissolution techniques have been described for the collection of other ectoparasite groups (Hopkins, 1949, pp. 395–398; Lipovsky, 1951; Cook, 1954; Henry and McKeever, 1971), these are unsatisfactory for fleas, which adhere tenaciously to the hairs of their host and are easily damaged by caustic chemicals. During this study, all fleas were recovered by vigorous brushing and careful searching, a process that generally required half an hour per animal. To prevent ectoparasite loss, these operations were performed against a large, white enameled tray.

RESULTS AND DISCUSSION

Remarkably severe weather prevailed throughout the collecting period. A destructive freeze in December 1972 was followed by an unusually dry spring and a prolonged summer drought. Ten consecutive months of dryness were finally ended by generous rains in September and October and record-breaking rainfall in November. Above-normal precipitation and temperatures characterized December, but the heavy rains of late January 1974 fell on ground that had been solidly frozen earlier in the month, producing serious floods over much of the Willamette Valley. On the whole, it appears that the normal weather patterns for western Oregon were exaggerated during the period of this study.

In 1973, the gray-tailed vole experienced a population peak throughout the Willamette Valley. This was followed in the spring of 1974 by a catastrophic decline after which few voles were seen until the end of the year (R. F. Hoyer, personal communication). Between February 1973 and January 1974, 428 gray-tailed voles—377 of them statistically comparable—and 251 surface nests were removed from the North, South, and West sites. This material yielded 22,641 specimens of eight flea species, including 6,761 imagines distributed as shown in Table 1. For most species, identification of larvae was not possible. Only *Atyphloceras multidentatus, Catallagia charlottensis, Hystrichopsylla occidentalis,* and *Peromyscopsylla selenis* are regular parasites of voles (Hopkins and Rothschild, 1962, 1971). *Corrodopsylla curvata* is a true shrew flea, *Monopsyllus wagneri* is a widespread western deer mouse flea, and *Nosopsyllus fasciatus* is the introduced northern rat flea. Owing to the rarity of *Rhadinopsylla* in collections and the resultant taxonomic confusion within this large genus, the identity and preferred hosts of specimens from western Oregon remain unknown.

Table 2 summarizes seasonal changes in the total flea population on all

Table 2. Seasonal changes in total flea population on the North, South, and West Corvallis Sites.

	1973											1974
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Mean number of fleas per vole												
North	0.80	0.50	1.5	0.0	0.12	0.0	0.27	0.38	1.0	1.9	3.5	1.5
South	0.77	0.37	1.3	—	—	0.0	0.21	0.33	1.3	0.75	4.8	1.8
West	1.2	1.2	2.3	0.60	0.25	0.17	0.17	0.37	0.78	2.4	1.4	1.3
Mean number of larval fleas per nest												
North	0	20	127	33	5	7	18	24	236	132	52	35
South	77	31	51	—	—	12	0	26	34	139	112	73
West	15	107	66	37	4	8	0	12	134	65	63	32
Mean number of adult fleas per nest												
North	53	65	42	11	5	2	3	14	25	49	71	59
South	45	25	3	—	—	6	2	9	15	76	86	40
West	15	11	19	10	4	2	1	7	21	33	42	22

three sites. Regardless of species or host preference, fleas were most abundant during the mild, moist months of spring and early winter and least numerous during the hot, dry summer. A midwinter decline also was evident. Thus, in the example of *Peromyscopsylla selenis,* which despite its generic name is typically a flea of microtine rodents (Jameson and Brennan, 1957), 85 (71%) of the 119 specimens in Table 1 were taken during March–April and October–December. On the other hand, *Corrodopsylla curvata* is specific to insectivores (Hubbard, 1947; Hopkins, 1957), but of 43 accidentals obtained from nests and pelts of the gray-tailed vole, 27 (63%) were taken during the peak spring and early winter months. *Hystrichopsylla occidentalis* is an impartial parasite of small mammals within its range (Hopla, 1964), but again of 237 specimens collected, 170 (72%) were from the same peak months. These observations are consistent with Holland's (1949) thesis that humidity and temperature are the principal factors influencing flea populations. Similar results were obtained by Howell (1955, 1957) in his investigations of fleas associated with nests of the desert wood rat (*Neotoma lepida lepida* Thomas) and by Parker (1958) in a study of fleas—particularly the ceratophyllid *Thrassis bacchi gladiolis* (Jordan)—on the antelope ground squirrel (*Citellus leucurus leucurus* (Merriam)). As expected, peaks in larval populations preceded those of adults; the sole departure from this pattern (North Site, April) probably was due to sampling error.

The mean number of fleas per vole or per nest is equivalent to a crude flea index, similar to one proposed early in this century by the British Plague Commission to monitor flea populations on synanthropic rats in India (Hirst, 1926, 1927; Muirhead-Thomson, 1968). The sensitivity of this index can be improved by treating each species separately and by restricting coverage to infested voles and nests (Cole and Koepke, 1947). Both of these modifications will be demonstrated in forthcoming papers, where the population dynamics of each flea species listed above will be discussed in detail.

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Foremost among the recipients of my gratitude is Dr. Gerald W. Krantz, Department of Entomology, Oregon State University, Corvallis, who enthusiastically supported a research program largely unrelated to his own profession of acarology. Sincere thanks are also due Mr. Richard F. Hoyer, long-time Corvallis naturalist, who collected most of the voles and nests used in this study and offered many important observations drawn from years of experience in field biology. Dr. Vernon J. Tipton and his colleagues at the Center for Health and Environmental Studies, Brigham Young University, Provo, Utah, kindly determined a synoptic series of the flea species discussed herein. The bulk of the flea collection on which this series is based has been donated to B.Y.U.

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HISTOLOGY OF THE MALE REPRODUCTIVE SYSTEMS IN THE ADULTS AND PUPAE OF TWO DORYLINE ANTS, *DORYLUS* (*ANOMMA*) *WILVERTHI* EMERY AND *D.* (*A.*) *NIGRICANS* ILLIGER (HYMENOPTERA: FORMICIDAE)

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Abstract.—This paper is the first comprehensive description of the histology of the male reproductive systems of the adults and pupae of the doryline ants, *Dorylus* (*Anomma*) *wilverthi*, and *D.* (*A.*) *nigricans.* The reproductive systems consist of the testes and vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the bound accessory gland duct, the ejaculatory duct and wedge, and the aedeagal bladder. The numbers of testicular follicles, the microanatomy of the organs, the types and amounts of secretions in the lumina of the organs, as well as the presence or absence of spermatozoa, are compared in the adults and pupae of these two species. Although similarities exist, significant differences are found in the microanatomy of the organs, in the types and amounts of secretions produced, and between organs of the adults and pupae. The histology is also compared with that in the Old World *Aenictus gracilis*, the New World *Neivamyrmex harrisi*, and other studies of Old and New World dorylines. Important differences exist between the male reproductive systems of the two African *Dorylus* species herein studied and the New World *N. harrisi.* The *Dorylus* species have a larger number of testicular follicles, the organs of the system are more complex and produce both acidophilic and basophilic secretions, the entrance of the ejaculatory duct into the aedeagal bladder, and the formation of a new dorsal duct at the posterior end of the bladder are different from those in other dorylines.

This paper describes the histology of the organs of the male reproductive system in the adults and pupae of *Dorylus* (*Anomma*) *wilverthi* and *D.* (*A.*) *nigricans.* In an earlier paper, the anatomy of this system in these two ants has been reported (Ford and Forbes, 1980). The histology described is compared with that in the Old World *Aenictus gracilis* (Shyamalanath and Forbes, 1983) and in the New World *Neivamyrmex harrisi* (Forbes and Do-Van-Quy, 1965) and with the histological comments and illustrations included in the study of army ant males by Gotwald and Burdette (1981).

Histological studies reveal differences that are not observable by dissection but that are significant in the microscopic structure of organs, in the types of secretions produced, and between organs of pupal and adult stages.

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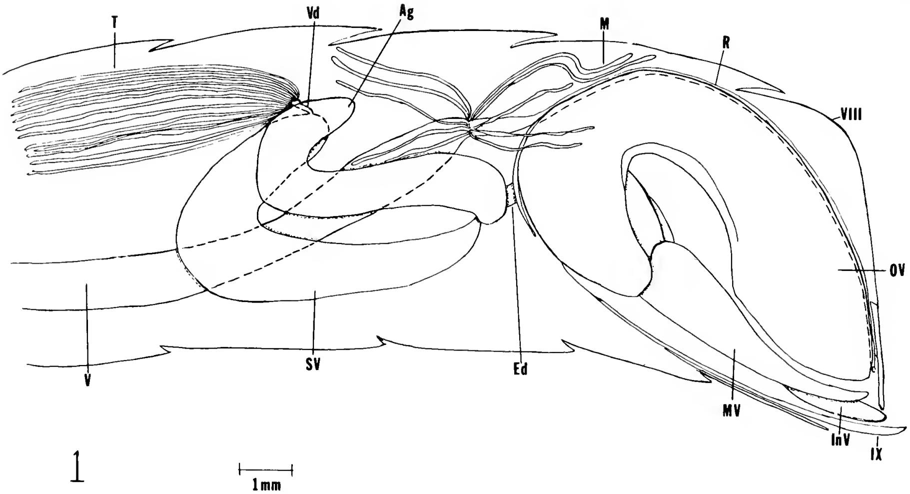


Fig. 1. Diagram of a lateral dissection of the posterior portion of the gaster of the adult male ant *Dorylus* (*Anomma*) *wilverthi.* Abbreviations: Ag, accessory gland; Ed, ejaculatory duct; InV, inner genitalic valve; M, Malpighian tubule; MV, middle genitalic valve; OV, outer genitalic valve; R, rectum; SV, seminal vesicle; T, testis; V, ventriculus; Vd, vas deferens; VIII–IX, Roman numerals designate abdominal segments. (From the original of Fig. 1, F. C. Ford and J. Forbes, J. New York Entomol. Soc. 88:135.)

MATERIAL AND METHODS

Seven to nine specimens each of the male adults and pupae were furnished by Albert Raignier, S.J. of Belgium, who collected them in the Republic of the Congo, Africa, now designated Zaire, in the town of Mayidi. The adults of *nigricans* were collected during June of 1956, the pupae of *nigricans* and the adults and pupae of *wilverthi* during November of 1957. The specimens were preserved in 80% ethyl alcohol. These specimens were sent to the late T. C. Schnierla of the American Museum of Natural History who gave them to J. Forbes for anatomical studies.

The pupae of both species were very well developed externally and internally and were probably close to eclosion. The gastral viscera were removed entirely and processed by a double infiltration technique (Trombetta and Forbes, 1977). Sagittal and transverse serial sections were cut at 10 μ, stained with Harris' haematoxylin and counterstained with eosin. Although the material had been fixed and stored in alcohol for a long period, most of it cut fairly well. The *nigricans* adults were in the poorest condition. Their organs and tissues were brittle when gross dissections were made and were more resistant to the embedding process, resulting in blocks that shattered during sectioning. During staining, each group of slides was processed similarly, but variations in the stained slides were apparent.

OBSERVATIONS

Throughout this section, the histology of the *wilverthi* adult system will be described first. Differences between that system and the pupal system will follow. Comparisons will be made with the adult and pupal systems of *nigricans.*

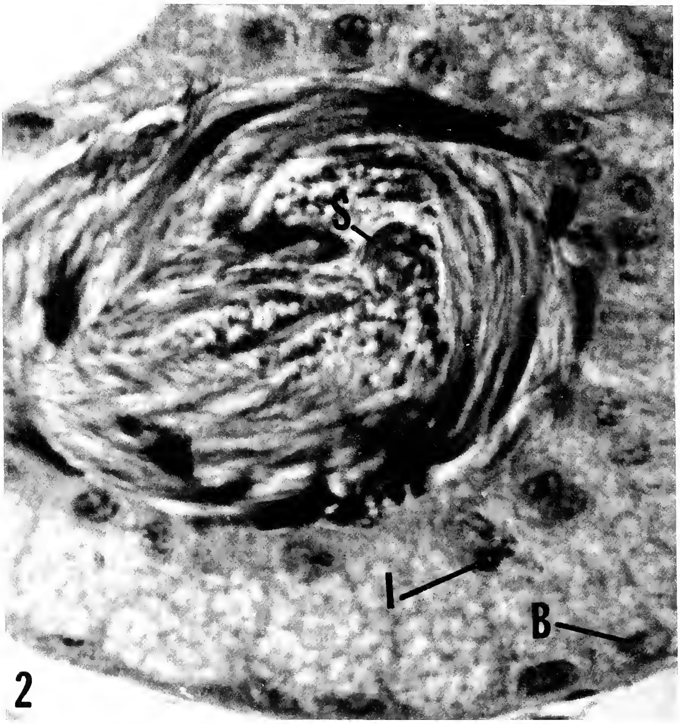
Testes (Figs. 1, 2, and 3). The testis of *wilverthi* consists of 35–40 long, slender, thin-walled follicles. The wall of the follicle is composed of two cell layers, a basal and an inner one, arranged around a distinct central lumen. The cells of the basal layer are large, generally cuboidal in shape with indistinct lateral margins, and they lie on a distinct basement membrane. The basally located nuclei of these cells have their long axes parallel to the basement membrane. The cytoplasm is highly vacuolate throughout but more granular basally. The inner cell layer consists of flattened nuclei lying in an irregular layer of cytoplasm above the basal cells. The lumina of the follicles are filled with clusters of closely packed spermatozoa. The heads of these sperm clusters lie toward the center, and the tails extend to the periphery.

The testes of both species are not covered with a capsule. The sections show a thin covering of many branching tracheae of various sizes. These tracheae continue into the spaces between the follicles, and they are attached to the basement membrane of the follicles by very fine, branching, nucleated fibers. Occasionally, clusters of fat cells are found in the network of tracheae between the follicles. Embedded in these clusters are a few spheroidal cells, about the size of adipocytes, that contain irregularly-shaped nuclei and have the cytoplasm filled with fine, basophilic granules and numerous vacuoles. These cells resemble urate cells. Acidophilic granular material is found in spaces between some of the follicles.

In the pupa of *wilverthi* the testis is similar in its overall histological arrangement to that of the adult, but the lumina of the follicles are smaller and contain a network of cytoplasmic strands not connected to the inner cell layer of the follicle. Clusters of sperm heads are found in the spaces of the network and are embedded in the cytoplasmic strands, and the tails extend to the periphery of the follicles.

In *nigricans* adults no testes were found macroscopically, but the sections revealed a posterior displaced mass of intertwined large and small tracheae within which was a large circular mass and a few smaller masses of spermatozoa; nothing else was seen. In *nigricans* pupae each testis consists of 50–55 tubules. The histology of the testicular follicles is similar to the arrangement in the *wilverthi* pupa.

Vasa efferentia. In *wilverthi* each testicular follicle ends in a narrow vas efferens. At the junction of the follicle and the vas efferens there is an abrupt transition from the larger, basal cells on the wall of the follicle to very low, columnar cells that form the epithelial lining of the vas efferens. The nuclei



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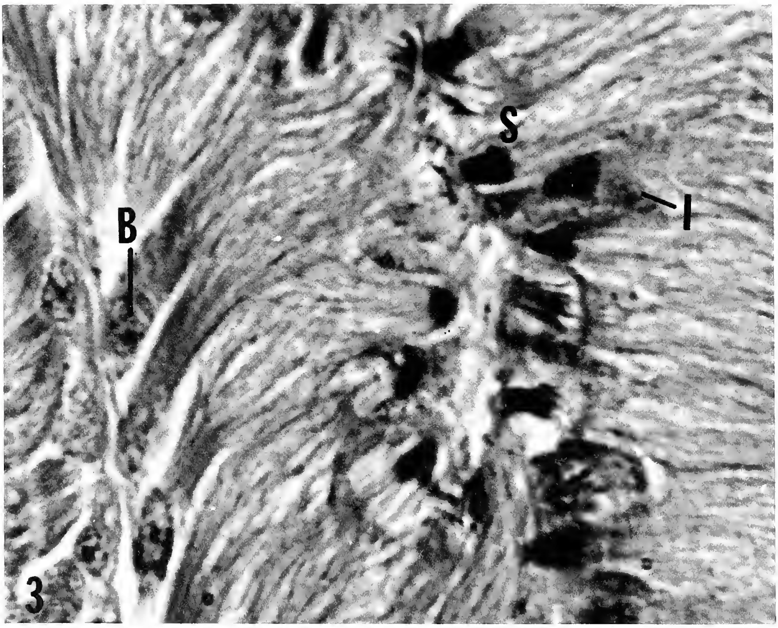

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are centrally located. A basement membrane is not evident, but small muscle fibers adhere closely to the bases of the epithelial cells and run obliquely around the vasa efferentia. Clusters of spermatozoa are found only at the anterior ends of many of these vas efferens. The thin capsule, that extends between the testicular follicles, continues between the vasa efferentia.

The histology of the vasa efferentia in the *wilverthi* pupa and in the *nigricans* pupa is similar to that of the *wilverthi* adult. No vasa efferentia were found in the *nigricans* adult.

Vas deferens. Where the vasa efferentia unite to form the short vas deferens, the low columnar cells immediately increase in height to form the columnar epithelium of the vas deferens. The nuclei of these cells are centrally located. Small clusters of sperm are present in the lumen. The vas deferens narrows as it proceeds toward the seminal vesicle. Vacuoles are present in the cytoplasm bordering the lumen. A very faint basement membrane is seen periodically, and the surrounding muscle coat consists of 2 or 3 obliquely arranged fibers. At the junction of the vas deferens with the seminal vesicle, the columnar cells merge with the tall columnar epithelium of the seminal vesicle. The muscle coat of the vas deferens continues into that of the seminal vesicle.

Seminal vesicles (Figs. 1 and 4). The epithelium of the prominent U-shaped seminal vesicles consists of columnar cells built on a distinct basement membrane. The cells are arranged in clusters of taller cells interspersed with one or a few shorter, irregularly distributed cells. The nuclei of the cells are centrally located, and the staining reaction of the cytoplasm is variable from the basal region to the free surface. The region from the base to just above the nucleus is packed with granule-filled vacuoles. In the subnuclear region these granules stain faintly basophilic, and in the region above the nucleus they stain more strongly. Above this region, there is a narrow band of strongly acidophilic-staining cytoplasm that extends to the free surface. Occasionally, in this strongly acidophilic layer, thin columns of basophilic granules extend toward the surface of the cells. The free surfaces of most of the cells are dome-shaped, and extensions from the free surfaces of some cells are pinched-off to form a secretion in the lumen. This secretion varies in composition and amount along the lumen of these organs. In the first part, the lumen is filled with a fine-granular, basophilic secretion and numerous spermatozoa. On the periphery of this secretion are scattered clusters of a larger, acidophilic granular secretion. Toward the middle region

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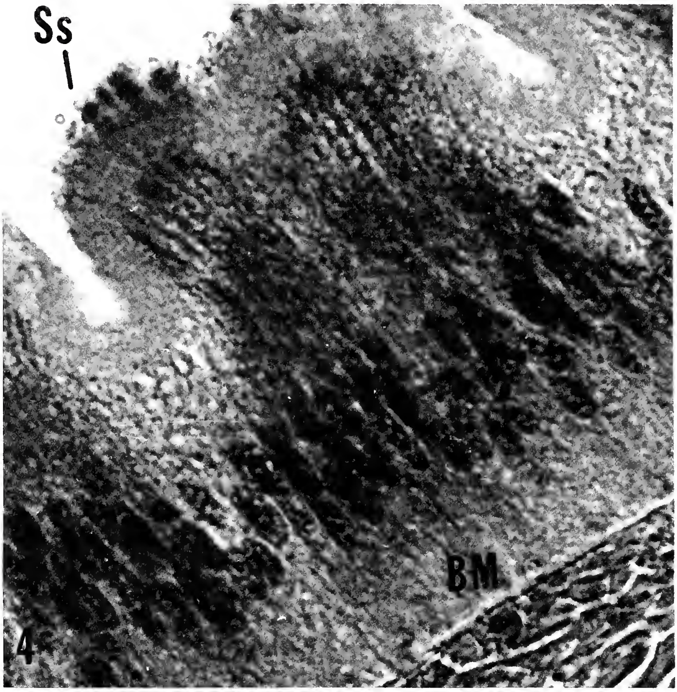
Figs. 2, 3. Photomicrographs of oblique sections of testicular follicles of *Dorylus wilverthi.* ×450. 2. Adult. 3. Pupa. B and I, nuclei of basal cell layer and of inner cell layer of testicular follicles; S, bundles of sperm.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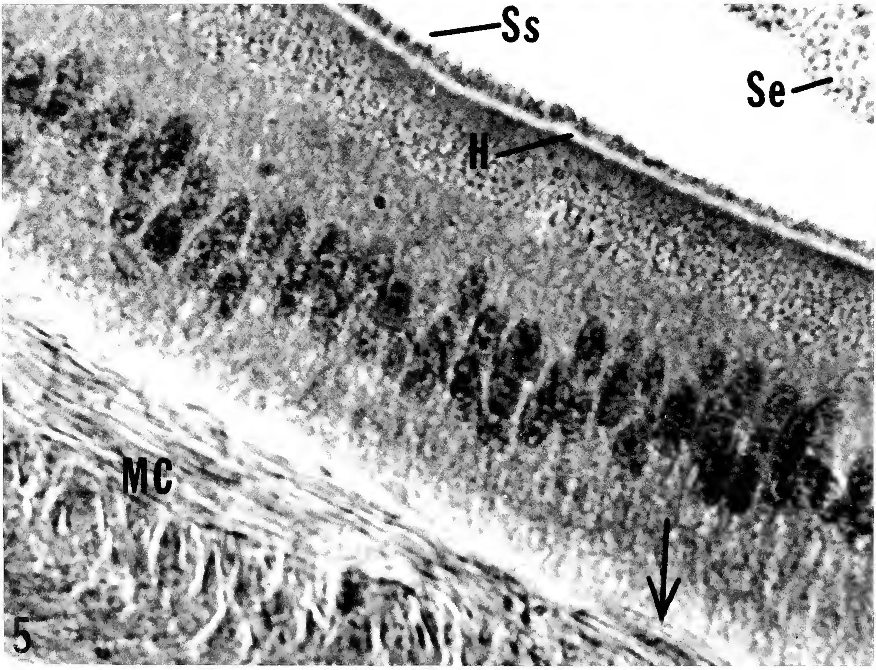
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the secretion is composed of large, acidophilic granules, and some sperm is present. In this region, also, there is a strongly acidophilic-staining, amorphous mass that can vary in amount within the seminal vesicles of the same ant. In the posterior region, the secretion is granular, stains distinctly basophilic, and no sperm were seen. The muscle coat is composed chiefly of obliquely arranged fibers, 4 or 5 fibers in thickness anteriorly and increasing by 2 or 3 more fibers posteriorly.

In the constricted posterior region of the seminal vesicle, the epithelial cells are reduced in height. The cytoplasm is basophilic in staining reaction, and in the upper third of many cells the vacuoles have coalesced to form a large, clear vacuole. The cytoplasm at the free borders is compact, and there is a granular, basophilic secretion in the lumen. The muscle coat has again increased by several fibers in thickness. This constricted end joins the lower, posterior part of the accessory gland, where it penetrates obliquely through the muscle coat of the accessory gland.

The organization of the tissues in the seminal vesicles of the pupa of *wilverthi* is similar to that of the adult, but no spermatozoa are present. A granular, basophilic secretion is present in the lumen. The histology of the seminal vesicles of the *nigricans* adult and pupa is respectively similar to that of the *wilverthi* adult and pupa.

Accessory glands (Figs. 1 and 5). The epithelium of these thick-walled, S-shaped glands consists of a single layer of cells that varies from cuboidal to exceptionally tall columnar. No basement membrane is evident. The epithelium is raised into 2 or 3 oblique folds that extend the length of the glands. Large, granular, ellipsoidal nuclei are located in the lower half of the cells. The cytoplasm, variable in appearance from the bases to the free surfaces, is basophilic in staining throughout the cells. In the basal region it is highly vacuolate but above the nucleus less so. Within the upper third the cytoplasm is packed with coarse, spherical, acidophilic-staining granules. In some regions above this granular, acidophilic layer and at the surface of the cells there is a thin, hyaline layer which stains lightly basophilic. Some columnar cells have the cytoplasm above the nucleus filled with acidophilic granules, and in these cells there is usually a thin separation in the cytoplasm between the nucleus and the granules. These cells break down to produce an apocrine secretion that probably contributes to the acidophilic secretion

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Figs. 4, 5. Photomicrographs of oblique sections of the seminal vesicle and the accessory gland in the adult of *Dorylus wilverthi.* ×450. 4. The seminal vesicle, showing the groups of alternating high and low epithelial cells. 5. The accessory gland, showing the variations in the staining reactions of the cytoplasm of the epithelial cells. Arrow points to muscle fibers attached to the bases of epithelial cells. BM, basement membrane; H, hyaline layer; MC, muscle coat; Se, secretion in lumen; Ss, surface secretion.

in the center of the lumen of these glands. The surfaces of some cells are ruptured, and the cell contents produce the fine-granular and the globular, basophilic secretions found just outside the cells. A well-developed, muscle coat of 8 to 12 obliquely arranged fibers lies outside the epithelium. Muscle fibers extend into the epithelial folds, and, in regions around the wall, the muscle fibers terminate in the basal cytoplasm of the epithelial cells.

Toward the lower ends of the accessory glands, close to where the seminal vesicles enter, the oblique folds of the epithelium become longitudinal in direction, and these are located dorsolaterally and ventromedially. Over the surface of the folds, the cells are exceptionally tall, and, between the folds, the cells are reduced in height to become cuboidal. In this region, the cytoplasm is acidophilic in reaction, less so in the subnuclear region of the cells. A very fine-granular, acidophilic secretion along the surface of these cells contributes to a fine-granular, but weakly staining, acidophilic secretion in the lumen of the ducts.

The median walls of the terminal portions of the accessory glands come together, the muscle fibers of these median surfaces fuse, and some of the outer fibers encircle these terminal portions to form a continuous layer. From here to the end of the system, macroscopically, there appears to be a single tube. However, histological sections of this single duct in its proximal region show two lumina; this region is the bound accessory gland duct.

The overall arrangement and appearance of the tissues in the accessory glands of the *nigricans* adult and pupa and the *wilverthi* pupa are similar to and resemble those of the *wilverthi* adult. In the pupal stage of these ants, fewer regions of the epithelium are breaking down, and there is a scattered, basophilic granular secretion in the lumen. In the *nigricans* pupa an acidophilic, granular secretion is present, also. In the *nigricans* adult small clusters of spermatozoa were seen in the lumen of these glands but only at the anterior ends.

Bound accessory gland duct. This is a short duct, and in the *wilverthi* adult the epithelium, lining the lumina, varies from low to tall columnar cells built on a basement membrane. The ventral halves of the lumina are lined with tall columnar cells that are taller on the median and lateral walls. The upper halves are lined with cells that are lower in height, and there is a middordsal fold in each lumen. The nuclei are basally located in all the epithelial cells. The subnuclear cytoplasm is dense and basophilic in staining. In the midregion of the cells. the cytoplasm is condensed into strands, and many large vacuoles containing basophilic granules lie between these strands. In the

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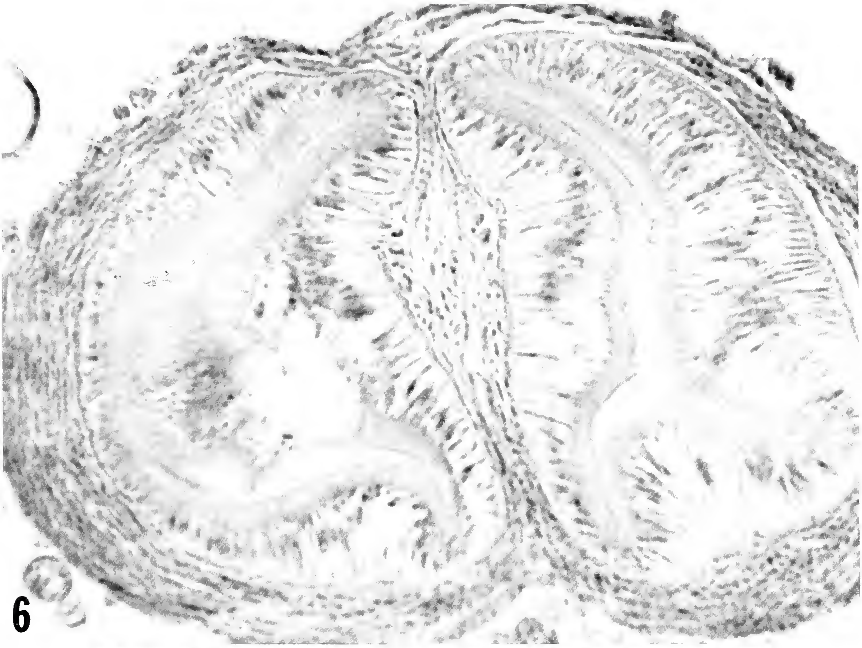
Figs. 6, 7. 6. Photomicrograph of a cross section of the bound accessory gland duct in the pupa of *Dorylus nigricans.* ×140. 7. Photomicrograph of a cross section through the anterior end of the ejaculatory duct in the adult of *Dorylus wilverthi.* ×140. Se, secretion in lumen.



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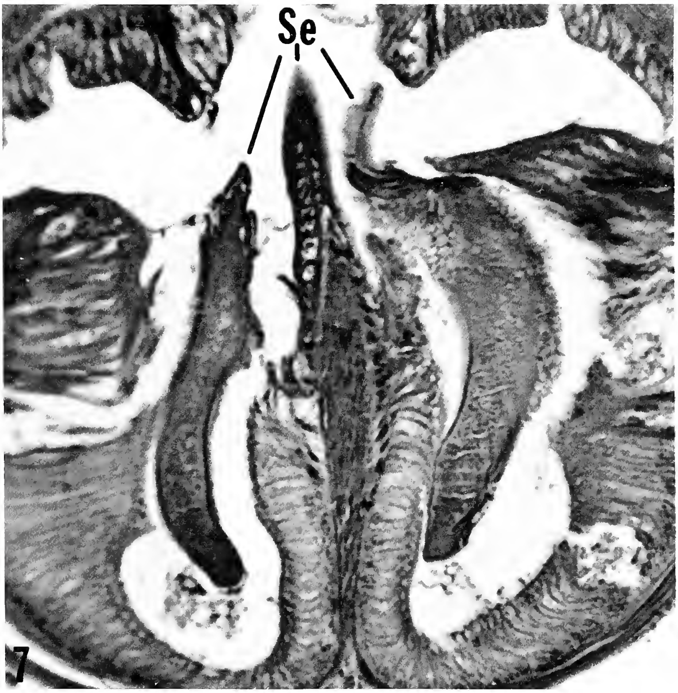

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ventral halves of the lumina there are large, compact, amorphous, acidophilic-staining secretions, which are covered dorsally with a basophilic, mucus-like layer. Scattered in the lumina, there is also a small amount of basophilic granular material. The muscle coat consists of an inner longitudinal and an outer circular or obliquely arranged layer of fibers. The inner longitudinal fibers are confined to the middorsal, the lateral, and the ventral walls. Middorsally, this muscle coat is about a dozen fibers in thickness, whereas on the lateral and ventral walls it is only a few fibers in thickness. In the median wall the muscle coat is circular and heavier in its midregion. As the bound accessory gland duct proceeds posteriorly, the median wall becomes thinner and disappears; first the dorsal half, then the remainder. The lumina now communicate with each other, and thus begins the ejaculatory duct (Fig. 7).

In the *nigricans* adult the bound accessory gland duct is similar in its organization to that of the *wilverthi* adult. In the pupae of *wilverthi* and *nigricans,* the epithelial cells are much taller, and only very small lumina are present (Fig. 6). A basement membrane is present beneath the epithelium. The ellipsoidal-shaped nuclei are centrally located in most of these cells. The subnuclear cytoplasm is compact and acidophilic in staining. The perinuclear cytoplasm in many cells is straplike and separated from that of the adjoining cells. The cytoplasm toward the surface of the cells is compact and distinctly acidophilic. The muscle coat is similar to that of the adult.

Ejaculatory duct and wedge (Figs. 1 and 7–14). The epithelium of the ejaculatory duct continues as simple columnar. The cells on the lateral and ventrolateral walls are very tall. On the dorsal wall the epithelium on either side of the midregion is elevated into a lateral fold. The cytoplasm of the cells on the dorsolateral and lateral walls is vacuolated. The acidophilic secretion in the lumen does not have the dorsal mucus covering. The underlying muscle coat consists of a number of circular and longitudinally arranged fibers. Longitudinally arranged fibers are clustered inside the circular layer under the epithelium of the dorsolateral folds and on the ventrolateral walls. The number of longitudinal muscle fibers under the dorsolateral folds increases, the folds become higher, and their median walls touch.

A very thin, cuticular layer now covers the lateral and ventrolateral folds (Fig. 8). This layer, thicker on the median surfaces of the ventrolateral folds, is the beginning of the lateral arms of the cuticular wedge. The ventrolateral

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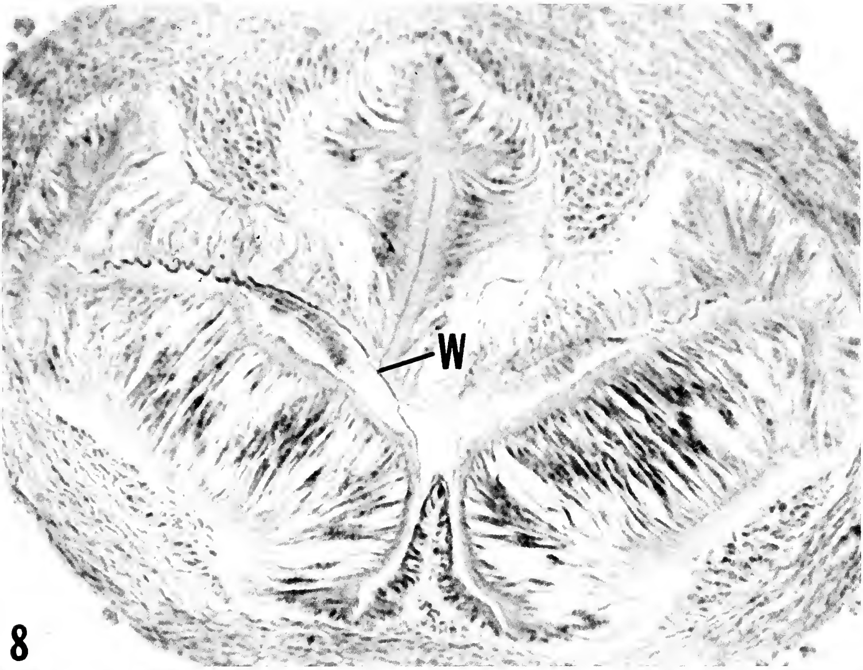
Figs. 8, 9. Photomicrographs of cross sections of the ejaculatory duct and wedge in *Dorylus.* ×140. 8. Section through the anterior arms of the wedge (W) covering the ventrolateral folds in the pupa of *D. nigricans.* 9. Section through the lower half of the duct showing the ventral ridges of the wedge (VR) in the adult of *D. wilverthi.* Se, secretion in lumen.



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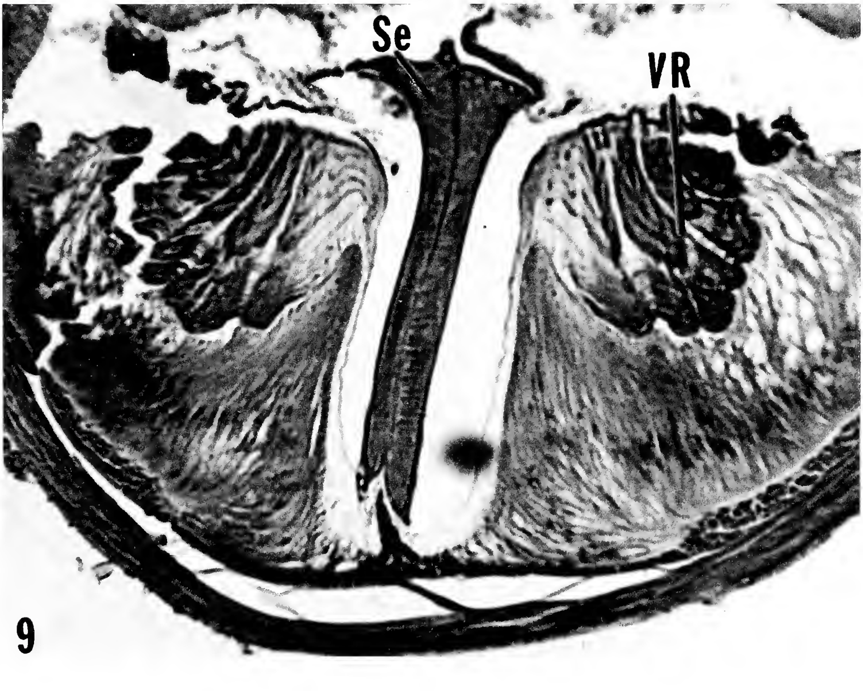

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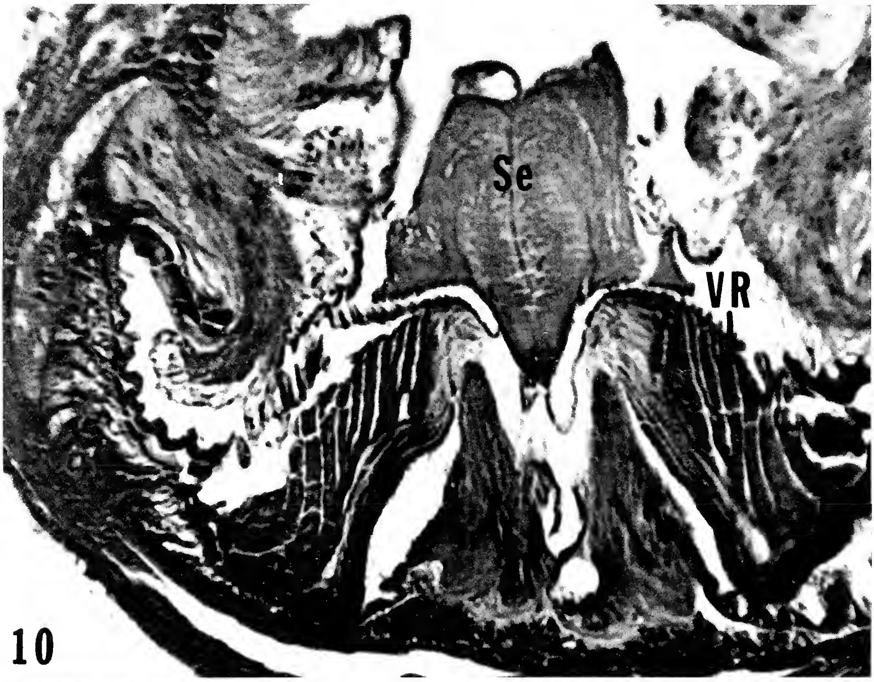

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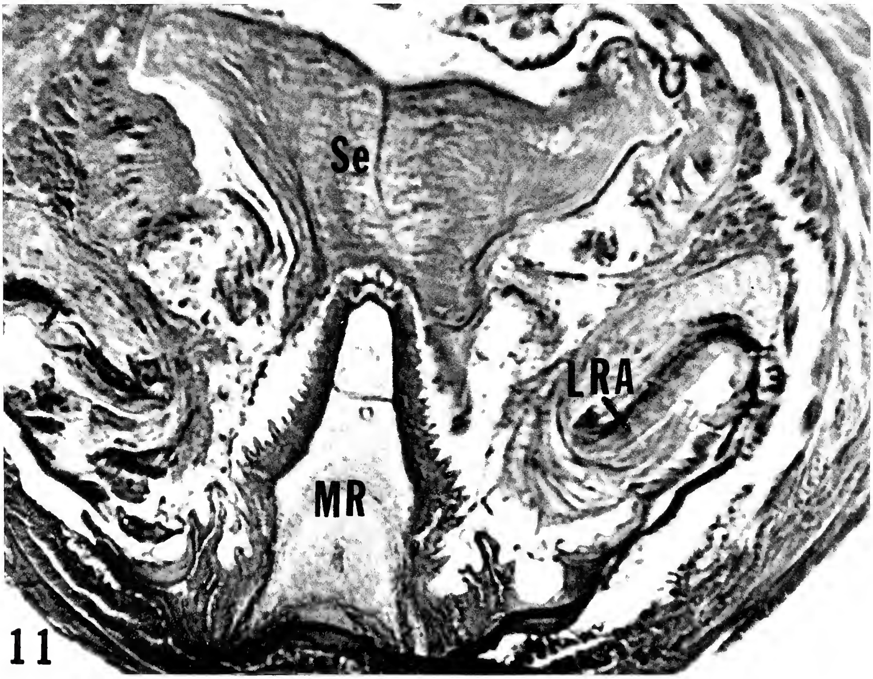

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folds increase in height, and the cuticular covering gets thicker on its underside and projects deeply into the epithelium of these folds (Fig. 9). These cuticular thickenings on the lateral arms of the wedge are set down in wavy horizontal layers that are basophilic in staining reaction. A thin surface layer on the arms of the wedge extends more laterally and is strongly acidophilic. The clear, cuticular covering of the median surfaces of the ventrolateral folds joins medially and forms a midventral groove (Fig. 9). A little further back the ventral ridges of the lateral arms of the wedge are directed medially and the epithelium on the inner sides of these ridges is displaced medially to form ventral epithelial folds. The midventral groove is elevated, and the arms of the wedge extend dorsally along the lateral walls of the duct and reflect medially on themselves. This surface layer is longitudinally ridged. At this level the epithelial cells on the lateral folds increase in height and bend downward under the reflected lateral arms of the wedge (Fig. 10). The epithelium on the dorsal and dorsolateral walls becomes lower. The secretion is still present in the lumen. The ventral epithelial folds disappear, the ventral ridges of the lateral arms diminish in height, and the elevated midventral groove extends upward to become a median ridge of the wedge (Fig. 11). This median ridge is covered with a thick, longitudinally ridged basophilic-staining layer. The cuticular material within this median ridge is less dense than the surface layer and does not fill the elevation; its tip is hollow. The middle portion of the median ridge is reduced to a small ridge. The epithelium beneath the ridge is low columnar and contains basophilic granules. Under the lateral arms of the wedge the epithelium is flattened. The wedge at this level is a ridged plate with its lateral arms reflected and tapering medially (Fig. 12). The remnant of the median ridge elevates slightly again, but soon disappears. The lateral reflected arms of the ridge are reduced and disappear. The surface of the wedge becomes smoother, tapers to a U-shaped trough, which gradually ends on the floor of the ejaculatory duct (Fig. 13). The epithelium on the dorsal and dorsolateral walls decreases in height, and the distinctly acidophilic cytoplasm along the surface of these cells is condensed. The amount of secretion in the lumen increases. The muscle coat consists of some dorsolateral and ventrolateral longitudinal fibers, which are surrounded by a heavy band of circular fibers. The ejaculatory duct extends a short distance beyond the end of the wedge and lies on the roof of the aedeagal bladder. Here the cells on the dorslateral, lateral, and ventral walls

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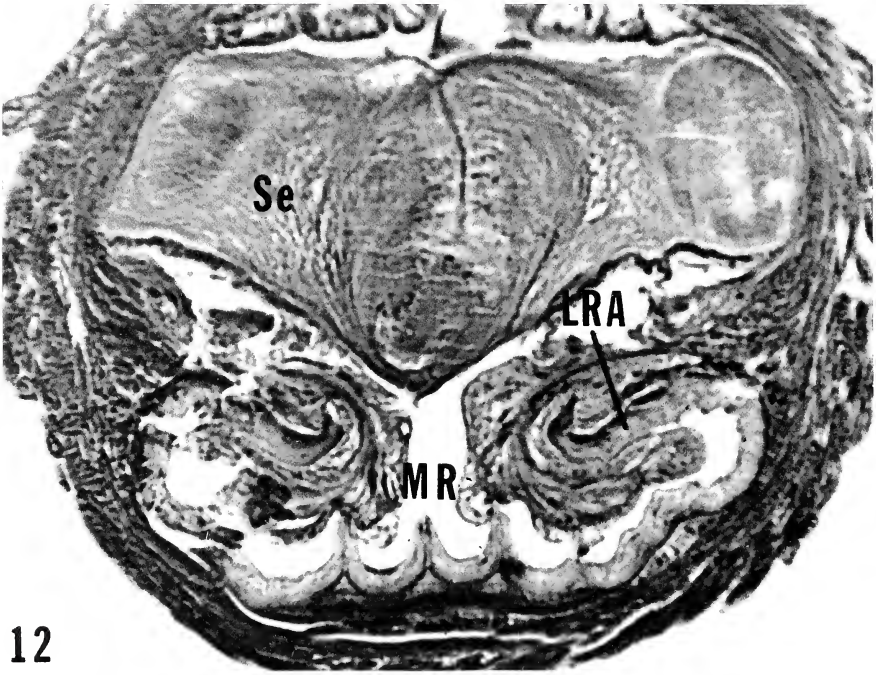
Figs. 10, 11. Photomicrographs of the lower part of cross sections through the ejaculatory duct and wedge in the adult of *Dorylus wilverthi.* ×140. 10. Shows the converging ventral ridges (VR) of the wedge. 11. Shows the median ridge of the wedge (MR) and the lateral reflected arms (LRA). Se, secretion in lumen.



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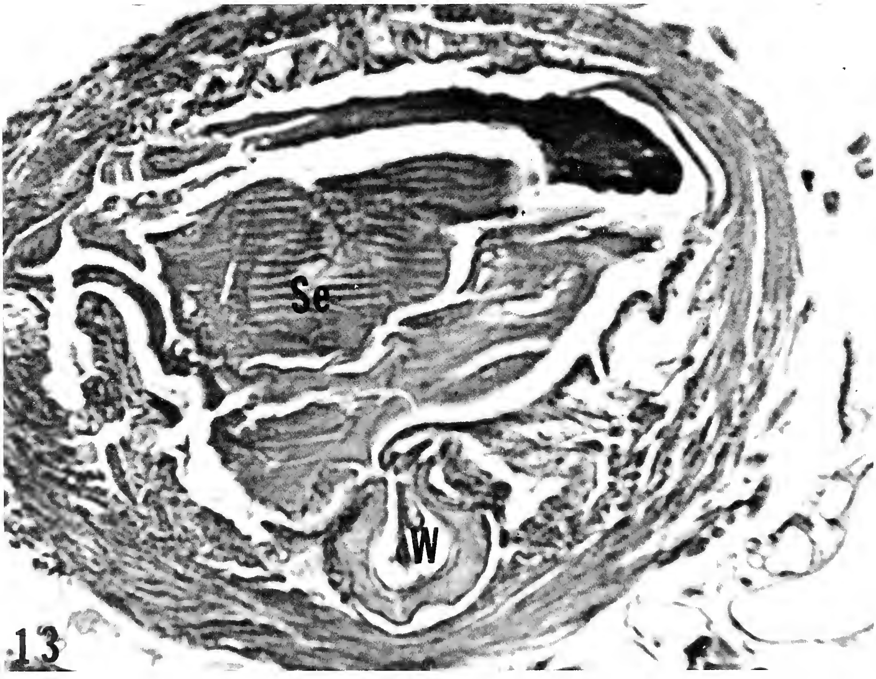

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of the ejaculatory duct are reduced to flattened squamous, and the cells on the ventral wall are covered with a thin cuticular intima. This ventral wall becomes folded, and the folds deepen when they contact folds on the dorsal wall of the aedeagal bladder. These deep folds break through, and the ventral wall of the ejaculatory duct quickly disappears (Fig. 14). The cuticular intima now covers the remaining epithelium of the ejaculatory duct, and this layer thickens. The duct decreases in height. Folds on the dorsal wall of the aedeagal bladder extend upward on either side of the ejaculatory duct and invade its circular muscle coat. The enclosed lateral walls of the ejaculatory duct disappear, and the roof of the ejaculatory duct continues for a short distance as the middorsal wall of the aedeagal bladder. Outside the epithelium, the visceral muscle fibers of the outer muscle coat of the ejaculatory duct continue for some distance along the dorsolateral walls of the aedeagal bladder, but the heavy, oblique, body wall muscle fibers of the dorsal wall of the aedeagal bladder move in from either side.

A cluster of unicellular gland cells is found at the posterior end of the ejaculatory duct. These cells are situated both outside and within the longitudinal muscle layer of the roof of the ejaculatory duct. The gland cells are large, spherical, and ellipsoidal in shape. The nucleus of each gland cell is vesicular, and the cytoplasm contains a granular, basophilic-staining secretion. These gland cells become smaller in size posteriorly. Minute ductules emerge from these gland cells and extend tortuously through the thick cuticle at the end of the ejaculatory duct. A large number of ductules is visible in some sections; this indicates numerous gland cells (Fig. 15).

In the *nigricans* adult, the histological organization of the anterior end of the ejaculatory duct is similar to that of *wilverthi.* Unfortunately, the tissue of the remaining portion of this system in the *nigricans* adult specimens was too brittle to be sectioned.

At the anterior end of the ejaculatory duct in the pupae of *wilverthi* and *nigricans,* the epithelium is all columnar and arranged into two dorsomedian folds and two ventrolateral folds. The cells over the dorsolateral folds are moderate in height, those over the ventrolateral folds are very tall, while those midventrally are the lowest. The nuclei of these cells are centrally located, and the cytoplasm along the free borders is condensed and more acidophilic in staining reaction than that of the remainder of the cell. A basement membrane is present under the epithelium, but beneath the epi-

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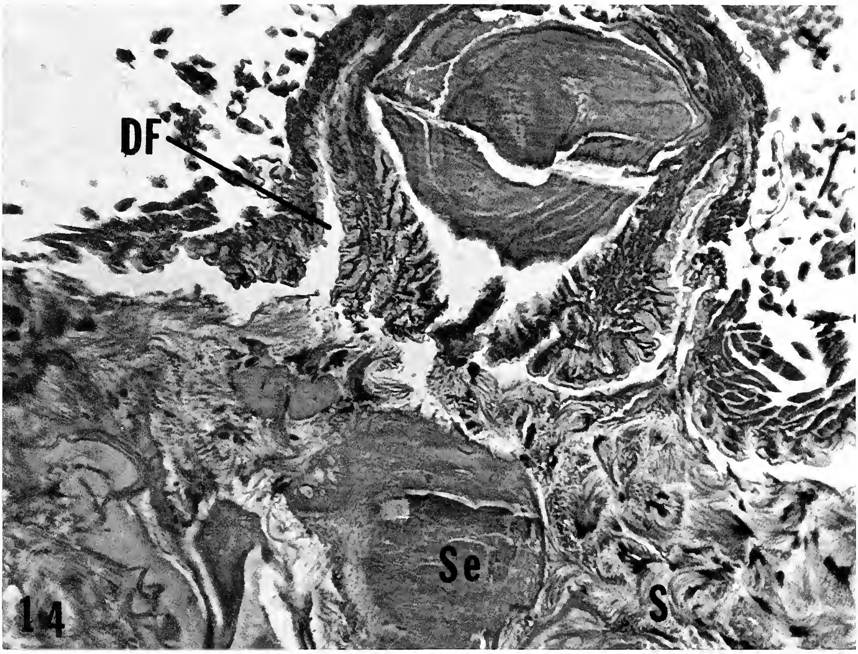
Figs. 12, 13. Photomicrographs of cross sections through the ejaculatory duct and wedge in the adult of *Dorylus wilverthi.* ×140. 12. The median ridge of the wedge (MR) has decreased in height. 13. The posterior tip of the wedge (W) is U-shaped. LRA, lateral reflected arms of the wedge; Se, secretion in lumen.


DF
Se
S
14

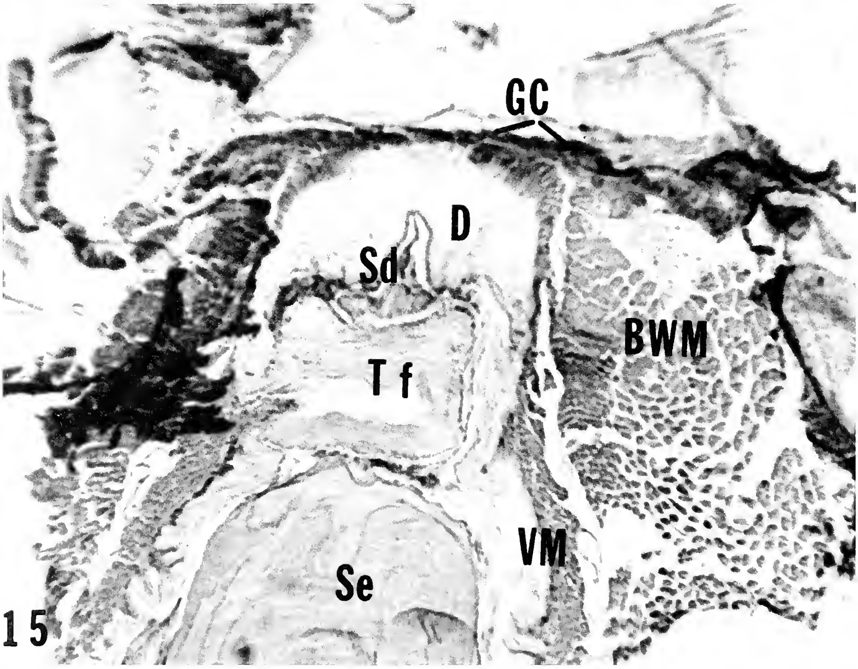

GC
D
Sd
BWM
Tf
VM
Se
15

Fig. 16. Photomicrograph of a cross section through the dorsal duct in the adult of *Dorylus wilverthi.* ×140. This section is a short distance beyond that in the previous figure and is cut through the anterior ends of the inner genitalic valves. The left side of the photomicrograph shows the wall of the dorsal duct fusing with the wall of the inner genitalic valve (InV).

thelium of the ventrolateral folds it is a distinct hyaline layer. The lumen is reduced to thin spaces between the folds of these cells. Throughout the remainder of the duct and including the wedge, the organization of the tissues is similar to that of the adult *wilverthi,* but the cells are taller. There is no secretion in the lumen of this duct in either pupa.

Aedeagal bladder (Figs. 14–16). The aedeagal bladder has a thick, tightly folded, cuticular lining, and the nuclei of the flattened epithelial cells lie between the folds of the cuticle. At the anterior end, the intima on the dorsal wall is thinner and less folded. In cross section this organ is shallowly V-shaped with the point of the V directed ventrad. An acidophilic-staining

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Figs. 14, 15. 14. Photomicrograph of a cross section through the opening of the ejaculatory duct into the aedeagal bladder in the adult of *Dorylus wilverthi.* ×70. DF, dorsal fold of the aedeagal bladder; S, bundles of sperm; Se, secretion in the bladder. 15. Photomicrograph of a cross section through the posterior part of the aedeagal bladder in the adult of *Dorylus wilverthi* showing the formation of a transverse cuticular fold (Tf) from the dorsolateral wall. This transverse fold forms a new duct, the dorsal duct, in the upper part of the aedeagal bladder. ×70. BWM, body wall muscles; D, gland ductules from the gland cells, GC; Sd, secretion in dorsal duct; Se, secretion in aedeagal bladder; VM, visceral muscle.

secretion, similar to that found in the accessory glands and ejaculatory duct, and bundles of spermatozoa fill the lumen, but the sperm and the secretion are not mixed (Fig. 14). In some of the lower portions of the lumen, layers of a basophilic secretion are interspersed with the acidophilic secretion. The muscle fibers covering the epithelium of the aedeagal bladder are similar in diameter to the body wall muscles, and these muscle fibers are generally oblique in direction. The outermost fibers of the muscle coat lie very close to the muscles of the external genitalia and insert on the anterior ends of the genitalic valves. When the valves of the genitalia are removed, the outer muscle fibers of the aedeagal bladder are disrupted.

Where the ejaculatory duct lies on the roof of the aedeagal bladder, dorsal folds extend upward on either side of the ejaculatory duct. Shortly thereafter the ejaculatory duct opens into the aedeagal bladder. The bladder then tapers posteriorly. At this posterior end of the aedeagal bladder, the cuticle thickens on the dorsal and dorsolateral walls, and a heavy transverse fold is formed from the right dorsolateral region (Fig. 15). This fold almost completely cuts off the dorsal region of the aedeagal bladder, but a small channel is still present on the left side, which connects the dorsal lumen with the remainder of the aedeagal bladder. More posteriorly a new lateral channel is formed on the right side of this fold. This results in a block of cuticular material between the dorsal lumen and the ventral bladder. The cuticular block soon expands laterally, closes the lateral channels, and completely separates the dorsal duct from the remainder of the aedeagal bladder. Muscle from the lateral walls of the aedeagal bladder now covers the ventral wall of the new dorsal duct. The ventral remaining aedeagal bladder becomes smaller in diameter and continues for a short distance as a blind pouch, still filled with a strongly acidophilic-staining secretion and bundles of spermatozoa.

At the posterior end of the aedeagal bladder, numerous unicellular gland cells, similar to those at the end of the ejaculatory duct, are found on the dorsal walls. Ductules from these gland cells extend through the thick, dorsal, cuticular wall of the dorsal duct. These gland cells may contribute to the secretion that is found in the lumen. The lumen of this dorsal duct is more or less triangular in shape with the base downward (Fig. 15), but it soon changes and becomes cruciform (Fig. 16). At this level the gland cells are on the lateral regions of the duct. This dorsal duct lies immediately under the spathe of the inner valves. More posteriorly, the heavily sclerotized plates of the anterior ends of the inner valves are present on either side of the duct, and the walls of the dorsal duct fuse with the median walls of the inner valves.

In the pupae of *wilverthi* and *nigricans* the histology of the aedeagal bladder is similar to that of the adult of *wilverthi.* However, there are neither spermatozoa nor secretion in the aedeagal bladder, so that the lumen is not distended, and the walls are more wrinkled. Also, the entrance of the ejaculatory duct into the aedeagal bladder is similar to that of the adult *wilverthi.*

DISCUSSION

While the histology of the internal male reproductive organs in the two African dorylines, *Dorylus wilverthi* and *nigricans,* agrees with that of some of the organs of two other dorylines similarly investigated, the Old World *Aenictus gracilis* (Shyamalanath and Forbes, 1983) and the New World *Neivamyrmex harrisi* (Forbes and Do-Van-Quy, 1965), significant differences do occur in other organs.

The thin walls of the testicular follicles in the adults of both *D. wilverthi* and *A. gracilis* are composed of two cell layers, and the arrangement of the sperm in the lumina is the same. The testes in *N. harrisi* were apparently undergoing degenerative changes; the walls of the follicles had only a single layer of cells, the follicles were filled with granules, and no sperm were present.

Recently Gotwald and Burdette (1981) investigated the male internal reproductive system for representative species of army ants. Most of their specimens were adults, but a few pupae were included in the New and Old World genera. They found functional testes in the pupae, but in most of the adults the testes had atrophied so that there was little evidence of their existence. Prominent testes were found in earlier dissections of adults of *Eciton hamatum* (Forbes, 1958). In this study, testes were not found in the adult of *D. nigricans,* but the histological sections revealed a few masses of spermatozoa surrounded by tracheae in the gaster. Sections of the testes in pupae show that only these organs are packed with sperm. In the pupa of *A. gracilis,* the sperm are contained in a large, central vacuole within each follicular cell. The number of testicular follicles in the pupae examined by Gotwald and Burdette were not determined. This number is important, because, from the papers previously cited and one on the male anatomy of *Dorylus wilverthi* and *nigricans* (Ford and Forbes, 1980), New World species have significantly fewer follicles than do Old World ones. The testes of the *Dorylus* species have no visible capsule, whereas a common capsule covers the testes in *A. gracilis* and *N. harrisi.* Each testis has its own capsule in *Eciton hamatum.*

The histology of the vasa efferentia and that of the vasa deferentia in the doryline adults reported is similar, and scattered sperm are present in the lumina. In the pupae, the epithlium is slightly taller and the lumina are more constricted in each of these organs, and no sperm are present.

The seminal vesicles have a distinctive histology in both the adult and the pupal stages that is different from that of the vasa deferentia regardless of whether sperm is present as it is in the adults or absent as in the pupae. Our findings, contrary to those of Gotwald and Burdette (1981), show that no sperm is stored in the seminal vesicles during the pupal stage. The epithelial cells of this organ are larger and taller than those in the vas deferens, and they are built on a distinct basement membrane. The two *Dorylus* species described have the nuclei of the epithelial cells centrally located, the cytoplasm is variable in its staining reaction from base to free surface, and the secretion in the lumen is both acidophilic and basophilic; this arrangement seems to be unique. Figure 14 of the Gotwald and Burdette (1981) paper, a high power photomicrograph of the wall of the seminal vesicle of a species of the subgenus *Anomma,* appears similar in many details to Figure 4 of this paper: The position of the nuclei of the epithelial cells is the same, and the cytoplasm appears variable in staining reaction but not as granular as it is in *wilverthi* and *nigricans.* In *N. harrisi* [the organ labelled *vas deferens* in Forbes and Do-Van-Quy (1965) has been correctly designed *seminal vesicle* by Hung and Vinson (1975)] and in *A. gracilis,* the nuclei in the epithelium are basally located and have their long axes parallel to the basement membrane. In the pupa of *A. gracilis,* the tall columnar cells almost occlude the lumen of this organ, and the cytoplasm is basophilic.

The accessory glands of the Old World *dorylines* are shorter than those of the New World species, and they are not coiled. The epithelium of these glands in *D. wilverthi, nigricans* and *A. gracilis,* which consists of low to tall columnar cells, is folded the length of the glands and produces both acidophilic and basophilic granular and globular secretions. The staining reactions in these cells are more variable in *Dorylus* than in *Aenictus,* but the acidophilic secretion in these glands is produced by an apocrine type of secretion in the species of both genera. The cells that produce the acidophilic secretion in the *Dorylus* species are scattered throughout the epithelium, whereas in *Aenictus* these cells are clustered. Within the epithelial folds in the *Dorylus* species, muscle fibers join directly to the bases of the epithelial cells. In the *Dorylus* specimens of the subgenera *Rhogmus* and *Anomma* examined by Gotwald and Burdette (1981), the lumina of these glands were empty of secretion, but some spermatozoa were present in limited areas in the lumen of these glands in *Rhogmus.* We found in *D. nigricans* small bundles of sperm in the lumen of these glands only at the anterior ends. In *N. harrisi,* the epithelium of this organ is similar to that of the Old World dorylines, but it is not folded. The cytoplasm of these cells is filled with fine, basophilic-staining granules, and the lumen contains a dense, homogeneous, basophilic secretion that is sometimes coiled and convoluted within the lumen. In the pupa of *A. gracilis,* the epithelium is more folded than that in the adult, these folds almost occlude the lumen, and some neutral-staining secretion is present in the lumen.

In the accessory gland ducts and in the bound accessory gland duct, epithelial folds are present, but the number and position of these folds differ. The cells over the folds are usually taller than those between the folds.

Along the lumina of the ejaculatory duct in the various male ants studied, the epithelial folds undergo changes, and the lateral arms of the wedge are developed on lateral or ventrolateral folds. The lateral arms of the wedges in *D. wilverthi* and *A. gracilis* arise similarly, but the thickening of the arms in each is accomplished differently. In both *wilverthi* and *gracilis* a prominent median ridge is formed on the base of the wedge, i.e., where the arms unite. The formation and appearance of the wedge in *N. harrisi* is different from that of the Old World dorylines. The cross-sectional configurations of the wedges are different in the species of the three genera compared. Throughout the ejaculatory duct and above the wedge in *D. wilverthi* there is a considerable amount of secretion, while in *A. gracilis* and *N. harrisi* no secretion is present. In the pupae of *D. wilverthi, nigricans,* and *A. gracilis,* the cells along the ejaculatory ducts are taller, the arrangement of the folds is different from that in the adults, and no secretion is present in the lumen. The ejaculatory duct in *N. harrisi* and in *A. gracilis* opens directly through the roof of the aedeagal bladder at its posterior region, but in the *Dorylus* species the end of the ejaculatory duct is accompanied by folds from the roof of the aedeagal bladder, which envelop it.

Unicellular glands, similar to those found at the posterior end of the ejaculatory duct and at the posterior end of the aedeagal bladder in the *Dorylus* species, were found at the posterior end of the ejaculatory duct in *N. harrisi.* No glands were seen in these regions in *A. gracilis.*

The aedeagal bladder, present in the dorylines, has the same histological organization in all those studied, and it opens between the inner genitalic valves. Gotwald and Burdette (1981) did not mention nor figure this organ in any of the New or Old World army ants they investigated. Of the dorylines histologically examined so far, it is only in the *Dorylus* species herein reported that the posterior part of the aedeagal bladder is divided by a transverse cuticular fold to form a new dorsal duct, that opens between the inner genitalic valves. No sperm was present in the aedeagal bladder of *N. harrisi* or *A. gracilis,* but bundles of spermatozoa and an acidophilic secretion filled this organ in the adult of *D. wilverthi,* and layers of a basophilic secretion were interspersed with the acidophilic in the deeper parts. This organ may be used to store sperm in the adults nearly ready for the nuptial flight.

More doryline male internal reproductive organs will have to be examined histologically to determine if there are further important generic or subgeneric differences within this group. This study of the male organs in *Dorylus* (*Anomma*) *wilverthi* and *nigricans* and comparisons with the other two dorylines similarly reported have shown that the seminal vesicles are distinct organs in both the pupal and the adult stages. These organs in species of the subgenus *Anomma* are more complex than those in *Aenictus gracilis* and in the New World *Neivamyrmex harrisi* in that they produce both acidophilic and basophilic secretions. The accessory glands of the Old World species also produce acidophilic and basophilic secretions, while those of *N. harrisi* produce only a dense, homogeneous, basophilic secretion. The cuticular wedges in the ejaculatory ducts arise in similar fashion but are developed somewhat differently in the three genera. The entrance of the ejaculatory duct into the aedeagal bladder and the formation of a new dorsal duct at the posterior end of the bladder in *D. wilverthi* and *nigricans* are different from those in other dorylines.

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ANATOMY AND HISTOLOGY OF THE MALE REPRODUCTIVE SYSTEM IN THE ADULT AND PUPA OF THE DORYLINE ANT, *AENICTUS GRACILIS* EMERY (HYMENOPTERA: FORMICIDAE)

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Abstract.—This paper presents the anatomy and histology of the reproductive system, the external genitalia, and the terminal gastric sterna in the male adult and advanced-stage pupa of the Old World doryline ant, *Aenictus gracilis.* The male reproductive system consists of the testes, the vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the short bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia. The testes are enclosed in a thin common capsule, and each testis is composed of about 32 follicles. The epithelium of the testicular follicle in the adult consiss of a basal and an inner layer of cells around a central lumen, which contains scattered or clustered spermatozoa. In the pupa, the epithelium is composed of irregularly-shaped cells, each with a large central vacuole filled with spermatozoa. The seminal vesicles are U-shaped in the adult and pupa. The epithelial cells in the pupa are taller than those in the adult. In the adult, spermatozoa were present throughout, but in the pupa, sperm were absent throughout. The accessory glands are tubular and bent around the proximal region of the intestine. The epithelium is more folded in the pupa than in the adult. In the adult, some regions contain an acidophilic secretion, some basophilic, and some both. In the ejaculatory duct, a cuticular wedge is present on the lateral and ventral walls; this wedge is more complex in its structure in the adult. The duct enters the dorsal, posterior surface of the aedeagal bladder. The epithelium of the bladder consists of small cells covered by a thick, wrinkled intima. The muscle fibers that surround the bladder are larger in diameter than the visceral muscles of the ejaculatory duct. The lumen of the bladder is devoid of secretion. The basal ring of the genitalia, the three pairs of valves, and the eighth and ninth sterna are described. They are quite different in shape from those of the New World dorylines, *Eciton hamatum* and *Neivamyrmex harrisi,* but in some respects resemble those of the Old World dorylines, *Dorylus wilverthi* and *nigricans.* Comparisons made with previously described Old and New World species have revealed structures and features that lend support to the concept of the triphyletic origin of the dorylines.

A review of the studies on the male reproductive system in ants was made by Forbes (1954), and further information has been added by Hung and Vinson (1975). The study of the male reproductive system in doryline ants was pioneered by Mukerjee (1926), who described the anatomy of this system in the Old World *Dorylus labiatus.* Descriptions of the anatomy and histology of this system that followed are those of *Eciton hamatum* (Forbes, 1958), *Neivamyrmex harrisi* (Forbes and Do-Van-Quy, 1965), *Dorylus wilverthi*

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and *D. nigricans* (Ford and Forbes, 1980, 1983). The morphology of the male internal reproductive system for representative species of Old and New World army ants has been described by Gotwald and Burdette (1981) to interpret phylogenetic implications of this morphology. After Clausen's work (1938), the genitalic valves have been studied in detail and used as the basis for the classification of ants even to the subspecies level (Forbes, 1952; Borgmeier, 1955; Krafchick, 1959).

This is the first anatomical and histological description of the reproductive system of the male adult and advanced-stage pupa of the Old World doryline *Aenictus gracilis.* Comparisons are made with an African *Aenictus* sp. (Gotwald and Burdette, 1981) and with other dorylines previously described.

The specimens and methods used in this study were those reported in the description of the male digestive system of this ant (Shyamalanath and Forbes, 1980).

OBSERVATIONS AND DISCUSSION

Anatomy of the reproductive system. This system in the male adult and pupa consists of the testes, the vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the short bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia (Fig. 1).

The testes are enclosed within a very thin, common testicular capsule and lie in a concavity on the dorsal, posterior half of the ventriculus from the middle of the 4th to the end of the 5th abdominal segments. Each testis is composed of about 32 slender follicles, which are longer in the pupa than in the adult. The tubules of each testis form a compact mass, and their anterior ends converge medially. The posterior end of each follicle leads into a short narrow duct, the vas efferens. The vasa efferentia of each testis unite to form the short, wider vas deferens. The distal end of the vas deferens is slightly constricted where it leads into a dilated, elongated, U-shaped tube, the seminal vesicle, situated along the outer margin of the testis. The first part of the seminal vesicle is convoluted only in the adult and lies beneath the posterior region of the testis. The proximal arm of the seminal vesicle lies beneath the distal one, and both arms are covered with the testicular capsule. The distal arm of the seminal vesicle continues backward, emerges from the capsule, and opens into the accessory gland at about the middle of its lateral margin. The seminal vesicle in the pupa is narrower than that in the adult. The tubular-shaped accessory glands are bent around the proximal region of the intestine and unite beneath it to form a short bound accessory gland duct that continues into the ejaculatory duct with the wedge. The ejaculatory duct opens into the dorsal surface of a thick-walled aedeagal bladder situated beneath the bound accessory gland duct and the ejaculatory

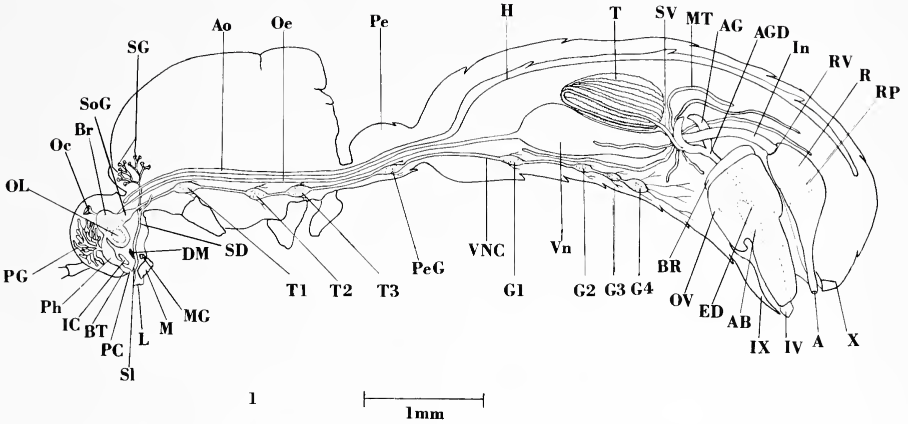

Fig. 1. Diagram of a lateral dissection of the adult male of *A. gracilis.* (From the original of Fig. 1, S. Shyamalanath and J. Forbes, J. New York Entomol. Soc. 88:18.)

duct. The posterior region of the aedeagal bladder lies between the median walls of the inner genitalic valves and opens to the outside near the ends of these valves. The aedaegal bladder in the pupa is larger and has a more spacious lumen than that in the adult.

The anatomy of the reproduction system of *A. gracilis* bears a close resemblance to that of an African *Aenictus* sp. (Gotwald and Burdette, 1981), except that the testes were absent in the adult of the African species; these authors also reported that testes were absent in the adults of some species of the subfamilies Ecitoninae and Dorylinae. The reduction in the length of the testicular follicles in the adult of *A. gracilis* from the length of the follicles in the pupa could be indicative of the shrinking and eventual total atrophy. *A. gracilis* with about 32 testicular follicles resembles the Old World dorylines that have comparatively more follicles, 35–40 in the adult and pupa of *Dorylus wilverthi,* 50–55 in the pupa of *D. nigricans* (Ford and Forbes, 1980), and a fair number in *D. labiatus* (Mukerjee, 1926). The New World *Eciton hamatum* has 20 follicles (Forbes, 1958) and *Neivamyrmex harrisi* 22–25 (Forbes and Do-Van-Quy, 1965). The common capsule surrounding the testes of *A. gracilis* is similar to that in *N. harrisi,* but no capsule covers the testes of *D. wilverthi, nigricans,* or *labiatus.* In general arrangement the seminal vesicles resemble those of the other dorylines. However, structures comparable to the collecting sac at the anterior end of the seminal duct and the dilated vesicula seminalis at the posterior end, reported to be present in *D. labiatus,* are not present in *A. gracilis.* The accessory glands of *A. gracilis* and the African *Aenictus* sp. are short, curved glands, which resemble those of *D. labiatus* in shape. These glands in *D. wilverthi* and *nigricans* are thick walled, S-shaped tubes and in *E. hamatum* and *N. harrisi* are tightly coiled tubes situated on either side of the intestine. The bound accessory gland duct is short and straight in the Old World dorylines, while in the New World dorylines it is much longer and in *E. hamatum* it encircles the ventriculus 5 or 6 times. The ejaculatory duct in all the dorylines examined opens into the dorsal, posterior end of the aedaegal bladder. The blind diverticulum found on the dorsal side of this duct by Mukerjee (1926) in a male of *D. labiatus* has not been seen in any other doryline examined or reported. The aedeagal bladder found in *A. gracilis* is present in *D. wilverthi* and *nigricans,* in *E. hamatum* and *N. harrisi.* It was not reported in *D. labiatus* nor in any of the army ants investigated by Gotwald and Burdette (1981).

EXTERNAL GENITALIA AND TERMINAL GASTRIC STERNA

The external genitalia are composed of a basal ring and 3 pairs of valves, the outer, the middle, and the inner, all of which are sclerotized. They are retracted into the genital chamber and only the distal ends of the outer and inner valves protrude beyond the posterior margin of the gaster (Fig. 1). The basal ring or lamina annularis is ring-shaped and situated in the posterior half of the 6th abdominal segment. Its anterior margin is attached to the reflected intersegmental membranes of the 9th segment. The dorsal surface of the basal ring is the broadest, its anterior margin is heavily sclerotized, and there is a distinct median process. Behind this median process there is a thin, nonsclerotized, V-shaped region that appears as a notch (Fig. 2). The outer valves or parameres are situated dorsally and laterally behind the basal ring to which they are attached by a thin membrane. Each has a broad anterior region, the lamina parameralis, and a narrow, finger-like posterior region, the paramere. The outer surface of both these regions is convex, and there is no suture or demarcation between the two regions; both regions are uniformly sclerotized. Ventrolaterally at the base of the paramere, there is a distinct indentation (Fig. 3). The laminae paramerales lie close to each other along the middorsal line, and ventrally their anterior halves are held together by a thick, nonsclerotized membrane. The parameres are separated

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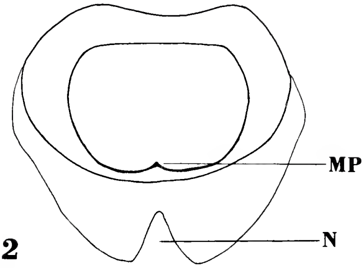
Figs. 2–7. Genitalic valves and terminal gastric sterna of the adult male of *A. gracilis.* All figures are drawn to the same scale. 2. Diagram of an anterodorsal view of the basal ring, the lamina annularis. The dorsal side is downward in this drawing. 3. Diagram of a lateral view of the right outer genitalic valve, the paramere. 4. Diagram of a lateral view of the right middle genitalic valve, the volsellaris, attached to an inner part of the lamina parameralis of the outer valve. 5. Diagram of a lateral view of the right inner genitalic valve, the lamina aedeagalis. 6. Diagram of a ventral view of the IXth abdominal sternum, the subgenital plate. Dotted lines indicate the margins of its dorsal plate. 7. Diagram of a ventral view of the VIIIth sternum.



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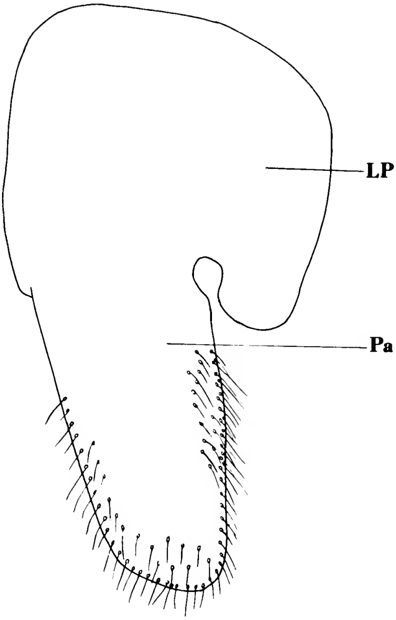

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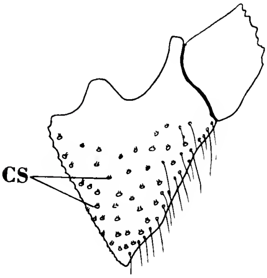

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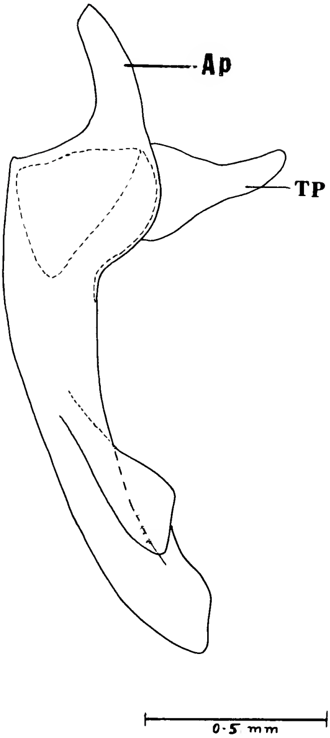

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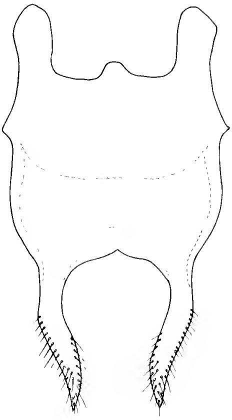

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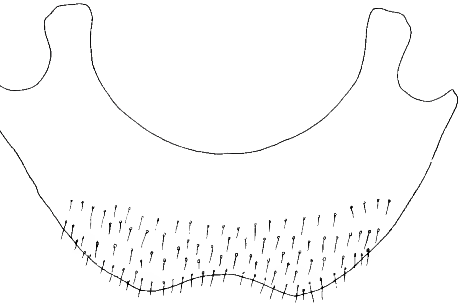

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from each other. Many sensory hairs are present along the upper and lower margins of the parameres, and some are present on their median surfaces. The middle valves or volsellares are the smallest of the valves and the most heavily sclerotized. Each is roughly quadrilateral in shape and is strongly attached along its anteroventral margin to the ventroposterior margin of the lamina parameralis (Fig. 4). It lies mediad of the paramere and is inflected upward. Campaniform sensilla are present on the posterior surfaces, and sensory hairs are only on the ventroposterior margin. The inner valves or laminae aedeagales constitute the male intromittent organ. These are moderately sclerotized, narrow, elongated valves lying close to each other. The posterior half in lateral view is bent downward. When viewed dorsally and ventrally, they are broader anteriorly and posteriorly and narrower in the midregion (Fig. 5). The dorsal and ventral inner margins of these valves are joined by thin membranes enclosing a narrow space that opens to the outside by a terminal orifice. The dorsal membrane is the spatha. Wavy flaps from the lateral margins of the posterior region fold ventrally and form a short ventral trough. The anterior ventral margins of the two valves are attached to the posterior half of the lateral sides of a triangular plate. The base of this plate is attached to the posterior margin of the membrane extending between the ventral anterior halves of the laminae paramerales. This plate is less sclerotized than the inner valves. Proximally, the aedeagus has a pair of anterodorsally directed arms, the aedeagal apodemes. These valves are devoid of sensilla or sensory hairs.

The IXth sternum or subgenital plate is located on the floor of the genital chamber. It has a broad, shield-shaped body that terminates in two widely separated processes, and this segment is heavily sclerotized (Fig. 6). The body consists of a dorsal and ventral plate fused along their lateral margins. The dorsal plate extends up to half the length of the ventral plate. The forward margin of the ventral plate has three anteriorly directed apodemes; the middle one is the shortest. Sensory hairs are found on the posterolateral regions of the body of this plate and on the terminal processes. The VIIIth sternum forms the anterior floor of the genital chamber, and it is roughly crescent-shaped (Fig. 7). The anterior margin has a pair of lateral arms, and the segment is heavily sclerotized between them. The posterior margin has a shallow notch in its midregion. Sensory hairs are present on its ventral posterior half. The external genitalia and terminal gastric sterna of the pupa are similar in all respects to those of the adult except that the component parts are less sclerotized.

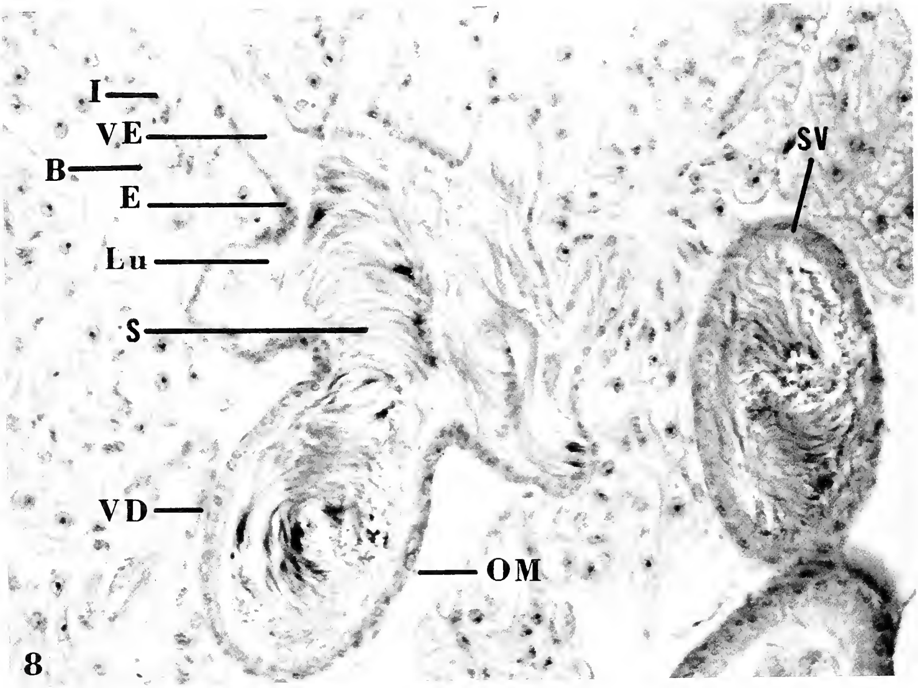
The external genitalia of *A. gracilis* conform to the doryline pattern in general organization and resemble those of the Old World dorylines, *D. wilverthi* and *nigricans* (Ford and Forbes, 1980). The shapes of the component parts are strikingly different from those of the New World dorylines, *E. hamatum* (Forbes, 1958) and *N. harrisi* (Forbes and Do-Van-Quy, 1965).

While the basal ring of *A. gracilis* resembles that of the African dorylines, *D. wilverthi* and *D. nigricans,* it has a sclerotized median process on the anterior margin of the dorsal surface and a posteriorly directed notch behind this process. The middorsal apodeme present on the ventral part of the basal ring of *D. wilverthi* and *D. nigricans* is absent in *A. gracilis.* Also, the outer valves of *A. gracilis* are not fused to the basal ring along their dorsal, anterior borders as they are in *D. wilverthi* and *nigricans.* The middle valves of *A. gracilis* are broad and roughly quadrilateral in shape while those of *D. wilverthi* and *nigricans* are finger-shaped. These valves of *A. gracilis* are strongly attached to the inner surfaces of the outer valves; this is not the arrangement in *D. wilverthi* and *D. nigricans.* The presence of many campaniform sensilla on the posterior surfaces of the middle valves of *A. gracilis* has not been reported in other dorylines. The shapes of the inner valves of all the dorylines described, the Old World as well as the New, are distinctly different. The presence of the triangular plate at the anteroventral margins of the inner valves is characteristic of *A. gracilis.* The IXth sternum is considered an integral part of the genitalia because it provides muscle attachment (Krafchick, 1959). In general shape, the IXth sternum of *A. gracilis* resembles that of other dorylines (Borgmeier, 1955; Forbes, 1958; Forbes and Do-Van-Quy, 1965; Ford and Forbes, 1980).

HISTOLOGY OF THE REPRODUCTIVE SYSTEM

The testicular capsule in the adult is a network of interlacing tracheae of varying diameters, and it continues inward between the testicular follicles. Fat cells are found on the surface of the capsule. In the pupa, the capsule is not as well formed; the tracheae are smaller and fewer. The epithelium of the testicular follicles in the adult consists of a basal layer and an inner layer of cells arranged around a central lumen (Fig. 8). The larger cuboidal or pyramidal cells of the basal layer have distinct cell boundaries. The cytoplasm of these cells is granular and highly vacuolated, and a large, ellipsoidal nucleus is located in the basal region. The smaller cells of the inner layer are without distinct cell boundaries. They have densely granular cytoplasm and small oval nuclei. The central lumen has clusters of spermatozoa or scattered spermatozoa and their tails extend into the cytoplasm of the basal cell layer. This arrangement of the testicular epithlium resembles that in the adult and pupa of *D. wilverthi* and in the pupa of *D. nigricans* (Ford and Forbes, 1983). In the pupa, large irregularly-shaped cells form the epithelium of the follicles and there is no central lumen. The cytoplasm is restricted to the periphery of the cells and encloses a large vacuole that is filled with spermatozoa (Fig. 9). This condition has not been reported in any of the other dorylines.

The epithelium of each vas efferens in the adult is a continuation of the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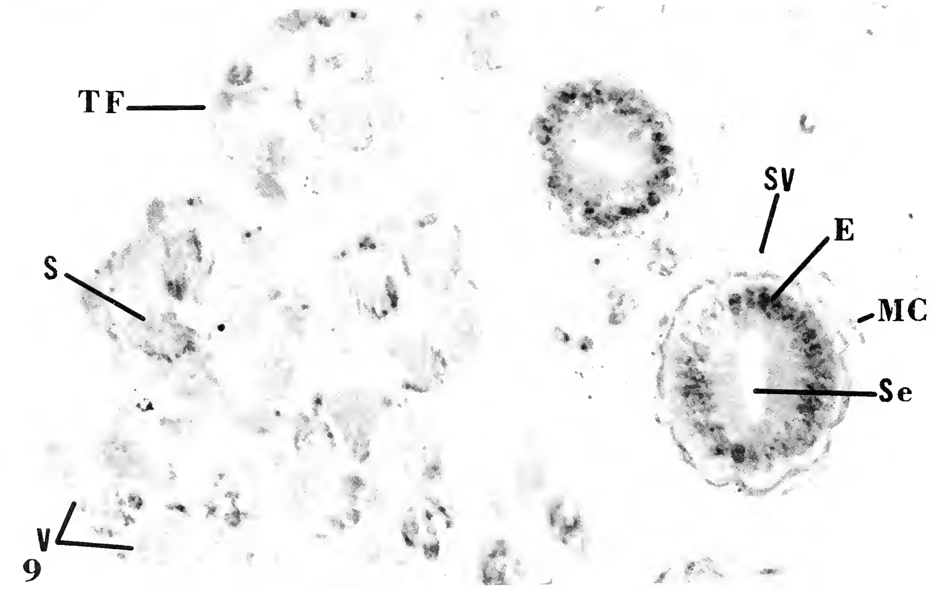
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basal epithelial layer of the testicular follicle. These basal cells decrease abruptly in size and become low and cuboidal in shape (Fig. 8). The nuclei are centrally located. The lumina of the vasa efferentia contain scattered or clustered spermatozoa. In the pupa, the cells of these organs are low and columnar with oval, basally located nuclei and basophilic cytoplasm. The lumina of the vasa efferentia are narrower than those of the adult and are devoid of spermatozoa, but they do contain a fine-granular, neutrophilic secretion that arises from the free surface of the cells.

The epithelial cells of the vas deferens of the adult are larger than those of the vasa efferentia, and the epithelium of the vas deferens is surrounded by a thin layer of small, obliquely arranged muscle fibers. The lumen contains scattered spermatozoa (Fig. 8). In the pupa the single layer of epithelial cells of this organ is taller than that lining the vasa efferentia, and the cytoplasm is still basophilic in its staining reaction. The lumen is narrower, is devoid of spermatozoa and has a secretion similar to that found in the vasa efferentia.

In the seminal vesicles, the epithelium is gradually transformed from the cuboidal cells of the vas deferens to low columnar. The cytoplasm is granular, and some vacuoles are present. Each cell has a basally located, ellipsoidal nucleus; the long axis of the nucleus is parallel to the basement membrane. A small amount of neutrophilic-staining, granular secretion was seen on the free surface of some of the cells (Fig. 8). The muscle coat gradually becomes thicker from the proximal to the distal region of this organ. In the narrow duct at the posterior end of the seminal vesicle, the epithelium increases slightly in height and the nuclei change their position to lie at right angles to the basement membrane. This position of the nuclei continues into the accessory glands. The lumen of this organ is filled with spermatozoa except in one adult where the sperm were confined to the testicular follicles. Spermatozoa were never found in the distal narrow duct (Fig. 10). In the pupa the epithelium consists of a single layer of tall columnar cells that almost occlude the lumen. The cytoplasm is more granular, basophilic and with fewer vacuoles. The lumen is filled with coarser granules that are less basophilic than those in the cytoplasm and no spermatozoa are present (Fig. 9).

The histology of the seminal vesicle and the distribution of spermatozoa are similar in the adults of the dorylines described. Variations in the secretions of this gland have been reported: In *N. harrisi* (Forbes and Do-Van-Quy, 1965) the secretion is granular and acidophilic in the constricted ter-

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Figs. 8, 9. Photomicrographs of sections through the testes of *A. gracilis*. 8. Adult testis that shows testicular follicles, vasa efferentia, vas deferens, and seminal vesicle. ×275. 9. Pupal testis that shows follicles and seminal vesicle. ×600.

minal region; in *D. wilverthi* and *nigricans* there is mixing of both acidophilic and basophilic secretions in the anterior region and basophilic in the posterior.

The epithelium of the accessory glands in the adult is folded and the cells vary in height from low cuboidal to tall columnar. The cytoplasm is granular and slightly vacuolate. The secretion in the dorsal half of the gland is distinctly acidophilic and is composed of coarse spherical granules that are formed in the supranuclear region of the cells (Fig. 10). The cells become packed with this secretion, the surface membrane of the cells disintegrates, and the secretion is discharged into the lumen. Only a thin basal layer of cytoplasm containing the nuclei remains of these epithelial cells that elaborated this secretion. In the ventral half of the gland, the secretion is acidophilic toward the median wall, basophilic toward the lateral wall, and a combination of both in the center of the lumen. The basophilic secretion, in contrast to the acidophilic, is developed within the cytoplasm of the entire cell and consists of small, fine granules concentrated in the upper ends of the cells and is discharged through the surface membrane into the lumen. The muscle coat is composed of an inner layer of 3 or 4 oblique fibers, 1 or 2 of which extend into the epithelial folds, and an outer layer of 2 or 3 circular fibers (Fig. 10). In the pupa the epithelium consists of a single layer of columnar cells that vary in height and is more folded than in the adult. These folds almost occlude the lumen. The cytoplasm is fine-granular throughout the cells but more dense in the supranuclear regions. A small amount of neutral staining secretion is present in the lumen.

Spermatozoa are normally absent in these glands, but their unusual presence has been reported at the anterior ends of these glands in the adults of *D. nigricans* (Ford and Forbes, 1983) and in limited areas in these glands in the subgenus *Rhogmus* (Gotwald and Burdette, 1981).

The accessory gland ducts are wider proximally, and their epithelial cells vary in height from cuboidal to columnar. In the adult, where each accessory gland enters its duct, there are two epithelial folds on the lateral and two on the medial walls. These folds alternate in position and might serve as a closing mechanism. The pupa has only two median folds, one dorsal and one ventral. In the adult the lumen contains a neutral, granular secretion which is absent in the pupa.

The bound accessory gland duct is formed by the two accessory gland ducts held together by a common peripheral muscle coat. Anteriorly, the

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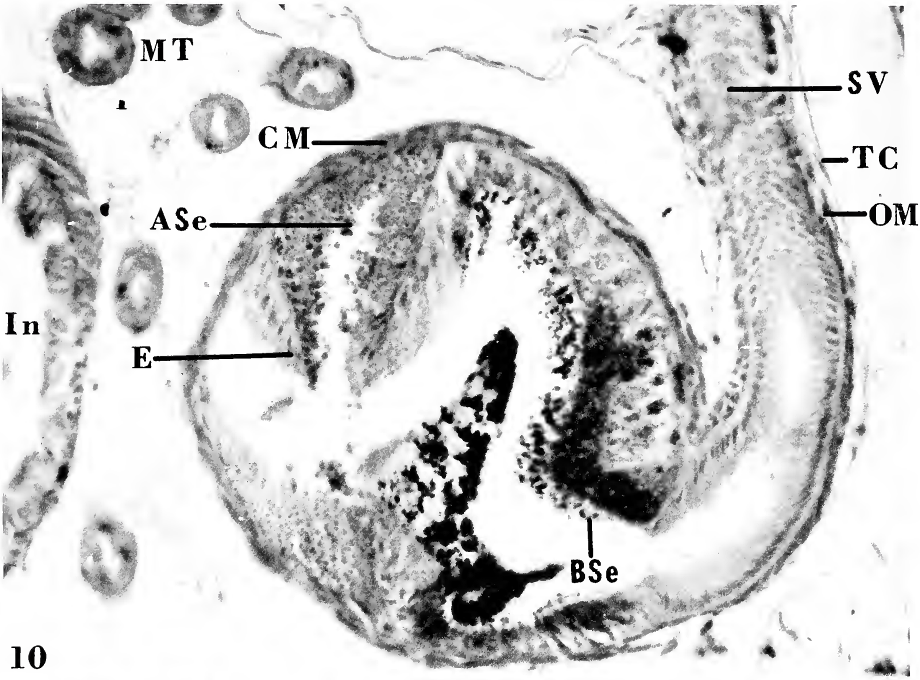
Figs. 10, 11. Photomicrographs of cross sections of organs in the adult of *A. gracilis*. 10. The accessory gland and the seminal vesicle opening into it. ×266. 11. The bound accessory gland duct. ×300.



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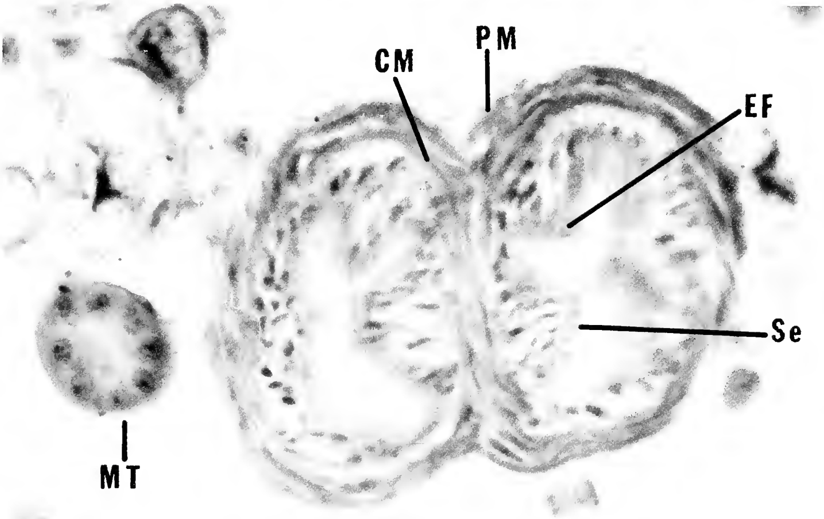

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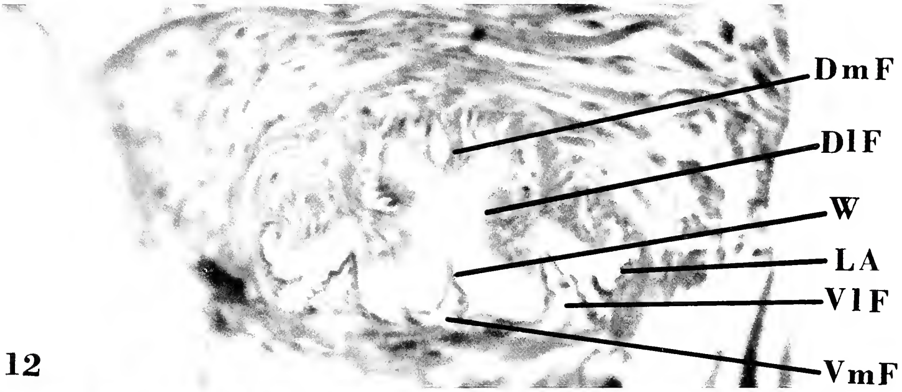

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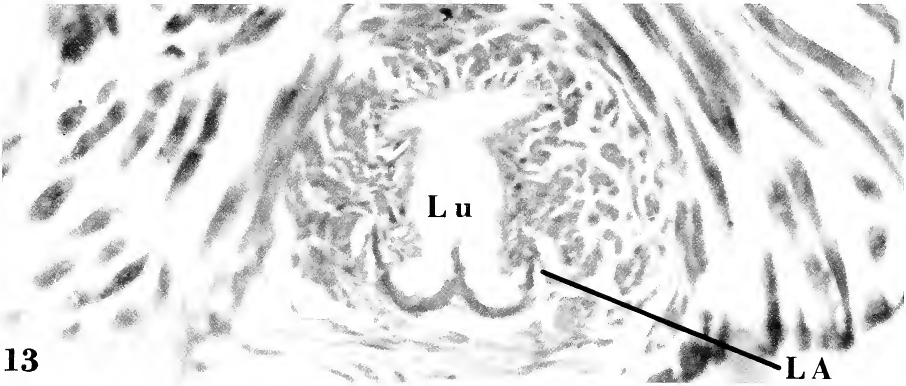

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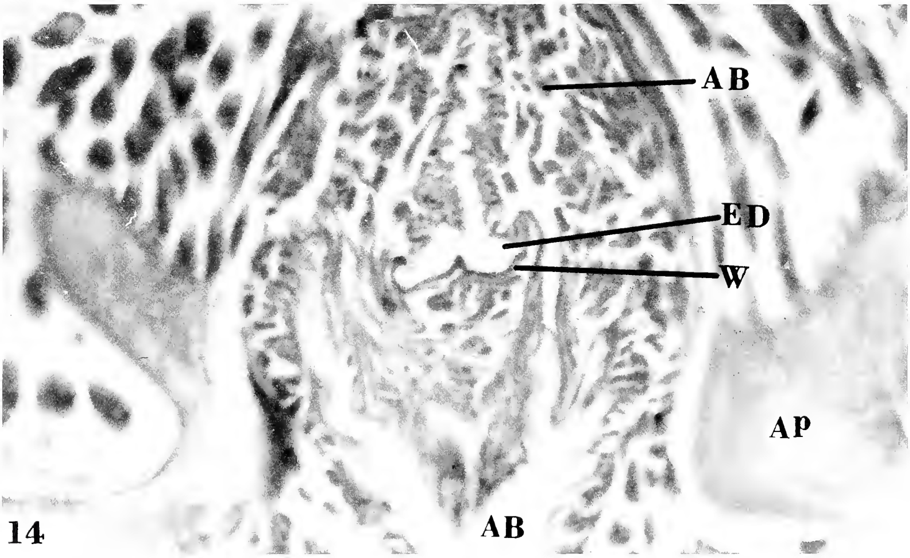

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epithelium in each duct has two folds, one dorsomedian and one ventromedian. The cells over these folds are columnar and the rest of the epithelium is cuboidal. Posteriorly, these folds gradually decrease in height and new folds are formed on the dorsal, lateral, and ventral walls. The lumina contain a neutrophilic, granular secretion. The muscle coat is composed of a few circularly arranged fibers around each accessory gland duct, and a few peripheral circular and oblique fibers that bind the two ducts together (Fig. 11). At the posterior end, the muscle fibers between the two ducts are reduced in number and disappear. The two lamina join into one and the duct formed is the ejaculatory duct. Histologically, the pupa is similar to the adult in this region.

The first part of the ejaculatory duct has two prominent dorsal folds and smaller lateral and ventral folds. The latter become more pronounced posteriorly. The columnar epithelium in this duct is taller over the folds. In the pupa, this region has narrow folds; three dorsal, two lateral, and one ventral. In the adult, the apices of the two dorsal folds become much broader, and, at this level, the formation of the cuticular wedge is first seen as a thin intima over the epithelium on the ventrolateral folds. The muscle coat consists of 2 or 3 inner oblique fibers and 1 or 2 outer circular fibers. More posteriorly, a fold is formed between the two dorsal folds, the small lateral folds broaden, and the ventral one becomes a tall narrow midventral fold. The cuticular wedge is now broadly W-shaped, thicker ventrally, and the lateral arms are thinner and wavy in appearance. In the pupa the wedge is short and is less complex in its structure. The muscle coat on the dorsal and lateral walls in the adult has increased by several fibers in thickness, and some of these fibers are longitudinally arranged (Fig. 12). In the pupa, the muscle fibers are not distinct and are being formed. Further along in the adult, the midventral portion of the wedge becomes thicker, broader for a short distance, and then narrows and extends upward into the lumen. The middorsal fold is reduced in height and disappears, and the midventral fold of the wedge lowers. The muscle coat becomes thicker laterally, and pushes the lateral folds inward. Toward the distal region, the lateral arms move mesially and the wedge is W-shaped (Fig. 13). The posterior tip of the wedge is thinner and flatter. The distal end of the ejaculatory duct extends through the dorsal wall of the aedeagal bladder at the level of the anterior region of the inner

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Figs. 12–14. Photomicrographs of cross sections through the ejaculatory duct and wedge in the adult of *A. gracilis*; all are magnified ×215. 12. This section is about at the midregion of the wedge and shows the extended lateral arms of the wedge. 13. This section shows the reduction of the lateral arms of the wedge, the formation of its base, and the laterally compressed lumen. 14. This section shows the end of the ejaculatory duct opening through the roof of the aedeagal bladder.

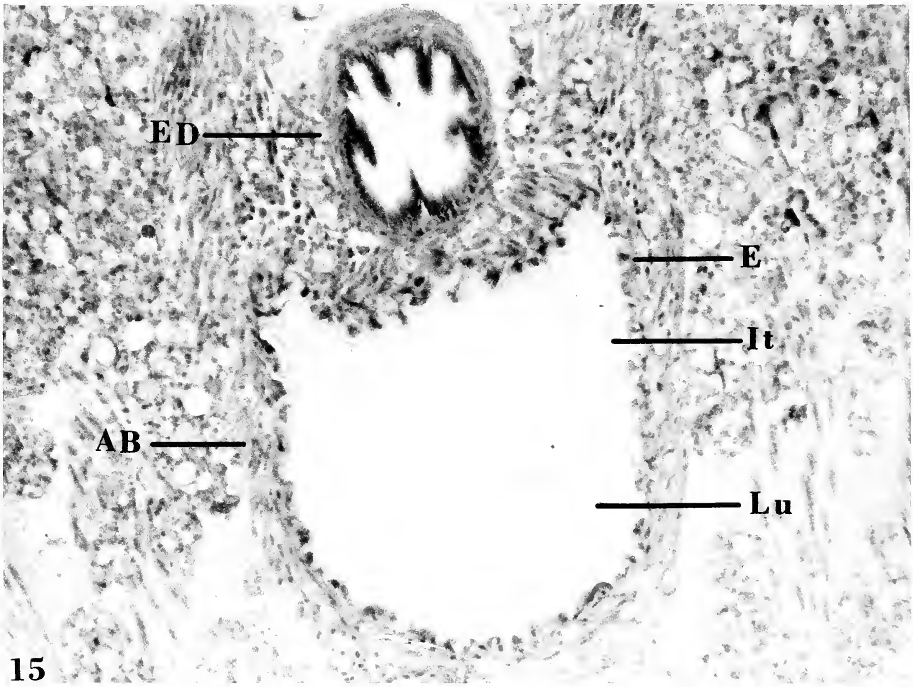

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Fig. 15. Photomicrograph of cross sections through the ejaculatory duct and the aedeagal bladder in the pupa of *A. gracilis.* ×210.

valves (Fig. 14), and just beyond the end of the wedge the floor of the ejaculatory duct opens into the aedeagal bladder. The muscles of the dorsal and lateral walls of the ejaculatory duct are incorporated into the dorsal wall of the aedeagal bladder. The lumen of the duct throughout, in both adults and pupae, is devoid of any secretion.

The cuticular wedge on the ventral surface of the ejaculatory duct, referred to as the chitinous "penes" in *D. labiatus* by Mukerjee (1926) and described in detail by Clausen (1938) in formicine ants, is present in all male ants in which the histology has been described. The shapes of the wedges and the histological organization of the ejaculatory ducts exhibit differences in all male ants. In the origin of the arms of the wedge from the ventrolateral folds of the duct and in the formation of a ventral median ridge on the base, *A. gracilis* resembles the Old World dorylines.

The wall of the aedeagal bladder consits of a thick, wrinkled intima and an underlying epithelium of small cells with prominent spherical or ellipsoidal nuclei. The epithelium is surrounded by a thick muscle coat of large inner circular and outer obliquely arranged fibers; the latter are inserted on the median walls of the inner valves at their anterior ends. In the adult, the dorsal and lateral walls in the anterior region of the bladder are deeply folded, and muscle fibers extend into these folds. In the pupa, the walls are not folded, the lumen is spacious (Fig. 15), and the dorsal wall is depressed in front of the point where the ejaculatory duct opens into the bladder. In the posterior region, in both the adult and the pupa, the intima is thin and not wrinkled, and there are small folds on the lateral walls. The lumen of the bladder opens between the inner valves. There is no secretion anywhere in the lumen of the aedeagal bladder.

Gotwald and Kupiec (1975), who analyzed the existing information on the morphology, behavior, and geographical distribution of the doryline tribes, indicate that the subfamily Dorylinae, as presently constituted, is triphyletic. The three lineages are the Ecitonini-Cheliomyrmecini, the Dorylini, and the Aenictini. They advocate the retention of the subfamily Dorylinae to include the tribe Dorylini and make a case for the creation of a subfamily Ecitoninae, already introduced by Brown (1973) to include the tribes Ecitonini and Cheliomyrmecini. The status of Aenictini, they conclude, remains to be determined by further investigation.

This report of the anatomy and histology of the reproductive system has brought to light several structures and features of phylogenetic importance. The larger number of testicular follicles, the histology of the testicular epithelium, the general structure of the accessory glands, the short straight bound accessory gland duct and ejaculatory duct, the formation of the chitinous wedge in the ejaculatory duct, and the structure of the genitalia are features in which *A. gracilis* is different from the New World dorylines. Some of these structures have been noted and described by Gotwald and Burdette (1981). It also differs from the Old World genus *Dorylus* subgenus *Anomma* in the presence of a capsule covering the testes, in the histology and secretion of the seminal vesicles, in the development of the wedge in the ejaculatory duct, in the entrance of the ejaculatory duct into the aedeagal bladder, in the absence of unicellular glands at the end of the ejaculatory duct and the aedeagal bladder, in the absence of a dorsal duct also at the end of the aedeagal bladder, and in the shapes of the genitalic valves and terminal sterna. These features exhibited by the male reproductive system in *Aenictus* lend support to the elevation of the tribe Aenictini to a subfamily rank, and to the triphyletic origin of the dorylines.

ABBREVIATIONS

A, anus; AB, aedeagal bladder; AG, accessory gland; AGD, accessory gland duct; Ao, aorta; Ap, apodeme; ASe, acidophilic secretion; B, basal cell layer; Br, brain; BR, basal ring; BSe, basophilic secretion; BT, buccal tube; CM, circular muscle; CS, campaniform sensilla; DlF, dorsolateral fold; DM, dilator muscle; DmF, dorsomedian fold; E, epithelium; ED, ejaculatory duct;

EF, epithelial fold; G1, G2, G3, G4, gastric ganglia; H, heart; I, inner cell layer; IC, infrabuccal chamber; In, intestine; It, intima; IV, inner genitalic valve; L, labium; LA, lateral arm; LP, lamina parameralis; Lu, lumen; M, mandible; MC, muscle coat; MG, mandibular gland; MP, median process; MT, Malpighian tubule; N, notch; Oc, ocellus; Oe, oesophagus; OL, optic lobe; OM, oblique muscle; OV, outer genitalic valve; Pa, paramere; PC, preoral cavity; Pe, petiole; PeG, petiolar ganglion; PG, postpharyngeal gland; Ph, pharynx; PM, peripheral muscle coat; R, rectum; RP, rectal pad or gland; RV, rectal valve; S, spermatozoa; SD, salivary duct; Se, secretion; SG, salivary gland; Sl, salivarium; SoG, suboesophageal ganglion; SV, seminal vesicle; T, testis; T1, T2, T3, thoracic ganglia; TC, testicular capsule; TF, testicular follicle; TP, triangular plate; V, vacuole; VE, vas efferens; VD, vas deferens; VlF, ventrolateral fold; VmF, ventromedian fold; Vn, ventriculus; VNC, ventral nerve cord; W, wedge; IX, 9th abdominal sternum; X, 10th abdominal tergum.

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CUTICULAR PIGMENT CHANGES IN WORKER YELLOWJACKETS (HYMENOPTERA: VESPIDAE)

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Abstract.—Unusual cuticular marks on the yellow regions of the gastral terga of worker yellowjackets of two species (*Vespula vulgaris* and *V. maculifrons*) were studied. These resembled marks found on the gastral terga of physogastric *Vespula* foundresses. The marks were associated with ovarian development among workers of queenless *V. vulgaris* colonies, and the change in structure of pigment granules was similar to that occurring in physogastric queens. Cuticular marks of *V. maculifrons* workers from queenright colonies were not related to ovarian development and the constituent pigment of the marks differed from that of foundresses and laying workers. The evidence presented supports the hypothesis of Ishay and Shimony that changes in structure of the pigment granules of ovipositing wasps are due to components of the granules being shunted to the production of nucleic acids.

Many social wasps of the subfamily Vespinae are aposematically colored with bright yellow or orange pigment on a contrasting dark background. The development of characteristic dark blotches on the otherwise lightly pigmented regions of the cuticle of physogastric queens is well known among these wasps (Heldmann, 1934; Spradbery, 1973). These marks typically appear medially on the posterior portions of gastral terga I–IV in late season foundresses (Edwards, 1980); their cause has variously been attributed to external wear, precipitation of pigments due to friction between sclerites, or oxidation of the pigments due to diffusion of substances through the cuticle (Marchal, 1896; Becker, 1937a; Spradbery, 1973). Ishay and Shimony (1982) presented evidence that the cuticular marks result from loss and change in structure of the pigment granules (xanthosomes) comprising the marks. The pigment granules are thought to contain pteridines (Becker, 1937b) which may be shunted to the production of nitrogenous bases for DNA synthesis.

In this paper I report the occurrence of anomalous dark marks on the yellow regions of the gastral tergites of workers of *Vespula vulgaris* (L.) and *V. maculifrons* (Buysson) similar to the marks found on aged queens. Evidence is presented to suggest that the mechanisms giving rise to the marks in workers are of two distinct types, with one apparently analogous to that occurring in aged queens.

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Table 1. Colony composition and population of five *Vespula* study colonies.

Colony	Date collected	Population				Foundress present	Size of worker sample taken
		☿	♂	♀	Total		
V. vulgaris							
V10	Aug. 27	1,420	—	—	1,420	no	80
V16	Sept. 16	713	96	—	809	no	79
V35	Nov. 1	15	—	—	15	no	15
V. maculifrons							
M26	Oct. 8	1,164	454	165	1,783	yes	80
M29	Oct. 15	1,215	552	154	1,921	yes	60

MATERIALS AND METHODS

Three colonies of *Vespula vulgaris* and two of *V. maculifrons* were collected during late summer and fall of 1982 in Tompkins County, New York. These colonies were part of a larger *Vespula* colony survey in which 35 colonies of five species were sampled; they were chosen for further study on the basis of observed cuticular anomalies of workers. The colonies were lightly anesthetized with ethyl ether, excavated, and transported to the laboratory in large plastic bags. The colonies were killed by freezing. Adults were counted and sorted according to sex and caste; colony composition and population are presented in Table 1. Workers and queens were held in a freezer at −10°C until subsequent examination.

Among the study colonies, the *V. vulgaris* colonies were queenless at the time of collection, while the *V. maculifrons* colonies possessed functional queens (Table 1). Queenlessness was inferred from non-recovery of a foundress, presence of workers with well developed ovaries, and presence of supernumerary eggs in the cells (Ross and Visscher, 1983).

The inner and outer surfaces of gastral terga of workers and queens were studied using light and scanning electron microscopy. The inner fold of the cuticle of the sclerites was teased away and the specimens were coated with a thin (250–350 A) layer of gold-palladium in a Balzers® sputter coater. The external and internal surfaces of the terga were observed with a AMR® Model 1000 SEM at 10 kilovolts.

Random samples of non-teneral workers from within the colonies were selected for wing wear analysis and dissection of the ovaries. Wing wear was determined subjectively on a zero (no wear) to three (greatest wear) scale. Degree of development of gastral cuticular marks was similarly rated on a zero (no marks) to two (extensive marks) scale. Ovarian development was assessed using a modification of Cumber's (1949) ovariole index.

Data were descriptively analyzed with Exploratory Data Analysis (Velle-

Table 2. Frequency of occurrence of anomalous cuticular marks on the gasters of workers of five *Vespula* colonies. Percentages of total are in parentheses.

		Number of workers with	
Colony	No marks	Intermediate development of marks	Strong development of marks
V10	72 (90%)	6 (7.5%)	2 (2.5%)
V16	52 (65.8%)	1 (1.3%)	26 (32.9%)
V35	11 (73.3%)	—	4 (26.7%)
M26	72 (90%)	—	8 (10%)
M29	43 (71.7%)	7 (11.7%)	10 (16.7%)

man and Hoaglin, 1981). When significant trends were suggested, data were further analyzed using conventional statistical tests.

RESULTS

Workers in the five study colonies possessed dark cuticular marks on the yellow portion of one or more gastral terga (Fig. 1). The frequency and degree of development of the marks among colony workers are shown in Table 2. The marks appeared identical to those of physogastric queens when the isolated terga were viewed under a dissection microscope from internal and external aspects. The marks occurred on the posterior portions of the terga and were most prominent medially; they consisted of areas of reddish-brown pigment bordered by dark bands. Immediately adjacent were areas of apparently normal yellow pigment. Clear spots throughout the marks represent the columnae (cuticular pillars between the infolding cuticle, see Becker, 1937b; Shimony and Ishay, 1981). The layer of reddish-brown pigment comprising the cuticular mark was dry, thin, and brittle and was easily removed as flakes, while adjacent layers of normal yellow pigment were considerably thicker and more malleable. Concentric dark rings throughout the reddish-brown area, conspicuous in physogastric queens (Fig. 1a), were absent from the marks of workers. Cuticular marks were not found in males or fall queens from the study colonies, nor were they found in workers randomly sampled from 30 other colonies of *V. vulgaris, V. maculifrons, V. germanica* (F.), *V. flavopilosa* Jacobson, or *V. vidua* (Saussure) collected during the same season.

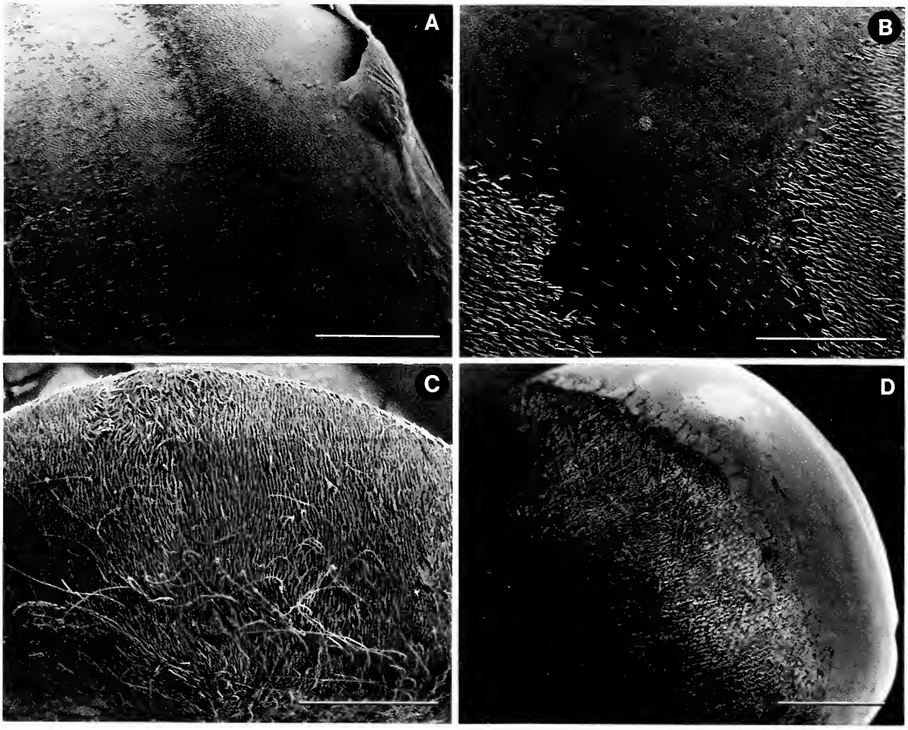
For *V. maculifrons* workers the marks were most commonly found on gastral tergum I (Fig. 1c), but occasionally also on T II. Many of these workers possessed dark discolorations of the lateral and ventral yellow regions of the gaster as well. For *V. vulgaris* workers the marks occurred on gastral terga I–V and were often spread laterally along the posterior margin of the segment

Figs. 1a–c. 1a. Cuticular marks on gastral tergites of physogastric queen of *V. maculifrons* (arrows). The yellow regions are faded in contrast to fall or spring queens (×6.6, bar = 4.0 mm). 1b. Cuticular marks on gastral tergites of laying worker of *V. vulgaris* (arrow). The yellow regions of the body are dull and faded in contrast to nestmates without developed ovaries (×8.2, bar = 3.0 mm). 1c. Anomalous cuticular mark on gastral tergite I of *V. maculifrons* worker (arrow) (×8.2, bar = 3.0 mm).

(Fig. 1b). These workers also commonly exhibited extensive lateral discoloration. The yellow pigment of *V. vulgaris* workers with marks was quite dull and faded in comparison to other nestmates, as is common for physogastric foundresses. In contrast, the yellow pigment of *V. maculifrons* workers with gastral cuticular marks was characteristically bright.

Many workers in the three queenless *V. vulgaris* colonies had developed ovaries (Ross, unpublished data) and were acting as functional reproductives. The presence and degree of development of cuticular marks were positively associated with ovarian index for workers in these colonies (ANOVA, F = 40.7, 23.2, and 103.6; all $P < 0.005$). Ovarian development was uncommon among workers in the two queenright *V. maculifrons* colonies and was not associated with development of gastral cuticular marks. Presence of the marks was not associated with wing wear in workers of the five study colonies.

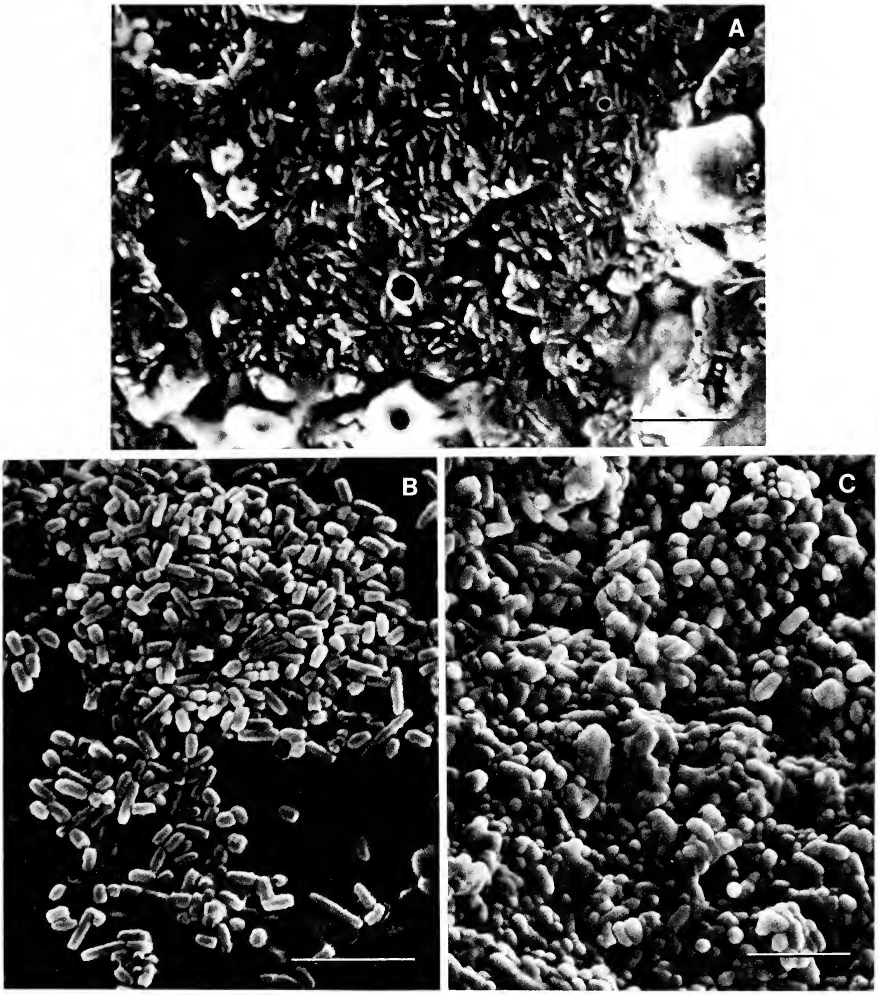
Scanning electron micrographs revealed loss of setae and hairs from the gastral terga of laying workers of *V. vulgaris*, similar to the loss of these structures in physogastric queens (Figs. 2a, b). Loss of the hair and setae occurred on the same segments as did cuticular marks. However, the areas of hair loss did not correspond to the exact areas of the cuticular marks.



Figs. 2a–d. 2a. Hair and seta loss on gastral tergum of laying worker of *V. vulgaris* (×69, bar = 0.5 mm). 2b. Hair and seta loss on portion of gastral tergum of physogastric *V. maculifrons* queen. Photograph shows the region in which the cuticular mark is found (×74, bar = 0.5 mm). 2c. Gastral tergum I of *V. maculifrons* worker with cuticular mark. Posterior of segment is to the top (×78, bar = 0.5 mm). 2d. Gastral tergum of virgin *V. maculifrons* queen collected in autumn. Posterior of segment is to the left (×30, bar = 1.0 mm).

Indeed, hair loss of physogastric queens often involved the entire yellow region of any given tergum. Workers of *V. maculifrons* with cuticular marks and virgin queens collected in autumn exhibited an abundance of hair and setae on the gastral tergites (Figs. 2c, d).

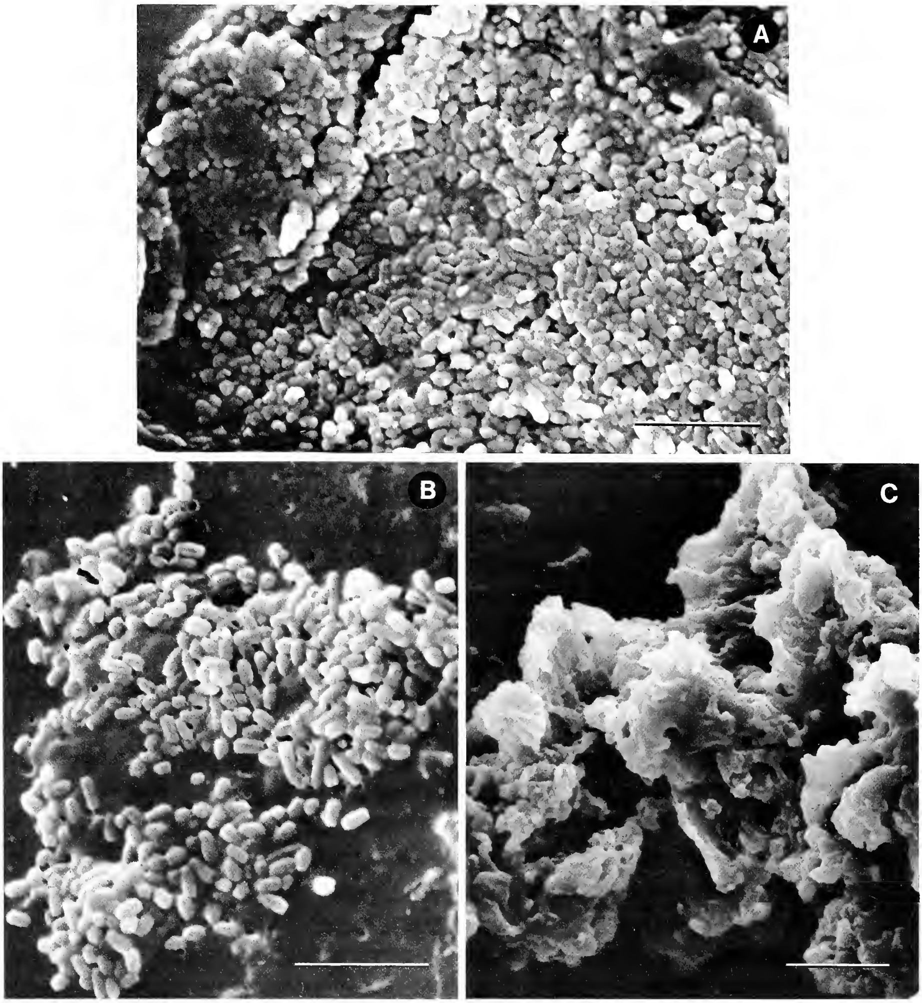
In virgin *V. maculifrons* queens, pigment granules were deposited in dense layers throughout the yellow portion of the tergum. The granules were cylindrical and elongate (ca. 0.8 μm long, Fig. 3a), as shown by Shimony and Ishay (1981) and Ishay and Shimony (1982) for various vespine species. Granules from the yellow pigmented areas surrounding the marks of physogastric queens were more sparsely distributed; many of the granules were shorter and more barrel-shaped than typical granules from virgin queens (ca. 0.6 μm long, Fig. 3b). All granules from the areas of the cuticular marks



Figs. 3a–c. 3a. Pigment granules from yellow region of gastral tergum of virgin *V. maculifrons* queen (×8,300, bar = 3 μm). 3b. Pigment granules from yellow region of gastral tergum of physogastric *V. maculifrons* queen (×10,300, bar = 3 μm). 3c. Pigment granules from area of gastral cuticular mark of physogastric *V. maculifrons* queen (×8,600, bar = 3 μm).

of physogastric queens lost their cylindrical structure to an even greater extent and became barrel-shaped or spherical (Fig. 3c).

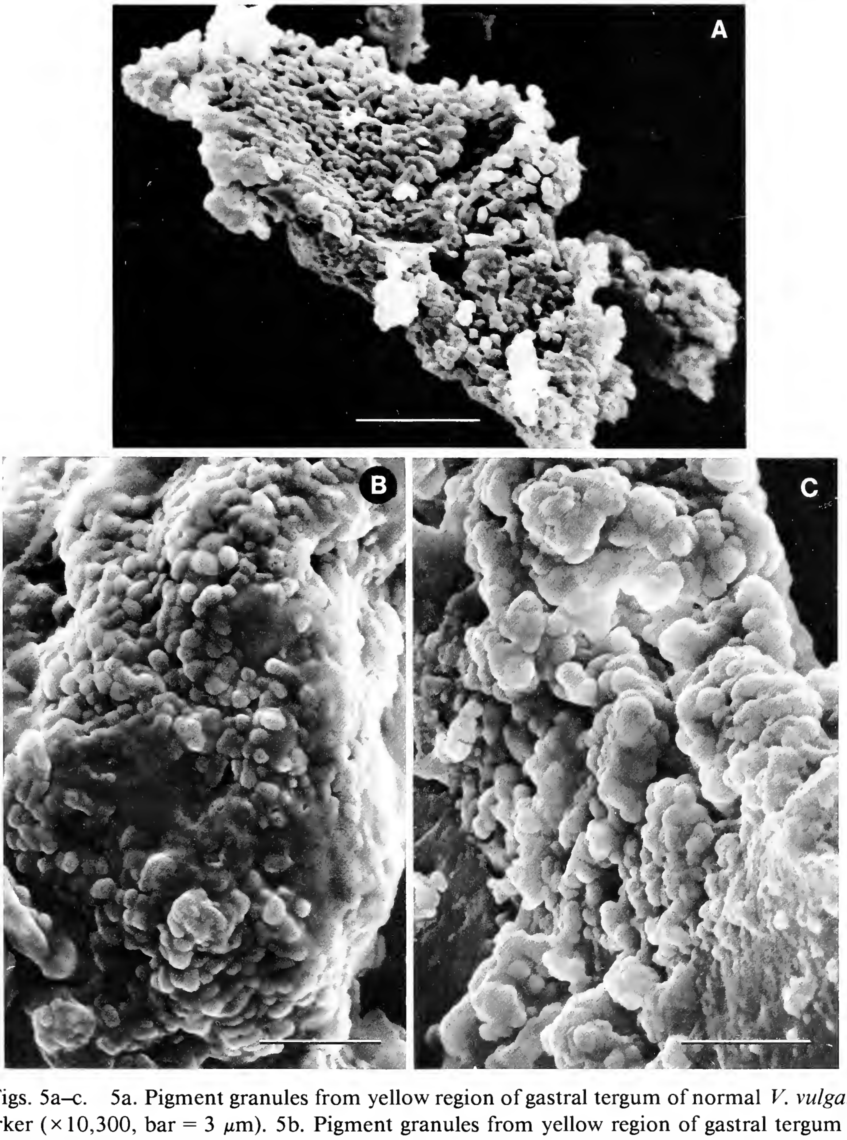
Yellow pigment granules from normal *V. maculifrons* workers exhibited a short, cylindrical structure (ca. 0.6 μm long, Fig. 4a). Granules from the yellow-pigmented regions adjacent to cuticular marks of *V. maculifrons*



Figs. 4a–c. 4a. Pigment granules from yellow region of gastral tergum of normal *V. maculifrons* worker (×10,500, bar = 3 μm). 4b. Pigment granules from yellow region of tergum of *V. maculifrons* worker with gastral cuticular mark (×10,900, bar = 3 μm). 4c. Pigment mass from area of gastral cuticular mark of *V. maculifrons* worker (×8,500, bar = 3 μm).

workers resembled granules from normal conspecifics in size and shape (Fig. 4b). Granules from the area of the cuticular mark lost their discrete, cylindrical character and formed amorphous masses of pigment (Fig. 4c).

Pigment granules from the yellow regions of gastral terga of normal *V. vulgaris* workers were cylindrical (ca. 0.6 μm long, Fig. 5a) and occurred in dense layers. As in physogastric queens, pigment granules from the yellow



Figs. 5a–c. 5a. Pigment granules from yellow region of gastral tergum of normal *V. vulgaris* worker (×10,300, bar = 3 μm). 5b. Pigment granules from yellow region of gastral tergum of laying *V. vulgaris* worker (×10,150, bar = 3 μm). 5c. Pigment granules from area of cuticular mark on gastral tergum of laying *V. vulgaris* worker (×10,600, bar = 3 μm).

portions of terga of laying workers appeared less dense in their distribution, and the granules became barrel-shaped or spherical (Fig. 5b). Granules from the areas of the cuticular marks lost their discrete structure to some extent and were without exception spherical or irregularly shaped (Fig. 5c).

DISCUSSION

How do the results of this study bear on hypotheses of the origin of cuticular marks on the gastral terga of foundress queens? As suggested by Ishay and Shimony (1982), development of cuticular marks in queens is associated with changes in the structure of the pigment granules found in the yellow regions of the wasps, and this change in the granules is associated with ovarian development. *V. vulgaris* workers with marks from the present study resembled physogastric queens in this altered structure of the yellow pigment granules, particularly in the area of the dark marks. These workers also exhibited significant development of the ovaries and loss of gastral hair and setae (probably resulting from friction between the gaster and cell wall during oviposition). These data suggest that the mechanisms underlying the development of cuticular marks in queens and in laying workers are identical. The development of cuticular marks in laying workers was first reported by Marchal (1896) for *Dolichovespula media* (Retzius) and is probably common to all laying vespine workers.

Spradbery (1973) suggested that cuticular marks in queens result from diffusion of substances through the normally impermeable cuticle via the sockets of worn-away hairs and setae. This hypothesis cannot be ruled out by the results of the present study, although two observations diminish the likelihood of its validity. First, the hair and seta loss in laying workers was not as dramatic as in physogastric queens, yet cuticular marks in workers were equally well developed. Secondly, the outline of areas of hair loss did not approximate the outline of the cuticular marks.

Becker (1937a) suggested that the cuticular marks of queens develop in response to friction between adjacent margins of gastral tergites due to distension of the physogastric queen's gaster. I observed no such friction or contact between tergal margins of laying workers, so this hypothesis also seems unlikely.

The development of cuticular marks in vespine queens is postulated by Ishay and Shimony (1982) to result from the conversion of pteridines in the yellow pigment granules to purines required for the synthesis of DNA. The conversion of the pteridine components of the granules results in the observed change in the structure of the granules. Significant amounts of nucleic acids presumably need to be manufactured for the large number of eggs produced by late-season foundresses. My findings that structural changes in the granules accompany ovarian development and oviposition in workers, as well as in queen yellowjackets, support this hypothesis.

The development of cuticular marks in *V. maculifrons* workers from the present study seems unrelated to the development of these marks in ovipositing wasps. The *V. maculifrons* workers with marks exhibited no significant ovarian development or loss of hair and setae from the gastral terga, and these workers did not differ from normal nestmates in level of foraging activity (deduced from amount of wing wear). Cuticular marks developed primarily on gastral tergum I in *V. maculifrons* workers, while these were most prominent on the more posterior segments of laying workers of *V. vulgaris* and of physogastric queens. The change in structure of the pigment granules from the marks of *V. maculifrons* workers seems to differ fundamentally from that occurring in ovary-developed queens and workers; granules from *V. maculifrons* exhibited virtually none of the discrete structure normally visible. Finally, the marks were confined to a significant proportion of the workers from only two *V. maculifrons* colonies collected; these colonies did not differ in any obvious respects from 13 other conspecific colonies collected during the same season. From these data I conclude that the cuticular marks of the *V. maculifrons* workers resulted from an anomaly during deposition of the yellow pigment layer, perhaps due to a genetic mutation. Ishay and Shimony (1982) report similar aberrations in patterns of pigmentation and structure of the granules in *Vespa orientalis* F. workers and males.

If components of the yellow pigment granules are indeed shunted to production of DNA in ovipositing wasps, then the pigment may be regarded as a vital storage substance. Given the variable proportions of yellow coloration in relation to dark coloration among vespine species, this storage product may be more limiting in some species than in others. Indeed, we may predict that the development of cuticular marks in those species with relatively low proportions of yellow-pigmented cuticle (e.g. *V. vulgaris, V. flavopilosa*) will be more extensive than in those species with high proportions of yellow-pigmented cuticle (e.g. *V. germanica*). My preliminary observations suggest that this prediction will hold true.

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ECOLOGICAL AND SENSORY ASPECTS OF PREY CAPTURE BY THE WHIRLIGIG BEETLE *DINEUTES DISCOLOR* (COLEOPTERA: GYRINIDAE)

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Abstract.—Whirligig beetles prey on a variety of small soft-bodied invertebrates that enter their surface film habitat from above or below. They also act as scavengers on dead floating invertebrates. Deficits in prey capture ability were produced by experimental deprivation of visual, tactile, or surface vibration cues. Visual deprivation and deprivation of surface vibration cues produced statistically equivalent deficits in whirligig predatory behavior. When tactile and surface vibration cues were both unavailable to the beetles, the deficits in their predatory behavior were more pronounced. These sensory systems are similar to those of Hemipteran predators that live in the surface film.

The way a predator locates its prey is determined by the predator's environment, its endowment of sensory structures, and the nature of its prey. For whirligig beetles, all three of these factors are unusual. These beetles live and feed on the surface film of bodies of fresh water, and gyrinid sensory structures are highly specialized for this environment. Their separate pairs of compound eyes above and below the water (Fig. 1) possess different spectral sensitivities suited to their respective surroundings (Bennett, 1967; Carthy and Goodman, 1964; Pappas, 1974). The Johnston's organs of their antennae, running between pedicel and flagellum (Fig. 2), are modified into extremely sensitive surface vibration detectors (Eggers, 1926; Wilde, 1941) which can sense vibrations with an amplitude as small as a few microns (Rudolph, 1967). Gyrinids potentially have available to them prey that enter the surface film from the air, from underwater or that live in the surface film itself.

I have examined the predatory activities of the river dwelling species *Dineutes discolor,* working in both the field and the laboratory to determine the natural diet of the beetles and what sensory systems were involved in their prey capture behavior. I investigated for the use of visual, tactile, and surface vibration cues in gyrinid predation, all three of which are used by surface film dwelling water striders or backswimmers (Murphey, 1971a, 1971b, 1973; Murphey and Mendenhall, 1973). Prey animals in the surface

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Fig. 1. Front and side views of the head region of *Dineutes discolor,* showing the separate dorsal and ventral pairs of compound eyes.

film are known to generate distinctive surface vibrations by their movements (Lang, 1980) which constitute an unusual stimulus available to any predator in contact with the water's surface.

MATERIALS AND METHODS

I studied an aggregation of whirligigs located on the Wisconsin River near Arena (Iowa Co.). Field observations were carried out with binoculars; for laboratory study beetles were removed from the river and maintained on a diet of live flightless *Drosophila.* Of the approximately 600 beetles examined for identification during the summers of 1976 and 1977, all but two were *Dineutes discolor.* This group composition differs from the multispecies rafts found in a lake habitat by Heinrich and Vogt (1980).

Beetles observed feeding in the laboratory belonged to one of four treatment groups. The first was normal beetles, which underwent no manipulation of their sensory structures. The second group was temporarily visually deprived, by exposing them to light from a Westinghouse DXC 500-W Photoflood from a distance of 30 cm. The exposure was carried out in a special reflector-lined aquarium freshly filled with cool water, so that the beetles were protected from elevated temperatures (they always submerged when the light was turned on). Once bright-light adapted, this group was observed feeding under a dim red light for 9 min. The combination of bright-light adaptation, a short observation period, and the insensitivity of the gyrinid eye to red light (Bennett, 1967; Carthy and Goodman, 1964) produced the visual deprivation. The third group was deprived of surface vibration cues by having their antennal flagellae removed. The Johnston's organ stretched between pedicel and flagellum (Fig. 2) depends upon relative motions of these two parts to detect surface vibrations (Eggers, 1926; Wilde, 1941). The fourth group was deprived of sensory cues by removal of both their antennal

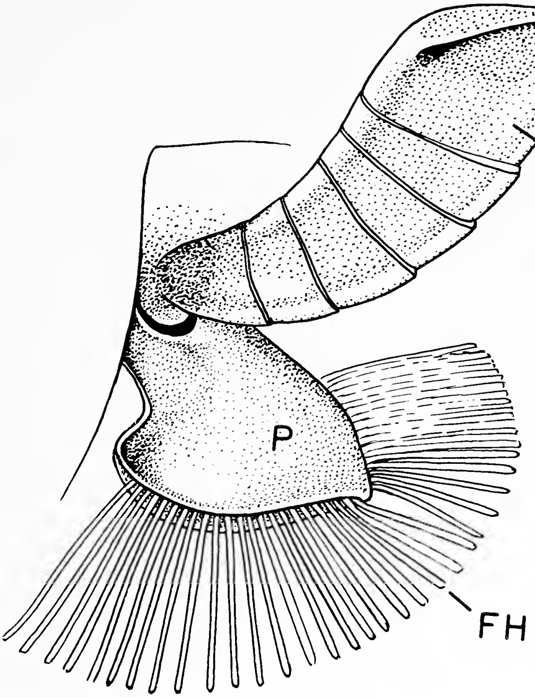

Fig. 2. The antenna of *Dineutes discolor.* Labelled parts are flagellum (F), pedicel (P) and socketed flotation hairs of the pedicel (FH).

pedicels and flagellae. Inspection with a scanning electron microscope revealed that the row of hairs on the pedicel have the typical individually socketed structure of mechanoreceptors, and so beetles with both pedicels and flagellae removed were deprived of tactile cues from these hairs as well as surface vibration cues. (Unfortunately it was impossible to eliminate the hairs on the pedicel and leave the surface vibration detectors intact, as these hairs supply the buoyancy that keeps the antennae afloat, and removing them causes unpredictable changes of the height at which the antennal pedicels are floating.)

Beetles were observed in the laboratory one at a time, feeding on live flightless *Drosophila* in a 122 × 122 × 30 cm tank that rested on inflated inner tubes to insulate it from extraneous environmental vibrations. Approximately 150 prey captures were recorded for each of the four treatment groups, with ten to twenty beetles comprising each group. Three or four days of food deprivation before observation periods was adequate to ensure hungry but otherwise healthy beetles.

Table 1. Objects close circled by *D. discolor* under natural conditions.

Objects close-circled	Consumed	Not consumed
Live invertebrates less than 3 mm long (gnats and collembolans)	4	3
Live mosquito larvae	3	88
Live flies, 3–5 mm long	2	—
Live flies, 5–10 mm long	1	1
Live coccinellid beetles	—	3
Dead spiders	18	—
Dead unidentified invertebrates	5	12
Duckweed plants	—	33
Unidentified objects	46	1,103

In both laboratory and field, *D. discolor* performs a stereotypic predatory sequence I call a close circle. The beetle approaches with its head directed toward its prey. Keeping its head very close to the prey the beetle circles around the prey. The raptorial forelegs of the whirligig, normally held in grooves under its body, reach out toward the prey during this circle. In the field, one, occasionally two, or rarely more, close circles were performed about prey animals before they were captured and consumed. For the laboratory data I compared the number of close circles required for prey capture as a measure of how the various sensory deprivations affected predatory ability.

RESULTS

A total of 1,322 close circles of objects in the surface film was recorded during the course of my field observations (Table 1). Identification of objects being close circled was often difficult due to their small size, as the categories in the table attest. Prey were only scored as "live" if I saw them move independently before being close circled by a gyrinid.

All of *D. discolor's* prey were soft-bodied invertebrates. They entered the surface film both from above (gnats, collembolans, flies, etc.) and below (mosquito larvae). Although small pieces of vegetation were close circled, I never observed the beetles eating any plant material. Beetles occasionally dove below the surface, but even when they were surrounded by animals they would have attacked at the surface film (mosquito larvae), I never saw a submerged gyrinid attack a prey animal.

In the laboratory, sensory deprivation in visual, surface vibration, and tactile stimuli all resulted in more close circles being required for prey capture. Figure 3 shows these data displayed as the cumulative probability of prey capture vs. the number of close circles performed, which is a form of

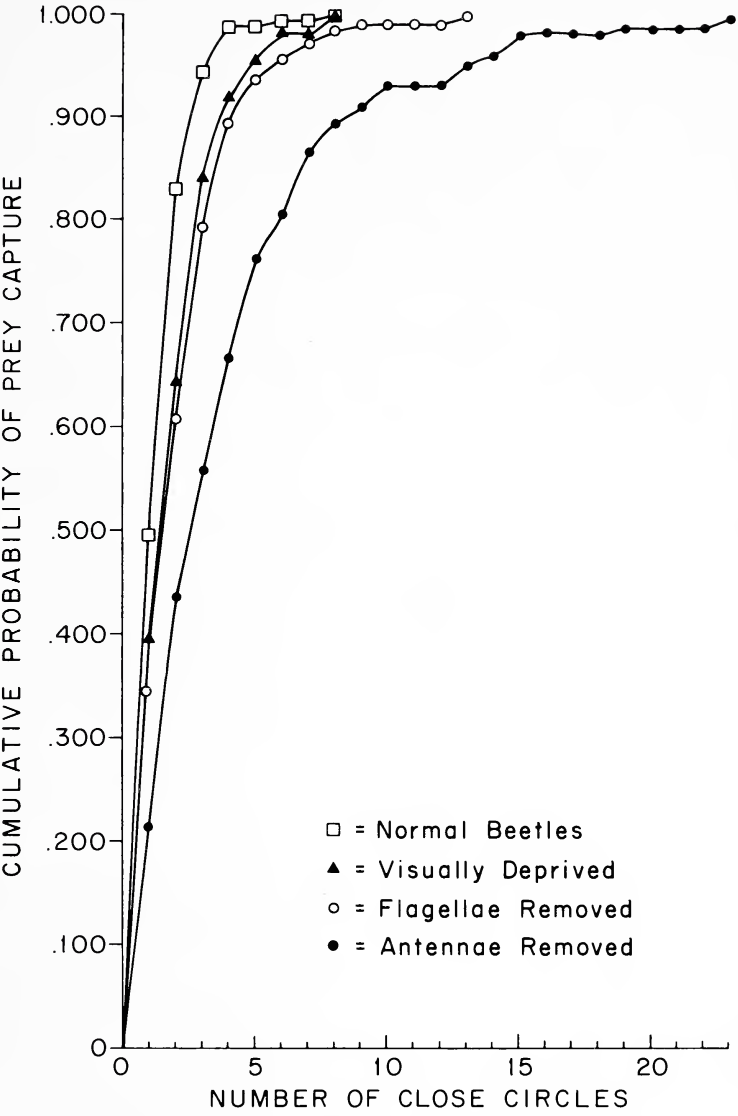

Fig. 3. The cumulative probabilities of prey capture by four experimental groups of *Dineutes discolor* fed live flightless *Drosophila* in the lab. The total number of prey captured is 150 ± 5 for each of the groups of beetles.

data organization amenable to analysis using the Kolmogorov-Smirnov test (Siegel, 1956). Each of the four groups of beetles includes data for 150 ± 5 prey captures.

Both visually deprived beetles and those deprived of their flagellae required more close circles than normal beetles to capture prey, with significance levels of 0.025 and 0.001 respectively. The visually deprived beetles and those deprived of surface vibration cues by flagellar ablation were statistically indistinguishable from one another in their number of close circles per prey capture, which can be seen by the virtual overlap of these two lines in Figure 3.

Beetles deprived of both surface vibration cues and tactile cues by having their antennae removed required even more close circles to capture prey, differing from all three previous groups at the 0.001 significance level. Presumably this deficit reflects an additional sensory deprivation due to the loss of mechanoreceptive hairs on their antennal pedicels.

DISCUSSION

Whirligig beetles capture and consume prey that enters the surface film from below and above, thereby taking advantage of aquatic insects that need to reach the surface for air, as well as flying or terrestrial invertebrates that may be blown down onto the water or landed in order to lay eggs. My limited ability to clearly distinguish small invertebrates and their movements from several meters distance undoubtedly skews Table 1 towards larger prey items and towards dead food materials more than is the actual case. Nonetheless, *D. discolor* clearly acts as both a predator and as a scavenger, and seems to feed on rather soft-bodied forms.

Virtually all of the live prey of *D. discolor* listed in Table I are very ephemeral objects from a whirligig's viewpoint. When approached by a predator in the surface film, mosquito larvae submerge, collembolans jump, gnats take off from the water's surface, etc. If a gyrinid is to successfully capture any prey, its predatory sequence must be as rapid as possible. The fewer number of close circles a gyrinid performs before prey capture, the more prey it will probably consume. This argument may also obtain for the dead invertebrates scavenged by the beetles. Not only do *D. discolor* live in moving water, but they also feed in aggregations and a dead invertebrate not captured immediately is apt to be swept downstream or consumed by a conspecific.

Previous studies have shown that backswimmers and water striders are capable of utilizing a variety of cues in locating and capturing prey, including visual, tactile and surface vibration cues (Murphey, 1971a, 1971b, 1973; Murphey and Mendenhall, 1973). Potential prey insects in the surface film generate distinctive vibration spectra (Lang, 1980) and the processes of surface vibration orientation are beginning to be unravelled (Lang, 1980; Reinig and Uhlemann, 1973; Weise, 1974).

D. discolor appears to use visual, tactile, and surface vibration cues in prey capture, as indicated by the increased number of close circles required in my laboratory groups. An alternative hypothesis for these deficits that must be considered is that the beetles were physically damaged in a more general sense by their laboratory treatments, but I do not believe this to be the case. Normal beetles in Figure 3 show probabilities of prey capture with one and two close circles, respectively, that correspond to 77 and 129 out of 155 total prey captured. The normal laboratory animals were therefore capturing prey with one or two close circles, much as beetles do in nature. The visually deprived beetles were exposed only to bright light and my apparatus ensured that they were not subjected to elevated temperatures, and they show deficits in capture behavior statistically indistinguishable from those of the beetles with their antennal flagellae removed. Experimental beetles who were operated on were as vigorous as normal animals, and did not display an increased mortality. Ideally I would have performed sham operations, but there is no obvious way to do so when the procedure involves an ablation rather than an incision.

Congeneric whirligigs such as *Dineutes hornii* are largely quiescent during the day and forage at night (Heinrich and Vogt, 1980). This nocturnal feeding may rely upon different sensory modalities than the diurnal predation by *D. discolor*. Whether whirligigs forage at night or during the day appears to depend on the motion of the water in which they live; those that live in a current must climb out of the water onto emergent vegetation at night in order to avoid being swept downstream while unable to use visual cues to maintain their position relative to the shore (Brown and Hatch, 1929; Folkerts and Donovan, 1973).

The wave patterns produced by swimming gyrinids have been well described by Tucker (1969), and the possibility of these waves reflecting off prey in a surface film borne echolocation system has seemed a natural possibility. However, the wavelengths of the waves produced by swimming gyrinids are very large compared to the portions of the natural prey items in contact with the surface film (siphons for mosquito larvae, legs for gnats, etc.) and so efficient wave reflection for echolocation seems unlikely. It is more probable that any echolocation used by gyrinids involves locating larger objects in the surface film, like rocks, conspecifics, etc.

ACKNOWLEDGMENTS

I am grateful to Professors Jeffrey R. Baylis, Jack P. Hailman, and Stanley Carlson who have supplied me with assistance and advice. I am also indebted to Clyde S. Gorsuch, Scott R. Robinson and Katherine C. Noonan for reading and commenting on various drafts of this paper. Cheryle Hughes produced the excellent illustrations.

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IRBISIA KNIGHTI, A NEW MIRINE PLANT BUG (HETEROPTERA: MIRIDAE) FROM THE PACIFIC NORTHWEST

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Abstract.—The new species *Irbisia knighti* is described and its distribution given.

Irbisia knighti, new species
(Figs. 1–8)

Diagnosis. Similar to *I. solani* (Heidemann) 1910 in size and surface features but is consistently recognizable by brachyptery of both sexes and white vestiture. *I. knighti* is separated from the brachypterous form of *I. sericans* (Stål) 1858 by the slightly punctate pronotum and white vestiture of the former species (Figs. 1 and 2).

Description. Holotype male. Brachypterous. Length 3.90–4.63 (all measurements in millimeters), width 2.18–2.30, shining black, moderately covered with shining white setae. HEAD: width across eyes 1.25–1.30, vertex 0.59–0.63, dorsal width of eye 0.35–0.36; triangular, smooth; temporal areas distinct, bordered basally by transverse short sulcus, glabrous median depression indistinct; basal carina moderately prominent, slightly rounded, declivous to level of vertex, straight, eyes broadly joined to frons, posterolateral margins arcuate posteriorly in dorsal view; distance from tylus to ventral margin of eye 0.61–0.63, height of the eye 0.50–0.53, maximum interocular width (anterior view of frons) 0.90–0.95. ROSTRUM: length 1.70–1.83, black, surpassing mesocoxae to just attaining apices of metacoxae. ANTENNAE: black; I, length 0.50–0.55, apices fuscous; II, 1.45–1.55; III, 0.78–0.93; IV, 1.02–1.20. PRONOTUM: length 0.86–0.88, anterior width 0.93–0.95, posterior width 1.45–1.55; subconical, slightly flattened, distinctly or confluently punctate, lateral margins straight, broadly rounded at junction with propleura, anterior angles rounded, indistinct in dorsal view, gently sulcate in lateral view; calli slightly convex, smooth, narrowly confluent anteriorly, with transverse depression on inner, and foveate depression of outer anterior angles reaching antero-lateral margins of pronotum. LEGS: black; coxae and femora with apices testaceous; tibiae testaceous with bases of knees black; tarsi black. HEMELYTRA: membrane reduced, extending

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slightly beyond apex of cuneus, cells not developed; apex of abdomen exposed in dorsal view. VESTITURE: dorsum clothed with suberect white setae; head and pronotum sparsely covered with thin setae; hemelytra moderately covered with sericeous setae basally, these setae grading into and being replaced by thin setae apically; venter moderately clothed with white setae; eyes with sparse minute pubescence between facets. GENITALIA: Left paramere (Fig. 3): evenly curved; sensory lobe developed but not set off by a dorsal suture, with numerous bristles; shaft truncate at apex, with numerous setae. Right paramere (Fig. 4): subcylindrical; with a single short apical process and a few short lateral setae. Vesica (Fig. 5): two smooth membranous lobes, each with a small preapical side lobe; sclerotized process furcate, primary process strongly serrate; ductus seminis expanded subapically.

Brachypterous female. More robust than male, but very similar in color, structure and vestiture. Length 4.40–4.95, width 2.40–2.50 HEAD: width across eyes 1.35–1.36, vertex 0.66–0.68, dorsal width of eye 0.35–0.38, distance from tylus to ventral margin of eye 0.66–0.68, height of eye 0.50–0.54, maximum interocular width 0.96–0.98. ROSTRUM: length 1.88–1.93, barely reaching apices of metacoxae. ANTENNAE: I, length 0.55–0.58; II, 1.53–1.55; III, 0.85–1.00; IV, 1.03–1.15. PRONOTUM: length 0.93–0.96, anterior width 1.02–1.04, maximum width 1.65–1.70. GENITALIA: Sclerotized rings (Fig. 6): sclerotized, area within rings narrow, postero-lateral region of rings with heavily sclerotized partial rings; dorsal wall extending anterior beyond rings, with a broadly truncate mesal margin. Maximum length 0.48, maximum width 0.99. Posterior wall (Fig. 7): A—structure curving, broadly truncate on ventral margin, with slight mesal indentation. B—structure protruding posteriorly, without indentations on ventral posterior surface; median process gradually expanded dorsad. Maximum length 0.22, maximum width 0.60.

Holotype. Male, Washington, Pacific Co., Nahcotta Oyster Research Station, 14 June 1979, ex. *Agropyron repens,* M. D. Schwartz (CAS type no. 15024). Paratypes: 15 males, 17 females, same data as holotype (AMNH, CAS, CNC, OSU, USNM).

Other specimens examined. 232 specimens were examined from the fol-

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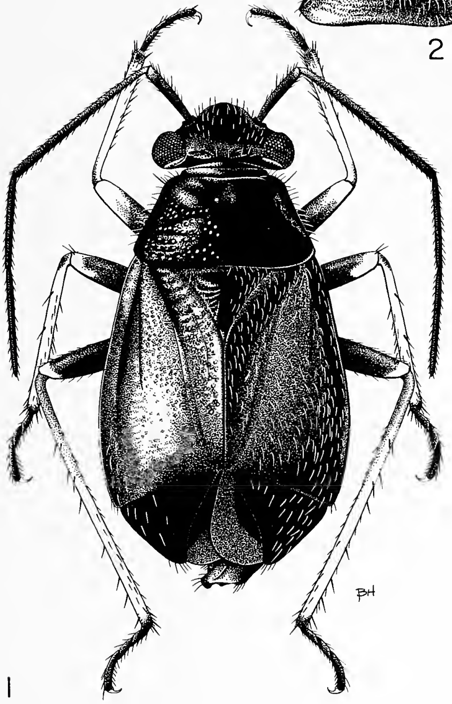
Figs. 1–8. 1. Dorsal view of body, *I. knighti.* 2. Dorsal view of pronotum, *I. sericans.* 3. Dorsal view of left paramere, *I. knighti.* 4. Dorsal view of right paramere, *I. knighti.* 5. Ventral view of vesica, *I. knighti.* 6. Posterior view of sclerotized rings and dorsal labiate plate, *I. knighti.* 7. Posterior view of inter-ramal sclerites, *I. knighti.* 8. Distribution map, *I. knighti.* Specimens illustrated are from Washington, Pacific Co. (OSU).



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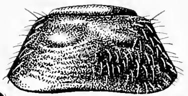

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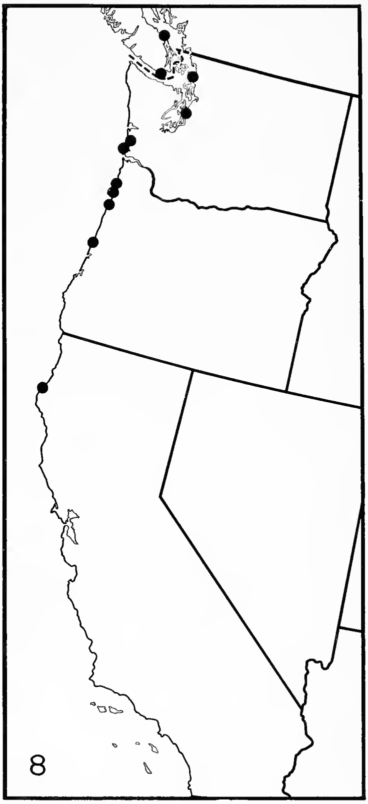

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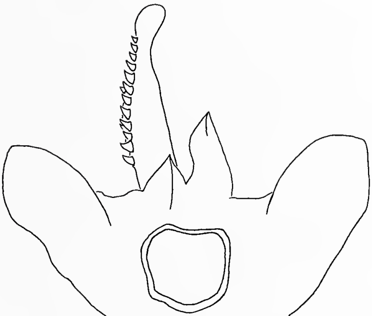

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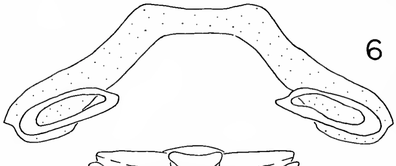

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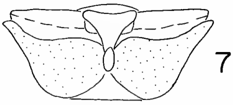

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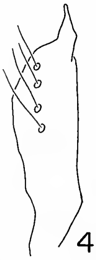

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lowing localities (Fig. 8): **CANADA:** BRITISH COLUMBIA: Jesse Island—(Nanaimo), 3 June 1925, 1♀ (USNM); G. J. Spencer, 1♂, 3♀♀ (UBC); 1♂ (UCB). Royal Oak, 3 June 1959, L. A. Kelton, 3♂♂, 3♀♀ (CNC). Victoria, 4 August 1912, J. B. Wallis, 1♀ (USNM); 25 June 1925, K. F. Auden, 3♀♀ (UCB); 1♀ (USNM); W. Downes, 1♂ (USNM); 15 July 1923, K. F. Auden, 1♀ (UCB); 3 June 1933, O. H. Swezey, 2♀♀ (CAS); 15 May 1928, W. Downes, 1♂, 1♀ (USNM). **UNITED STATES:** CALIFORNIA: *Humboldt Co.,* 5 mi. W Loleta—tidal mud flat, 9 June 1963, Ball, Freitag, Lister, McDonald, 1♀ (UALB). OREGON: *Lane Co.,* 12 mi. N Florence—Big Creek Rd.—Siuslaw Nat. For., 30 May 1979, ex. *Holcus lanatus,* M. D. Schwartz, 1♂, 2♀♀ (OSU). *Tillamook Co.,* 2.3 mi. N Neskowin on rt. 101, 21 May 1979, ex. *Festuca rubra, Holcus lanatus, Poa pratensis,* M. D. Schwartz, 27♂♂, 8♀♀ (OSU); 0.1 mi. N Rockway on rt. 101, 1 June 1979, M. D. Schwartz, 1♂ (OSU); Sand Beach Cmpgrd.—2 mi. W Sand Lake, 13 June 1972, ex. *Poa* sp. & *Carex* sp., J. D. Lattin, 9♂♂, 21♀♀ (OSU); Sand Lake, 7 July 1962, G. C. Eickwort, 3♂♂, 2♀♀ (MSU); Tierra del Mar, 13 June 1972, J. D. Lattin, 1♂ (OSU). WASHINGTON: *King Co.,* Seattle, 20 May 1916, 14♂♂, 8♀♀ (OSU); 24 May 1928, 1♂ (OSU); 25 May 1928, 1♂ (OSU). *Pacific Co.,* Bay Center, 30 June 1931, 1♀ (OSU); Nahcotta, 14 June 1979, ex. sweeping grasses just above tide line on bay shore, R. T. Schuh, 14♂♂, 6♀♀ (AMNH); G. M. Stonedahl, 1♂ (OSU); Wallapa Bay—near Nahcotta, 12 June 1971, W. J. Turner, M. Wiebers, J. A. Novak, D. N. Feno, 29♂♂, 25♀♀ (WSU). *Skagit Co.,* Mt. Vernon, 25 May 1961, M. C. Lane, 1♂ (OSU).

Etymology. Named in honor of the late Dr. Harry Hazelton Knight of Iowa State University, the renowned worker of the North American Miridae. The junior author, during his undergraduate years at Iowa State, had the good fortune to work with Dr. Knight who kindled the former's interest in the Hemiptera.

Discussion. The genus *Irbisia* contains 23 species; all are Nearctic (Schwartz, 1981). The junior author found this species with specimens borrowed from WSU. In addition, the senior author upon examining the Knight collection, at the United States National Museum at Washington, D.C. found five specimens of *Irbisia* with Dr. Knight's characteristic red labels indicating a "new species." These specimens are of *I. knighti.*

This species is narrowly distributed along the coastal flatlands of the Pacific Northwest. It occupies a very restricted portion of the Vancouveran Zone as defined by Van Dyke (1939). Adult specimens were collected from these hosts: *Agropyron repens* (L.) Beauv., *Carex* sp. (a sedge), *Festuca rubra* L., *Holcus lanatus* L., *Poa pratensis* L., and *Poa* sp. None of these grasses (*Carex* sp. is a doubtful host) are obligatorily associated with the apparent restricted habitat of *I. knighti.* Collection dates are from 15 May to 15 July. All localities are from sea level to 45 meters (150 feet) elevation.

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The authors wish to thank Ms. Bonnie B. Hall, for the dorsal view illustration. The following institutions and curators kindly loaned specimens: American Museum of Natural History, New York (AMNH), Dr. Randall T. Schuh; California Academy of Sciences, San Francisco (CAS), Dr. Paul H. Arnaud, Jr.; Canadian National Collection, Ottawa (CNC), Dr. Leonard A. Kelton; Montana State University, Bozeman (MSU), Ms. Sharon D. Rose; University of Alberta, Edmonton, Canada (UALB), Dr. George E. Ball; University of British Columbia, Vancouver, Canada (UBC), Dr. Geoffrey G. E. Scudder; University of California, Berkeley (UCB), Dr. Jerry A. Powell; United States National Museum, Washington, D.C. (USNM), Dr. Richard C. Froeschner and Mr. Thomas J. Henry; James Entomological Collection, Pullman, Washington (WSU), Dr. William J. Turner.

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DESCRIPTIONS OF THE NYMPHAL INSTARS OF *OECLEUS BOREALIS* (HOMOPTERA: FULGOROIDEA: CIXIIDAE)[1]

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Abstract.—The 5 nymphal instars of *Oecleus borealis* Van Duzee are described and illustrated. Features useful in separating nymphal instars include the size, and form of teeth and spines on the profemora and tibiae, size of body and wingpads, and the numbers of pits, and metatarsomeres.

Oecleus borealis Van Duzee has been recorded from New York south to Florida and west to Michigan, Kansas, and Texas (Kramer, 1977). Adults have been collected on apple (*Malus* sp.), hickory (*Carya* sp.), New Jersey tea (*Ceanothus americanus* L.) and desert willow (*Chilopsis linearis* DC.) (Kramer, 1977). Information on the immatures of any cixiid is very limited as they are subterranean: Cumber (1952) described the immatures of *Oliarus atkinsoni* Myers, Myers (1929) described some immature stages of *Mnemosyne cubana* Stål and *Bothriocera signoreti* Stål. Wilson and Tsai (1982) recently provided detailed descriptions of the immatures of *Myndus crudus* Van Duzee. We describe the five immature stages of *Oecleus borealis* Van Duzee in this paper.

MATERIALS AND METHODS

Specimens to be described were collected by Tsai and Thompson at two localities in peninsular Florida (collecting data given below) and preserved in 70% ethyl alcohol. The first instar is described in detail, but only major changes from previous instars are described for subsequent instars. Comparative statements refer to previous instars (e.g., more numerous). Measurements are given in mm as mean ± SE. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the thorax,

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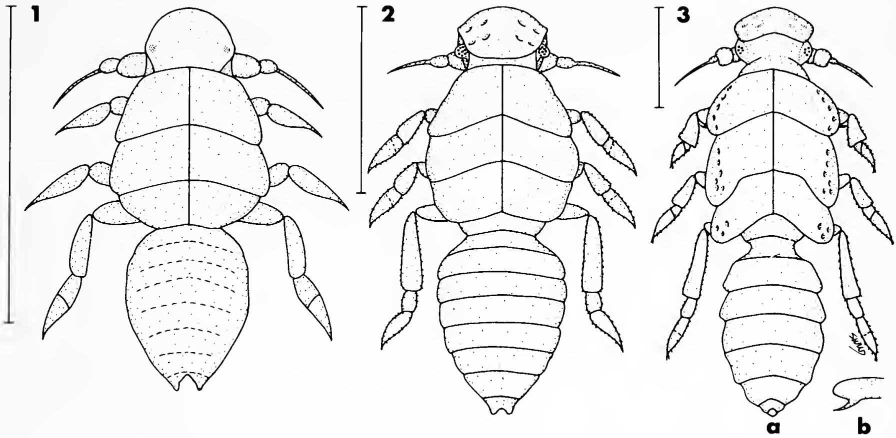


Figs. 1–3. Nymphs of *O. borealis.* 1. First Instar. 2. Second Instar. 3. Third Instar, a. Nymph, b. Median aspect of apex of profemur. Vertical bars = 0.5 mm.

and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum.

Nymphs of *O. borealis* were first discovered in January 1975 by the junior author (CRT) in sand pine woods [*Pinus clausa* (Chapman)], 27–32 km east of Silver Springs, Marion Co. Florida in Ocala National Forest. The subterranean nymphs were found 30–45 cm deep in white sand areas where vegetation consisted of saw-palmetto [*Serenoa repens* (Bartram)] and turkey oak (*Quercus laevis* Walter) as well as sand pine. Nymphs were subsequently found in similar habitats in Orange and Broward counties. An adult reared from a late instar nymph was identified as *O. borealis* by J. P. Kramer, USNM. The economic importance of this insect is unknown.

Collecting data for the specimens used in the descriptions are: FLORIDA: Broward Co.: Ft. Lauderdale, 28 May 1982 (2 first instars), 23 July 1982 (1 third instar); Orange Co.: Orlando, 18 November 1982 (5 fourth instars, 12 fifth instars); Marion Co.: Ocala National Forest, 15 September 1982 (1 fourth instar), 18 June 1979, (1 first instar, 7 second instars, 3 fourth instars, 3 fifth instars; same locality, no date—1 third instar, 3 fifth instars).

DESCRIPTIONS OF THE NYMPHAL INSTARS

First instar (Fig. 1). Mean length 0.69; thoracic length 0.27; width 0.26. Three specimens examined.

Form elongate, subcylindrical, slightly flattened dorsoventrally, widest across junction of meso- and metathoraxes. Vertex, frons, thoracic nota, and abdominal tergites with a few (less than 10) shallow indistinct pits. Body white.

Vertex broadly rounded anteriorly, slightly narrowing posteriorly. Frons with lateral margins convex and forming shelf-like carinae beneath eyes. Clypeus narrowing distally. Beak apparently 3-segmented [based on comparison with later instars and first instars of other cixiids e.g., *Myndus*; see Wilson and Tsai (1982)]; extending just beyond metacoxae. Eyes reduced, barely visible in ventral view, reddish. Antennae 3-segmented; scape and pedicel subcylindrical and subequal; flagellum bulbous basally, filamentous distally, bulbous portion ca. ½ length of pedicel.

Thoracic nota divided by a longitudinal mid-dorsal line into 3 pairs of plates. Pronotum longest laterally; each plate subquadrate, anterior margin almost straight, posterior margin slightly concave, lateral margin broadly curved. Mesonotum with median length subequal to that of pronotum; each plate subquadrate, posterior margin slightly concave, lateral margin slightly convex. Metanotum with median length ca. ⅔ that of mesonotum; each plate subquadrate, lateral margin sharply angled posteromedially. Pro- and mesocoxae posteromedially directed; metacoxae smaller, obscured by trochanters. Profemora with a slightly swollen appearance. Pro- and mesotibiae very short, ca. ½ length of tarsi; metatibiae elongated, slightly longer than metatarsi. Tarsi 2-segmented, divisions between tarsomeres obscure; with a pair of tiny apical claws.

Abdomen apparently 9-segmented (although specimens were cleared in 10% KOH, segments were very difficult to see; the supposed number of segments is based on comparison with later instars and first instars of other cixiids (e.g., *Myndus*; see Wilson and Tsai, 1982), subcylindrical, widest basally; posterior-most segment surrounding anus.

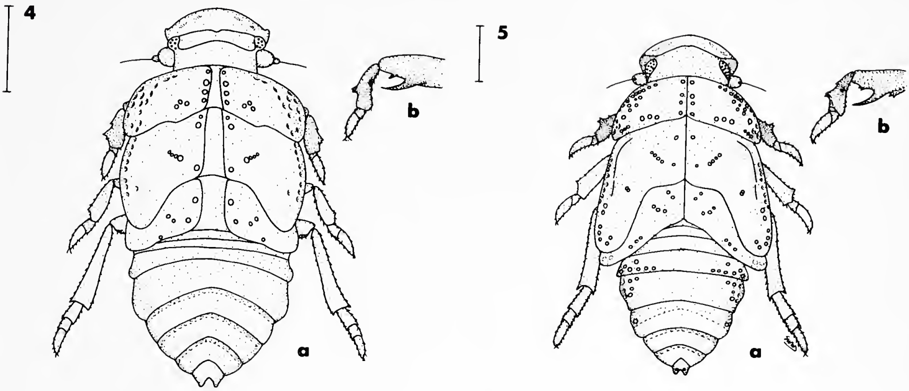
Second instar (Fig. 2). Length 1.05 ± 0.05; thoracic length 0.46 ± 0.03; width 0.46 ± 0.03. Seven specimens examined.

Widest across mesothorax. Thoracic nota with pits generally more numerous. Pro- and mesotibiae with lengths subequal to those of tarsi. Otherwise, similar to first instar.

Third instar. (Fig. 3). Mean length 1.95; thoracic length 0.73; width 0.79. Two specimens examined.

Frons and clypeus with a continuous row of ca. 11 tiny black dotlike pits paralleling lateral margins. Beak with segment 2 ca. 2× length of segment 1; segment 3 subequal to 2. Antennae with bulbous portion of flagellum ca. ¼ length of pedicel.

Thoracic nota with pits generally more numerous. Pronotum with each plate bearing 4 pits paralleling median line and ca. 13–15 total pits on plate. Mesonotum with median length ca. 1½× that of pronotum, distinctly lobate posterolaterally. Metanotum with median length ca. ⅔ that of mesonotum; each plate with 1 pit in anteromedial corner, ca. 4 pits near middle and ca.



Figs. 4, 5. Nymphs of *O. borealis*. 4. Fourth Instar. 5. Fifth Instar, a. Nymph, b. Median aspect of apex of profemur, protibia, and protarsus. Vertical bars = 0.5 mm.

3 pits laterally. Profemora with ca. 0.05 mm curved spine in distal ½. Pro- and mesotibiae subequal in length to tarsi; protibiae with small spine in distal ½, metatibiae with a row of 5 very small spines apically.

Fourth instar (Fig. 4). Length 2.47 ± 0.19; thoracic length 0.98 ± 0.03; width 1.03 ± 0.05. Nine specimens examined.

Frons and clypeus with a continuous row of ca. 20 tiny black dots paralleling lateral margins. Antennae with scape reduced and ring-like. Pronotum with each plate bearing 4 pits paralleling median line and ca. 20 pits on plate. Mesonotum with each plate bearing 1–2 pits near anteromedial corner, 1 pit near posteromedial corner, an oblique row of 4 pits near middle and an irregular row of very shallow pits (apparently absent in some specimens) paralleling lateral margin; wingpad lobate and covering ca. ⅔–¾ of metanotal plate laterally. Metanotum with each plate bearing ca. 5 pits. Profemora with ca. 0.15 mm curved spine in distal ½ and a very small tooth between spine and apex. Protibiae with a large bifid tooth in distal ½, a small tooth proximal to it, and 1 large tooth on median aspect (Figs. 4A, B). Metatibiae with a row of 5 small black-tipped spines apically. Metatarsi 3-segmented; tarsomere 1 cylindrical with a row of 4 very tiny black-tipped spines apically; tarsomere 2 cylindrical with a small black-tipped spine on either side at apex; tarsomere 3 subconical, slightly curved and bearing a pair of slender apical claws.

Abdominal tergites 6–8 each with dorsoposteriorly oriented white waxpads in intermembranous areas posterior to tergal plates; waxpads probably paired and present but indistinct in earlier instars (see Wilson and Tsai, 1982).

Fifth instar (Fig. 5). Length 3.23 ± 0.11; thoracic length 1.34 ± 0.02; width 1.52 ± 0.04. Eighteen specimens examined.

Frons and clypeus with a continuous row of ca. 16–25 tiny black dots paralleling lateral margins. Antennae with bulbous portion of flagellum ca. ⅙ length of pedicel.

Pronotum with each plate bearing 4 pits paralleling median line and ca. 30 or more total pits on plate (many pits very shallow and obscure). Mesonotum with each plate bearing 1–2 pits near anteromedial corner, an oblique row of 5 pits near middle of plate and numerous shallow pits paralleling lateral margins; wingpad extending to or nearly to apex of metanotal wingpad. Metanotum with each plate bearing ca. 6–8 shallow, obscure pits. Profemora with ca. 0.2 mm curved spine in distal ½ and a small unifid or bifid tooth distal to it on median aspect; on lateral aspect with 2 small teeth in basal ½ and 1 small tooth in distal ½. Protibiae with bifid tooth in basal ½ in median aspect, bifid tooth near apex and 1 small tooth in basal ½ of anterior aspect, and 1 tooth in basal ½ of lateral aspect. Metatarsomere 1 with an apical row of 5 black-tipped teeth.

Abdomen with pits generally more numerous.

KEY TO THE NYMPHAL INSTARS

1\. Metatarsi subdivided into 3 tarsomeres; profemur with small tooth distal to curved spine (Figs. 4, 5) 2
– Metatarsi subdivided into 2 tarsomeres; profemur without small tooth distal to curved spine or spine lacking (Figs. 1–3) 3
2\. Mesothoracic wingpads extending to or nearly to apex of metathoracic wingpads (Fig. 5); metatarsomere 1 with an apical row of 5 spines .... Fifth Instar
– Mesothoracic wingpads extending at most ¾ length of metathoracic wingpads (Fig. 4); metatarsomere 1 with an apical row of 4 spines .... Fourth Instar
3\. Profemur with curved spine in distal ½ (Fig. 3b); thoracic length greater than 0.7 mm .... Third Instar
– Profemur without curved spine in distal ½; thoracic length less than 0.6 mm 4
4\. Protibia ca. ½ length of protarsus; thoracic length less than 0.35 mm (Fig. 1) .... First Instar
– Protibia subequal in length to protarsus; thoracic length greater than 0.35 mm (Fig. 2) .... Second Instar

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ON THE BIOLOGY OF CAVE INHABITING ANTILLOCORINI WITH THE DESCRIPTION OF A NEW SPECIES FROM NEW GUINEA (HEMIPTERA: LYGAEIDAE)[1]

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Abstract.—Botocudo cavernicola is described as a new species from bat guano in a cave in New Guinea. Comments on the cave habitat are included. This is thought to be the first record of a lygaeid inhabiting caves in the Eastern Hemisphere. The biology of *Cligenes subcavicola* Scudder, Darlington and Hill is discussed. It is reported to feed on the seeds of *Piper* sp. found in bat guano in caves and abandoned buildings on Trinidad. The species is reported from a cave in Peru for the first time where it feeds at least in part on the seeds of species of *Ficus.*

The only species of Lygaeidae previously known to inhabit caves is *Cligenes subcavicola* Scudder, Darlington and Hill. Recently I have had the opportunity to observe this species in the field in Trinidad.

Through the kindness of Mr. W. R. Dolling and Dr. T. E. Woodward I have also been able to study a species that inhabits a bat cave in New Guinea and which is described below as a new species. To my knowledge these are the only lygaeids thus far known to live in caves where presumably both feed on mature seeds that have passed through the digestive tracts of frugivorous bats.

All measurements are in millimeters.

Botocudo cavernicola, new species
(Fig. 1)

Body broadly elliptical. Head, pronotum, scutellum, antennal segments I, II, and III, abdomen and thoracic pleura bright red brown. Apex of scutellum white. Base of head between ocelli darker. Hemelytral ground color white; area within corial furrow nearly to outer closely set row of punctures translucent, widening posteriorly. Corium with strongly contrasting red brown markings as follows: posterior ¾ of lateral corial margin; a large transverse

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vitta at level of claval commissure extending broadly along lateral margin, extending mesad to corial furrow and continued caudo-mesal along outer margins of translucent area to reach apical corial margin just laterad of where apical margin becomes strongly concave; remainder of apical corial margin red brown terminating in a very large brown terminal macula. (This coloration thus creating a large white ovoid spot distally on corium.) Membrane translucent. Legs and labium uniformly pale yellow. Fourth antennal segment (except for base) white. Pronotal and scutellar punctures colored as rest of surface; hemelytral punctures dark red brown. Body lacking upstanding hairs; dorsal surface nearly glabrous but with scattered, very short, sericeous hairs present, these more prominent on head, where anteriorly directed.

Head non-declivent, tylus nearly attaining distal end of first antennal segment. Eyes sessile, in contact with antero-lateral pronotal angles. Length head 0.50, width 0.68, interocular space 0.40. Pronotum broadly trapezoidal, lateral margins very strongly narrowing anteriorly, slightly sinuate; no transverse impression; posterior margin evenly and shallowly concave. Length pronotum 0.68, width 1.40. Scutellum lacking a median elevation. Length scutellum 0.84, width 0.81. Hemelytra with lateral corial margins nearly straight, explanate. Apical corial margin deeply concave on inner third. Membrane slightly exceeding end of abdomen. Length claval commissure 0.20. Midline distance apex clavus-apex corium 0.70. Midline distance apex corium-apex membrane 0.60. Metathoracic scent gland auricle strongly bent posteriorly, acute at distal end. Evaporative area small, occupying only a small area around auricle, outer margin slightly convex. Fore femora slender, mutic. Labium extending well between mesocoxae. Length labial segments I 0.40, II 0.46, III 0.36, IV 0.26. Antennae slender, terete. Length antennal segments I 0.36, II 0.66, III 0.56, IV 0.66. Total body length 3.40.

Holotype ♀. PAPUA NEW GUINEA: West Sepik District of Tedi nr. Tabubil VII–IX.1978 (N. Plumley) (Woltem Cave: on moist guano). In British Museum (Natural History). Paratype: 1 female. Same data as holotype. In J. A. Slater collection.

Discussion. This strikingly colored species is readily separable from any *Botocudo* species yet described from the Eastern Hemisphere. It is larger than any known species; of those previously described only *assimilans* Bergroth (Philippines) exceeds 3 mm in length. However, *assimilans* has a bicolored pronotum in which the posterior pronotal lobe has a broad whitish fascia and brown rather than pale yellow front legs. Bergroth (1918) relates *assimilans* to *signandus* Distant.

China (1930) in his description of *swezeyi* from Samoa states that it is "readily distinguishable from all other species by the uniformly red-brown pronotum and scutellum." This is true of *cavernicola.* However, the two species are readily distinguishable. *B. swezeyi* is only 2.3 long (the subspecies *major* reaches 2.7), has a fuscous brown rather than white fourth antennal segment, shining meso- and metapleura and dark spots on the pronotal humeri. The illustration in China's paper shows a straight apical corial margin but this is probably an artist's error.

The most interesting feature of this new species is its habitat. It is the first species of lygaeid that, to my knowledge, has been taken in a cave in the Eastern Hemisphere.

Mr. Noel Plumley who collected the type material has kindly sent me information on the habitat from which the material was taken. Woltem Cave is located at 5°14′S, 141°13′E in the Victor Emanuel Region of Papua New Guinea. The lygaeids were taken from bat guano in the entrance series near where a stream bed enters. The guano in the area was damp, moderately firm in consistency and probably no more than 5 cm in depth. A large number of small seeds similar in size to millet seeds were present in this guano. Mr. Plumley says that a large species of flying fox inhabited part of the entrance series. It is probable that droppings from these flying foxes provided the seeds upon which the insects were feeding. A smaller bat species occurred deeper in the cave but lygaeids were not collected in that area.

Thus we appear to have the independent acquisition of members of the same lygaeid tribe of the habit of feeding in caves upon seeds that have passed through the digestive tracts of the fruit eating bats.

Cligenes subcavicola Scudder, Darlington and Hill

Scudder, Darlington and Hill (1967) described *Cligenes subcavicola* from the Tamana Caves in Trinidad. This was the first record of a lygaeid living and breeding in underground caves. The Tamana Caves are limestone caves inhabited by both insectivorous and frugivorous bats. *C. subcavicola* was reported as living on the floor of the cave on and in the surface layers of bat guano in large numbers, in some instances reaching a density of the order of 100,000 per square meter. These authors did not establish the feeding habits but did suggest that they may have been feeding on the many seeds present in the guano or that they were predatory upon organisms in the guano. They described the egg and commented upon features of the nymphs.

A year after the publication of Scudder, Darlington and Hill's paper Drs. C. W. and L. B. O'Brien collected a series of *C. subcavicola* from Lechuzas Cave in Peru (Cueva de Lechuzas, Huanuco Province, near Tingo Maria, 12.VII.1968, C. W. and L. B. O'Brien).

Three years later Dr. R. T. Schuh visited Lechuzas Cave and has been kind enough to make his field notes available to me. In general his obser-

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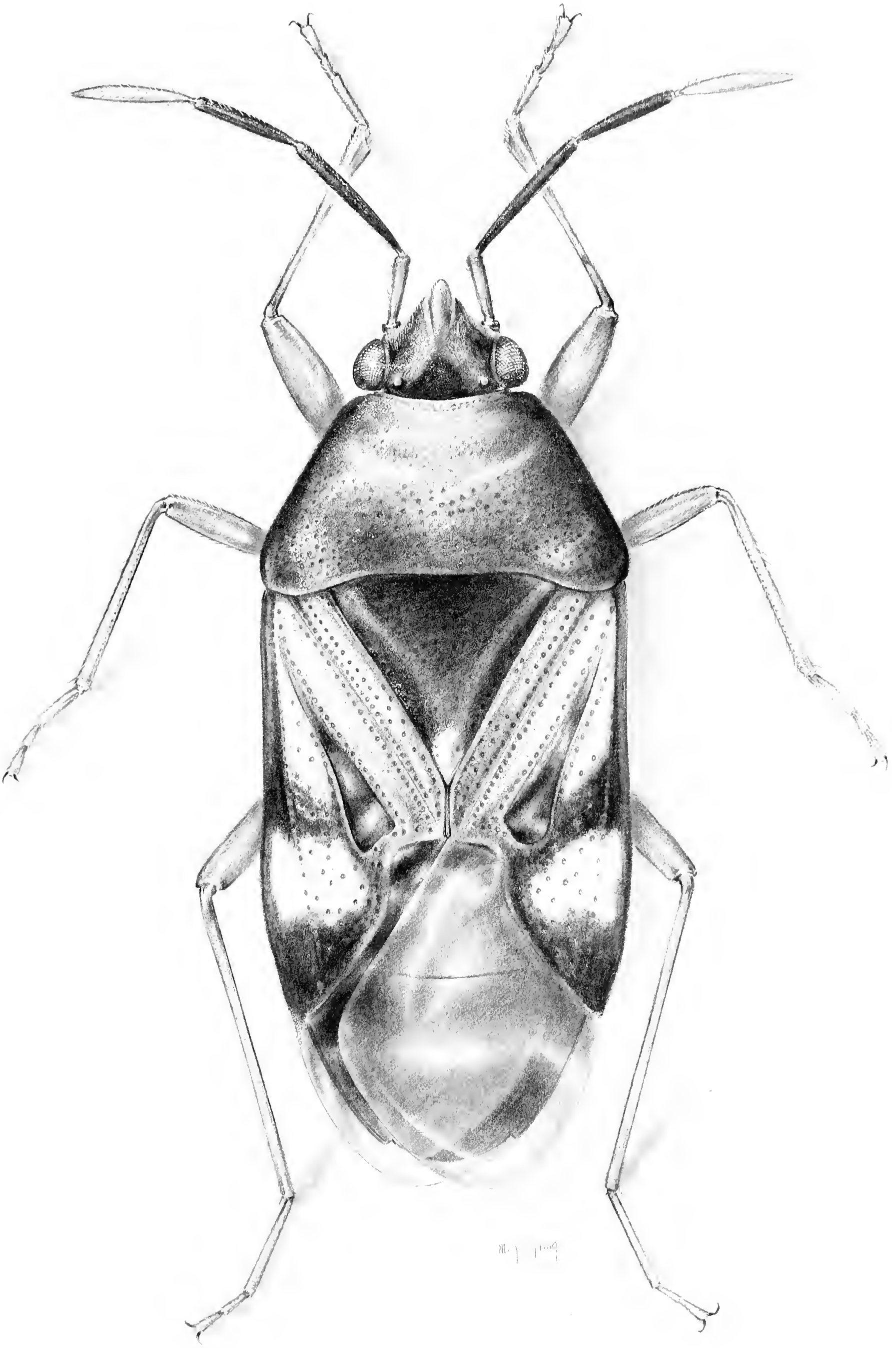
Fig. 1. *Botocudo cavernicola* new species. Holotype, dorsal view.



vations agree with the situation at the Tamana Caves on Trinidad and at Woltem Cave in New Guinea. Dr. Schuh's notes indicate that the main part of the cave is divided into two distinct caverns. The first chamber is large (about 150–200 feet long) and rather cubic in design with considerable light entering from the outside. The second chamber is somewhat smaller with very little light present. The lygaeids were concentrated in the outer two-thirds of the first chamber. The floor of the cave in this area was almost devoid of large seeds which are primarily those of palm and laurel fruits. These form the principal dietary items for the oil birds *Steatornis,* which occupy the inner portion of the first chamber and all of the second. The floor of the outer two-thirds of the first chamber consisted of thousands of tiny seeds mixed with soil and bat and parrot guano. Dr. Schuh found the *Cligenes subcavicola* population to be almost exclusively confined to this outer area of the cave where they occurred in "unbelievably large numbers" (one bagful of soil collected contained literally (!!!) thousands of lygaeids) and could be found in the "soil" to a depth of 3–4 inches.

Dr. Schuh feels that a great proportion of the small seeds in the lygaeid habitat were of one or more species of *Ficus.*

It is of interest to note that Dr. Schuh also collected litter living lygaeids immediately outside the cave, in fact inside the outermost overhang of the cave. He found small seeds in the litter and a species of rhyparochromine present but not a single specimen of *Cligenes subcavicola.* This is an additional indication that the latter may be confined to caves and other closed habitats where bat guano is present.

Recently Dr. R. M. Baranowski discovered a large breeding colony of *subcavicola* in an abandoned building at the Simla Subtropical Station in the Arima Valley of the North Range on Trinidad. Our collecting party (R. M. Baranowski, R. Clayton, M. Hassey, J. and E. Slater) visited this site on August 23, 1982. The building is constructed of concrete blocks. It apparently was used for photography and sound control work as there is a single entry with an interior wall to screen out light. The interior is completely dark during daylight hours. It is functionally a "cave" and is known to local investigators as the "bat house" because of the large colony of bats present. *C. subcavicola* is abundant on and in the upper layers of bat guano as described by Scudder et al. (1967). The insects climb upward for a foot or more on the vertical walls and move about actively, each carrying a small seed impaled on the end of the rostrum. Most of these seeds are of a species of *Piper,* the fruit of which forms a considerable part of the diet of the frugivorous bats inhabiting the building. Nymphs of all instars were present and there is no doubt but that this is a thriving population that is feeding upon seeds that have passed through the digestive systems of the bats.

The occurrence of *Cligenes subcavicola* in caves as far removed from each other as Trinidad and Peru raises at least two questions. (1). Is the species confined to caves? (2). If it is there must still be considerable dispersal or the populations would presumably show geographic differentiation.

C. subcavicola as noted by Scudder et al. (1967) does not show any of the adaptations usually associated with true cavernicoles such as loss of body pigmentation and reduction of the wings, eyes, and ocelli. The insects also do not occur in the deeper parts of either the Tamana or Lechuzas Caves. This suggests that they may not be confined to caves. When the first report appeared I had thought this was primarily an adventitious adaptation to a plentiful food source. However, the occurrence of the same species in bat guano in two separate places in Trinidad and in a cave in Peru together with its complete absence in collections from any other habitat (including light traps where many other antillocorines are taken in abundance) suggests that the occurrence is certainly not fortuitous but an adaptive strategy of the species.

The degree of host specificity in the Antillocorini is also very poorly understood. The only other species of *Cligenes* (*distinctus*) does appear to be restricted to fallen seeds of various species of *Ficus*. I have collected long series of this species on several islands of the West Indies and in southern Florida, always in this habitat.

Botocudo cavernicola also does not show any obvious adaptations to cave dwelling. It is in fact one of the more brightly colored species of *Botocudo* with large eyes and ocelli. It will probably prove to have similar habits to those of *Cligenes subcavicola.*

The carrying of small seeds on the end of the rostrum by *Cligenes subcavicola* is very reminiscent of the actions of species of *Stilbocoris* in Africa. Carayon (1964) has given a fascinating account of the activity of members of this genus. Here the male injects salivary secretion into the mature fallen seeds of *Ficus* and offers the softened seed to the female who only then will allow the male to copulate. *Cligenes subcavicola* (and probably also *Botocudo cavernicola*) can be readily maintained in laboratory culture and it would be valuable to know if the complex behavior found in species of *Stilbocoris* is more widespread in the Rhyparochrominae.

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THE TYPES OF SOME AMERICAN *CERCERIS* WITH LECTOTYPE DESIGNATIONS (HYMENOPTERA: PHILANTHIDAE)[1]

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Abstract.—The primary types of 37 species-group taxa of American *Cerceris* are discussed, and lectotypes are designated for 32 species-group taxa. Four previously designated neotypes are shown to be invalid, and three holotypes are identified.

As part of a study of North American and Caribbean wasps of the genus *Cerceris* the primary types of most of the described taxa have been studied. Cresson (1916, 1928), Scullen (1965, 1972), and Ferguson (1983) designated lectotypes for many species, most of which are located in type repositories in the United States. Most of the lectotypes designated in this paper involve species described by F. Smith, Saussure and Cameron and are located in European institutions. In a few cases the specimens comprising a syntype series are not conspecific; in other cases the specimens of a syntype series are located in more than one institution. All lectotypes and holotypes discussed herein agree with the original descriptions unless otherwise noted. The synonymy and taxonomic status of the species discussed below will be treated in a forthcoming synonymic list. Abbreviations used in the text for type repositories are explained in Acknowledgments.

Cerceris acolhua Saussure, 1867:90.

Described from at least two males from "Mexico. In planitie alta (terris frigidis), . . ." and from "provincia Mechoacan". A male in Geneva labelled "Mexico t.f." is here designated lectotype. A second conspecific syntype male in Vienna is rather badly damaged.

Cerceris azteca Saussure, 1867:97.

Described from eight females from Cuantla and two females from Orizaba, Mexico. A female in Vienna bearing a "Cuantla t.c." label, a printed red

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"Type" label, a handwritten "*Cerceris azteca* Sauss." label, and an "*azteca* Type det. Sauss." label is here designated lectotype.

Cerceris bakeri Cameron, 1904:67.

Described from an unstated number of females from "Chinandega, Nicaragua". A female in the BMNH labelled "Chinandega, Nicaragua, Coll. Baker" is here designated lectotype. It also bears a circular red margined "Type" label, a printed "Cameron Coll. 1904-313" label, a handwritten "3055" label, a handwritten "*Cerceris bakeri* Cam. Type Nicaragua" label, and a printed "B. M. Type Hym. 21.1, 371" label. Scullen (1972) saw a second female at Pomona College, but it has not been found in the USNM where most of the Baker collection of Hymenoptera is now housed.

Cerceris binodis Spinola, 1841:117.

Described from two males from Cayenne, French Guiana. Two conspecific syntype males are in the Spinola collection in Torino. These have been standing under the header label "*Philanthus binodis* m., *Didesmus Spinolae* Dlbm., D. Buquet, M. Le Prieur". The specimens are otherwise unlabelled. The larger of the two specimens is here designated lectotype.

Cerceris bothriophora Schletterer, 1887:456.

Described from an unstated number of both sexes from "Reg. V. Subreg. 3. (Mexico)". One female and two males in Vienna bear handwritten "*bothriophora* det. Schletterer" labels. These specimens agree with the original description including the fact noted by Schletterer, that the fossette present on tergum I of the female is absent in the males. The female also bears the labels "Withm." and "Newhaven" (handwritten and almost illegible). It is a specimen of *Cerceris atramontensis* Banks, a common species in the area of New Haven, Connecticut. Scullen (1972) designated and labelled this specimen neotype, but this designation is rejected as invalid since it was not shown that the original syntype series was lost or irretrievably damaged. Although not from Mexico, the female agrees with the original description, and it seems clear that Schletterer thought it was from a Mexican locality.

One male is labelled "Georg. Am. 1877 II" and is a specimen of *Cerceris compar* Cresson. Although the specimen agrees with the rather incomplete original description, the possibility exists that it is not a syntype because of the locality label.

The second male has a handwritten "Aug." label and a printed "Bilimek, Mexico, 1871" label with an illegible handwritten word below the printing. This specimen also agrees with the original description and is here designated lectotype, since the label agrees with the type locality given in the original description.

Cerceris chinandegaensis Cameron, 1904:66.

Described from an unstated number of males from Chinandega, Nicaragua. Scullen (1972) saw four males: one each at BMNH and Cornell, and two at Pomona College. I have seen three conspecific males: one each at the BMNH, Cornell, and the Baker collection now at the USNM. The second male from Pomona College reported by Scullen has not been located. The three specimens examined are labelled "Chinandega, Nicaragua, Coll. Baker". The BMNH specimen bearing a circular, red margined "Type" label, a printed "Cameron Coll. 1904-313" label, a handwritten "3054" label, a handwritten "*Cerceris chinandegaensis* Cam. Type Nicaragua" label, and a printed "B. M. Type Hym. 21.1, 374" label is here designated lectotype.

The USNM specimen bears a "*Cerceris kennicottii bakeri* Cameron det. H. A. Scullen" label. The Cornell specimen bears a printed "Cornell U. Lot 546 Sub 207 Baker Coll." label, and a "*Cerceris kennicottii* Cresson det. H. A. Scullen" label.

Cerceris clypeata Dahlbom, 1844:221.

Described from both sexes from "Carolina meridionali . . . Dr. Zimmerman". Number of specimens not stated. A female and male in Lund are not conspecific. The female bears a handwritten "105" label, a "E. Sudcarolina Zimmerman" label, an unmarked red label, and a blue "1982-402" label. It is here designated lectotype. The male bears a handwritten "104" label, a "S. Carolina" label, a "*Cer. clypeata* Kl. Mus. Berol." label, and a blue "1982-403" label. It is a male of the homeochromic *Cerceris halone* Banks.

Cerceris cribrosa Spinola, 1841:119.

Described from two females and one male from Cayenne, French Guiana. I have studied a syntype female and a conspecific male syntype from the Spinola collection in Torino. Scullen (1972) designated the female as neotype, but this designation is invalid since a syntype cannot become a neotype. I here designate the same female as lectotype. The male has the gaster missing beyond the first segment.

Cerceris crotonella Viereck and Cockerell, 1904:139.

Described from one female from Las Cruces, New Mexico. Cresson (1928) does not list this species. A female in the type collection of the ANSP from Las Cruces, N. Mex. bears a handwritten "*Cerceris crotonella* V. & C." label and is accepted as the holotype. Cresson's ledger in the ANSP has a line drawn through his entry No. 10039, *C. crotonella* with the notation "off in coll. Ckll". The number 10039 is not on the specimen. Apparently the specimen was subsequently returned to the ANSP collection.

Cerceris crucis Viereck and Cockerell, 1904:139.

Described as *Cerceris rufinoda* var. *crucis* from two females from Las Cruces, New Mexico. This taxon is not listed by Cresson (1928). The specimen in the type collection at ANSP bears a "Las Cruces, N. M." label and a handwritten "*Cerceris rufinoda* var. *crucis* V. & C. Type" label, and it is here designated lectotype. The second specimen has not been located. Scullen

(1965) was incorrect in stating that the type of *crucis* carried the ANSP No. 10393 as this number applies to quite a different wasp (see Cresson, 1928, p. 42). The lectotype does not bear an ANSP type number.

Cerceris deserta Say, 1825:343.

Scullen's (1965, p. 479) statement designating a neotype for this species is not clear as to whether he or Banks made the designation. Neither the labels on the specimen nor Banks' (1912) only published reference to *deserta* give any indication that he designated a neotype. The specimen [MCZ] carries a neotype label affixed by Scullen, although it also bears a *Cerceris deserta* Say determination label apparently in Banks' handwriting. The neotype designation is clearly that of Scullen (1965).

Cerceris dilatata Spinola, 1841:118.

Described from two females and one male from Cayenne, French Guiana. I have examined a syntype female and a conspecific syntype male from the Spinola collection in Torino. Scullen (1972) designated the male as neotype, but this designation is invalid since a syntype cannot become a neotype. The female is here designated lectotype, since it is the more distinctive of the two sexes.

Cerceris elegans F. Smith, 1856:467.

Described from an unstated number of males from "Hab. East Florida (coll. E. Doubleday, Esq.)." Two conspecific males in the BMNH are each labelled "E. Doubleday, St. John's Bluff, E. Florida." One male bearing a circular orange margined "Type" label, a handwritten "*elegans* Sm. Type" label, and a printed "B. M. Type Hym. 21.1 365" label is here designated lectotype. The second male has the gaster missing beyond the first segment.

Cerceris exsecta F. Smith, 1873b:410.

Described from an unstated number of both sexes from "Hab. Mexico." I have examined one female syntype and three conspecific males from the BMNH. The female bearing a small circular "Mex." label, a handwritten "*Cerceris exsecta* Smith" label, a circular orange margined "Type H. T." label, and a "B. M. Type Hym. 21.1, 429" label is here designated lectotype. One male labelled "Mex" is probably a syntype. A second male bears a "F. Smith Coll." label, and the third male has a "Smith Coll. pres. by Mrs. Farren White, 99-303" label. Both carry a "Mexico" locality label, but it is questionable whether or not they are syntypes.

Cerceris feralis Cameron, 1890:113.

Described from an unstated number of males from "Hab. Mexico (coll. Saussure)". I have examined six conspecific males from the BMNH of which two are probably not syntypes. A male bearing a "Cuantla t.c." label, a circular orange margined "Type H. T." label, a handwritten "*Cerceris feralis*

Cam. Type B.C.A. ii, 113" label, and a printed "B. M. Type Hym. 21.1 372" label is here designated lectotype. Two males labelled "Cuantla t.c." and one labelled "Mexiq. Orizaba" each bears a "P. Cameron Coll. 1914-110" label. The italicized type face of the locality labels indicates that they are from the Saussure collection; these are accepted as syntypes. Two males each bearing a "N. Yucatan Gaumer" label and a "Cameron Coll. B. M. 1914-110" label are not from the Saussure collection and are probably not syntypes. The latter two specimens each bears a "*Cerceris compar geniculata* Cam. det. H. A. Scullen" label.

Cerceris flavida Cameron, 1890:116.

Described from an unstated number of both sexes from "Hab. Mexico, Cordova (Coll. Saussure)." A female in the BMNH bearing a "Cordova t.c." locality label, a circular blue margined "Syntype" label, a handwritten "*Cerceris placida* [sic] Cam" label, and a "Syntype *Cerceris flavida* Cam. det C. R. Vardy" label is here designated lectotype of *Cerceris flavida* Cameron. Despite the "*placida*" label the specimen has the aberrant wing venation described by Cameron in the original description. The second cubital cross vein is missing on the left front wing but represented by a stub on the right front wing. The first cubital cross vein is partially missing on the right front wing.

Cerceris flavomaculata Cameron, 1890:115.

Described from an unstated number of both sexes from "Hab. Costa Rica, Rio Susio, Cache (Rogers)." A female and a male syntype in the BMNH are not conspecific. The female bearing a circular blue margined "Syntype" label, a printed "R. Susio, H. Rogers" label, and a printed "B.C.A. Hymen. II *Cerceris flavomaculata* Cam." label is here designated lectotype. The male bears a circular blue margined "Syntype" label, a circular orange margined "Type" label, a printed "Cache, Costa Rica, H. Rogers" label, a printed "B. C. A. Hymen. II, *Cerceris flavomaculata* Cam." label, a handwritten "*Cerceris flavomaculata* Cameron, Type, B. C. A. ii, 115" label, and a printed "B. M. Type Hym. 21.1, 376" label. The specimen is without a gaster and very dirty. The portions of the specimen that can be clearly seen indicate that it is a male of *Cerceris cooperi* Scullen.

Cerceris geniculata Cameron, 1890:113.

Described from an unstated number of females from "Hab. Mexico, Cuantla (Coll. Saussure)." A female in the BMNH bearing a "Cuantla, t.c." locality label, a "P. Cameron Coll. 1914-110" label, and a handwritten "*Cerceris geniculata* Cam." label is here designated lectotypes. A second conspecific female bears a "Mexiq. Orizaba" label, a "P. Cameron Coll. 1914-110" label, a red margined circular "Type H. T." label, a "B. M. Type Hym. 21.1, 366" label, and a handwritten "*Cerceris geniculata* Cam. Type B. C. A. ii, 113" label. The Orizaba locality was not mentioned in the original description.

Cerceris hebes Cameron, 1890:124.

Described from the male from "Hab. Mexico, Chilpancingo in Guerrero 4500 feet (H. H. Smith)". Number of specimens not stated. A male in the BMNH bears a "Valladolid, Yucatan, Gaumer" label, a printed "B. C. A. Hymen. II *Cerceris hebes* Cam. Type" label, and a handwritten "(? locality G.C.C.)" label. A head glued to the thorax is that of *Eucerceris montana* Cresson (=*Cerceris sonorensis* Cameron) and is not conspecific with the remainder of the specimen. The pygidium agrees with the figure accompanying the original description and is sufficient to identify the thorax and gaster as that of a male of *Cerceris graphica* F. Smith. The thorax and gaster is accepted as the holotype despite the discrepancy in the locality label of the specimen versus the locality stated in the original description. The locality label on the specimen was "questioned by G. C. C." Nevertheless the species is identifiable from the original description and accompanying figures.

Cerceris intricata F. Smith, 1856:459.

Described from an unstated number of males from "Hab. Brazil (Santarem). (Coll. H. W. Bates)". A male in the BMNH bearing a blue circular handwritten "Braz. Santarem" label, a circular orange margined "Type" label, a handwritten "*intricata* Sm. Type" label, a printed "B. M. Type Hym. 21.1, 407" label, and a "Syntype. Another at Oxford prob. conspecific. det. C. R. Vardy 1976" label is here designated lectotype. A second conspecific male in the BMNH bears a "Para" label, a blue handwritten "*intricata* Smith" label, and a "Smith coll. pres. by Mrs. Farren White 99-303" label, but it is probably not a syntype.

Cerceris krugi Dewitz, 1881:200.

Described from five specimens of both sexes from Puerto Rico. One female and two male syntypes, all conspecific, from Berlin have been studied. The female bearing a green "Portorico Krug" label; a red, printed "TYPE" label; a white printed "22041" label; and a green, handwritten "*krugii* [sic] Dewitz" label is here designated lectotype.

One male has a green "Portorico Moritz" label; a red, printed "TYPE" label; a white "4439" label; and a green "*krugii* [sic] Dewitz" label. The second male is similarly labelled, and, in addition, has a large, green, handwritten "*krugi* Dewitz, Berliner ent. Zeit. XXV" label. The latter specimen has the head and tergum VII badly damaged. The location of the remaining two syntypes is not known.

Cerceris laevigata F. Smith, 1856:465.

Described from both sexes from Santo Domingo. Number of specimens not stated. A syntype female and conspecific syntype male in the BMNH are labelled "St. Dom. 55.1". The female bearing a circular orange margined "Type" label, a handwritten "*laevigata* Sm. Type" label, and a printed "B. M. Type Hym. 21.1, 377" label is here designated lectotype. The left hind leg is glued to a point. The male bears only the locality label.

Cerceris montezuma Cameron, 1890:108.

Described from an unstated number of females from "Hab. Mexico (coll. Saussure)". There are four specimens in the BMNH under this name of which two are conspecific females and agree with the original description. The female bearing a handwritten "Mex. Mayo [and an illegible word]" label, a "P. Cameron Coll. 1914-110" label, and a handwritten "*Cerceris montezuma* Cam." label is here designated lectotype. A second conspecific female has a handwritten "Mex." label, a printed "F. Sm. Coll. 79.22" label, and a handwritten "*montezuma*" label. Since the F. Smith collection was not mentioned in the original description, the lectotype may in fact be a holotype. However, the F. Smith collection was available to Cameron, and it seems prudent to make the lectotype designation.

A third female bears a "Omilteme, Guerrero, 8000 ft. Aug. H. H. Smith" label, a "P. Cameron Coll. 1914-110" label, a "in B. M. 1973 under *C. graphica*" label, and a handwritten "*montezuma*" label. It does not agree with the original description, but it is a specimen of *Cerceris dreisbachi* Scullen.

The fourth specimen consists of a thorax and part of the gaster on a pin with a head and the remaining part of the gaster glued to the second label. It is a male of which the head appears to be that of *Cerceris californica* Cresson and the remaining parts appear to be *Cerceris erythropoda* Cameron. It bears a "Presidio, Mexico, Forrer" label, a printed "B. C. A. Hymen. II, *Cerceris montezuma* Cam." label, a handwritten "probably wrongly named GCC" label, and a handwritten "*Cerceris montezuma* Cam. Type, B. C. A. iii, 108" label. The composite specimen bears no resemblance to the original description.

Cerceris nigra Ashmead, 1900:227.

Described from two females from "St. Vincent–Windward side" [B. W. I.]. A female in the USNM bears a printed "Windward side St. Vincent, W. I., H. H. Smith" label, a red "Type No. 6410 USNM" label, and a handwritten "*Cerceris nigra* Ashm. Type" label. It is here designated lectotype. A second female in the BMNH also carries a handwritten "*Cerceris nigra* Ashm. Type" label. I have not seen it, but according to comments received from C. R. Vardy (pers. comm.) it is conspecific.

Cerceris obsoleta Cameron, 1890:118.

Described from an unstated number of females from "Hab. Mexico, Teapa in Tabasco (H. H. Smith)". Two conspecific females in the BMNH each bears a Teapa, Tabasco, locality label. One bearing a "Teapa, Tabasco, March H. H. S." label, and a printed "B. C. A. Hymen. II *Cerceris obsoleta* Cam." label is here designated lectotype. The second specimen is very dirty and bears a "Teapa, Tabasco, Feb. H. H. S." label, a circular orange margined "Type" label, and a handwritten "*Cerceris obsoleta* Cam. Type B. C. A. ii 118" label.

Cerceris otomia Saussure, 1867:99.

Described from five males from ". . . urbis Mexico" and "Zinapecuaro in provincia Mechoacan", and three females and six males from ". . . Cordillera orientali . . . ." A female in Vienna bearing a "Mexico, Saussure, Type 1880" label, a handwritten "*otomia* Type det. Sauss." label, and a printed red "Type" label is here designated lectotype.

Cerceris pullata F. Smith, 1873a:105.

Described from two females from "Hab. St. Paulo". Two conspecific syntype females in the BMNH each bears a blue circular "St. Paul" label. One of these bearing an orange margined circular "Type" label, a handwritten "*Cerceris pullatus* [sic] Smith" label, and a printed B. M. Type Hym. 21.1, 409" label is here designated lectotype. The second female bears only the locality label. A third conspecific female bears a handwritten "*Cerceris pullatus* Smith St. Paulo" label and a printed "Smith coll. pres. by Mrs. Farren White 99-303" label, but it is probably not a syntype.

Cerceris rufopicta F. Smith, 1856:467.

Described from an unstated number of males from "Hab. E. Florida". Two male syntypes in the BMNH are conspecific. One specimen bearing a circular orange margined "Type H. T." label, a circular white label with illegible markings on both sides, a printed "R. Foster, St. John's Bluff, E. Florida" label, a handwritten "*rufopicta* Sm. Type" label, a circular blue margined "Syntype" label, and a "B. M. Type Hym. 21.1, 364" label is here designated lectotype. The second male bears a small handwritten "'71" label, a printed "E. Doubleday, St. John's Bluff, E. Florida" label, a handwritten "*rufopicta* Smith" label, a printed "Smith Coll. pres. by Mrs. Farren White, 99-303" label, and a circular blue margined "Syntype" label.

Cerceris simplex F. Smith, 1856:462.

Described from an unstated number of both sexes from "Hab. Brazil (Santarem), (Coll. H. W. Bates)". A female in the BMNH bearing a blue circular handwritten "Santarem" label, a circular orange margined "Type" label, a handwritten label with illegible marks, a handwritten "*simplex* Sm. Type" label, and a printed "B. M. Type Hym. 21.1, 438" label is here designated lectotype. A male syntype has not been located.

Cerceris simulans Saussure, 1867:87.

Described from a male from "Mexico Temperata: in Cordillera orientali". The type has not been located. A headless female in Geneva was designated neotype by Scullen (1972), but this designation is invalid since the original description was based on a male and the headless female disagrees with the original description in several important respects. Furthermore, *C. simulans* Saussure is readily identifiable from Saussure's original description and figures. The headless female is identifiable as *Cerceris scapularis* Schletterer which belongs to quite a different species group from *C. simulans.*

Cerceris smithiana Cameron, 1890:119.

Described from an unstated number of females from "Hab. Mexico, Atoyac in Veracruz (H. H. Smith)". Two conspecific females in the BMNH each bears an "Atoyac, Veracruz, May. H. H. S." label and a printed "B. C. A. Hymen. II *Cerceris smithiana* Cam." label. One of these is here designated lectotype. The second specimen also bears a circular orange margined "Type" label, a handwritten "*Cerceris smithiana* Cam. Type B. C. A. ii 119" label, and a printed "B. M. Type Hym. 21.1, 369" label, but it is very dirty.

Cerceris strigosa Cameron, 1890:110.

Described from an unstated number of both sexes from "Hab. Mexico, Ciudad in Durango 8100 feet (Forrer)". Two conspecific females in the BMNH each bears a "Ciudad Mex., 8100 ft., Forrer" label, a printed "B. C. A. Hymen. II *Cerceris strigosa* Cam." label, and a handwritten *Cerceris strigosa* Cam." label. One of these also bears a circular orange margined "Type" label and a notation on the handwritten label "Type B. C. A. ii 110", and it is here designated lectotype. It is also the cleanest of the two specimens.

Cerceris subpetiolata Saussure, 1867:95.

Described from "Mexicanus ager. Terrae calidae", "In Puebla viejo apud Tampico" two males, and "Cordillera orientalis" one female. A female in Vienna bearing a "Saussure type 880" label, a "Cordova t.c." label, a "*subpetiolata* type det. Sauss." label, and a red printed "Type" label is here designated lectotype. A conspecific syntype male bears a "Cordova t.c." label, a "Saussure type 880" label, and a "*subpetiolata* det. Sauss." label.

Cerceris townsendi Viereck and Cockerell, 1904:140.

Described from a male from Las Cruces, New Mexico. The species is not listed in Cresson (1928). A male in the type collection of the ANSP bears a "Las Cruces, N. M." label, a red "Type No. 10389" label, and a handwritten "*Cerceris acanthophiloides* V. & C." label. Cresson's ledger at the ANSP contains the entry "*C. xanthophiloides* [sic] V. & C." under his number 10389. The specimen agrees in all details of structure and coloration with the original description of *C. townsendi,* and I have no doubt that this specimen is the holotype. Apparently Viereck and Cockerell changed the name in publication and neglected to change the label on the specimen. I have affixed a label to the specimen indicating that I consider it to be the holotype of *Cerceris townsendi.*

Cerceris truncata Cameron, 1890:121.

Described from an unstated number of both sexes from "Hab. Mexico, Temax in North Yucatan (Gaumer)". I have seen six females and four males from the BMNH. All are conspecific, and all are apparently syntypes. One female and two males each bears a "Temax, N. Yucatan, Gaumer" label; and five females and two males each bears a "N. Yucatan, Gaumer" label. Each of the ten specimens bears a printed "B. C. A. Hymen. II *Cerceris truncata* Cam." label. The female labelled "Temax, N. Yucatan, Gaumer" is here designated lectotype since the locality label agrees precisely with the original description. One female labelled "N. Yucatan, Gaumer" also bears a circular orange margined "Type" label, a "B. M. Type Hym. 21.1, 433" label, and a handwritten "*Cerceris truncata* Cam. Type" label, but it is in rather poor condition.

Cerceris vulpina F. Smith, 1856:463.

Described from an unstated number of males from "Hab. Brazil". A male in the BMNH bearing a blue circular "Santarem" label, a circular orange margined "Type" label, a handwritten "*vulpina* Sm. Type" label, and a printed "B. M. Type Hym. 21.1, 418" label is here designated lectotype. A second conspecific male bears a circular white handwritten "Braz." label, a handwritten "*C. vulpina* Sm." label, and a printed "Smith coll. pres. by Mrs. Farren White 99-303" label, but it may not be a syntype.

Cerceris zapoteca Saussure, 1867:89.

Described from two males from "prope Tampico". A male in Vienna bearing a "Cordova t.c." label, a handwritten "Saussure Type 1880" label, a handwritten "*zapotecus* [sic] Type det. Sauss." label, a handwritten "*Cerceris zapotecus* [sic] Sss." label, and a red printed "Type" label is here designated lectotype. A second conspecific male in the BMNH with the same locality label is the presumed second syntype.

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TYPE DESIGNATIONS AND NEW SYNONYMIES FOR NEARCTIC SPECIES OF *PHYTOCORIS* FALLEN (HEMIPTERA: MIRIDAE)

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Abstract.—Thirty-seven lectotype and two neotype designations are made for Nearctic species of *Phytocoris* (Hemiptera: Miridae) described by O. M. Reuter, P. R. Uhler, and E. P. Van Duzee. One holotype is identified, and eight species are considered as new synonyms. Species are listed alphabetically; and for each, year of publication, original page number, exact label data, type depository, pertinent body measurements, and discovered paralectotypes are given. Comments are provided on distributions, hosts, identification keys, and male genitalia.

Prior to this study, 230 species of the plant bug genus *Phytocoris* were recognized from Canada and the United States. Most of these were described by H. H. Knight, O. M. Reuter, P. R. Uhler, and E. P. Van Duzee. Van Duzee (except for species treated in this paper) and Knight regularly designated holotypes for their species, thus satisfying Article 73(a) and Recommendation 73A of the 1961 *International Code of Zoological Nomenclature.* However, because of the lack of holotype designations and the frequency of mixed syntype series of species described by Reuter and Uhler and some by Van Duzee, the remaining species of *Phytocoris* are often difficult to identify with certainty. We have found a number of specimens bearing labels such as "typus," "lectotype," "allotype," and "paratype," indicating that someone at the respective museums recognized that these specimens belonged to the original type series of the species; these designations, however, as far as we can determine, represent in-house curation and have never been validated through publication. To insure nomenclatorial stability in the North American species of *Phytocoris,* we feel it is important to make proper type designations, or in a few cases select necessary neotypes.

We have located most of the original specimens of Reuter and Van Duzee in the California Academy of Sciences and in several European museums.

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The remaining *Phytocoris* types, including most of Uhler's, were discovered in the U.S. National Museum of Natural History. We have not found types for *interspersus* Uhler and *minutulus* Reuter.

In this paper we select 37 lectotypes, identify one holotype, and assign two neotypes for the North American *Phytocoris* described by Reuter, Uhler, and Van Duzee. Eight species names are recognized as new synonyms. When syntypes were located in the U.S. National Collection and also in European collections, we have selected the best specimen as the lectotype and have labeled the remaining syntypes as paralectotypes. If possible, we have chosen males as lectotypes, or if males are in poor condition, a female was selected. We recognize a holotype only when the author stated he had a single specimen; in all other cases, even when we could locate only one specimen, we assumed that there was a series. The lectotypes, neotypes, and holotype are identified with red rectangular labels having the appropriate type printed at the top; paralectotypes are identified with blue rectangular labels.

The list of taxa below is arranged alphabetically by species with year of publication and original page number given after the author. In the same paragraph, exact label data, set in quotes, are given for each primary type, followed by type depository, condition of primary type, measurements of major body structures of primary type, and list of secondary types located. Synonyms are listed in a new paragraph with the same data as for the valid name; species listed without this data (e.g., those described by H. H. Knight) indicate that a holotype was properly designated and accompanied by a description and measurements. A remarks section under each taxon includes such information as notes on synonymy, confused identities, sources of keys, and other pertinent comments. All junior synonyms are listed alphabetically in the text and cross referenced to the valid senior synonym; e.g., *Phytocoris bipunctatus* Van Duzee [See *annulicornis* Reuter].

The following measurements, in millimeters, are given for each primary type: Body length = BL (from apex of tylus to apex of wing membrane); body width = BW (greatest width across hemelytra, usually just above cuneus); head width = HW (width across eyes); vertex width = V (greatest distance between eyes); rostrum length = RL; length of antennal segments = AI, AII, AIII, AIV; pronotal length = PL (mesal length); pronotal width = PW (basal or posterior width).

The following abbreviations are used for institutions serving as type depositories of the *Phytocoris* species: CAS (California Academy of Sciences, San Francisco, California); TMB (Termeszettudmanyi Muzeum, Budapest); LACM (Los Angeles County Museum, Los Angeles, California); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts); NRS (Naturhistoriska Riksmuseet, Stockholm); USNM (United States National Museum of Natural History, Washington, D.C.), and UZMH (Universitetets Zoologiska Museem, Helsinki).

Phytocoris americanus Carvalho

Phytocoris angustulus Reuter, 1909:29 [name preoccupied by *Phytocoris angustulus* Germar and Berendt, 1856 (fossil mirid)]. Type data (Fig. 1).—Lectotype male (here designated): Label 1, "F[or]t. Pendl[e]t[o]n, 10-7, W[es]t V[irgini]a"; 2, "O. Heidemann Collector"; 3, "*Phytocoris angustulus* n. sp. [handwritten], O. M. Reuter det."; 4 (here added), "Lectotype: *Phytocoris angustulus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100402; condition good, except the antennae and one fore- and one hindleg are missing]. Measurements of lectotype: BL 5.92; BW 1.92; HW 0.92; V 0.32; RL 2.52; antennae missing; PL 0.92; PW 1.60. Paralectotypes: No other syntypes located.

Phytocoris americanus Carvalho, 1959:190 [new name for *Phytocoris angustulus* Reuter].

Remarks. Knight (1923) correctly recognized this species (as *angustulus*), figured male genitalia, and gave eastern hemlock, *Tsuga canadensis* (L.) Carr., as the host. Knight (1941) recorded *americanus* (as *angustulus*) from New York, North Carolina, Nova Scotia, Vermont, and West Virginia; Wheeler and Henry (1977) added Pennsylvania.

Phytocoris angustulus Reuter

[See *americanus* Carvalho]

Phytocoris annulicornis (Reuter)

Compsocerocoris annulicornis Reuter, 1876:70. Type data.—Lectotype male (here designated): Label 1, "Texas"; 2, "Belfrage"; 3, "Paratypus"; 4, "307 82"; 5, "Riksmuseum Stockholm"; 6 (here added), "Lectotype: *Compsocerocoris annulicornis* Reuter, by Henry and Stonedahl, 1983" [NRS; condition good, except most of left wing membrane and the 4th antennal segments are missing]. Measurements of lectotype: BL 4.58; BW ca. 1.28 (wings spread); HW 0.82; V 0.32; RL 2.08; AI 0.96; AII 2.04; AIII ca. 1.40 (slightly curled); AIV missing; PL 0.64; PW 0.72. Paralectotypes: 2 males and 1 female, same data as for lectotype [NRS].

Phytocoris annulicornis: Reuter, 1909:33 (new combination).

Phytocoris bipunctatus Van Duzee, 1910:77. **NEW SYNONYMY**. Type data.—Lectotype male (here designated): Label 1, "7-Oaks, Fla., May 1, '08, Van Duzee"; 2, "Lectotype *bipunctatus*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris bipunctatus* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 1995; condition fair, left antenna, right foreleg, and right hindleg missing; antennal segment III on right side broken, segment IV missing; membrane of right hemelytron chipped; anterolateral margin of left clavus chipped]. Measurements of lectotype: BL 5.08; BW 1.44; HW 0.87; V 0.33; RL 2.05; AI 1.04; AII 2.21; AIII broken or missing; AIV missing; PL 0.72; PW 1.19. Paralectotypes: 1 male and 1 female, same data as for lectotype; 1 male, Sanford, Fla., Apr. 27, '08, Van Duzee; 1 female, St. Petersbg., Fla., 4-28-08, Van Duzee; 1 female, Tampa, Fla., May 2, '08, Van Duzee; 1 female, Ft. Myers, Fla., May 3–5, '08, Van Duzee. All paralectotypes are deposited in the collection of the CAS.

Remarks. Phytocoris annulicornis is recorded from Maine, south to Florida, west to California, and south to Panama (Carvalho, 1959). We suspect that the far western records (California, Colorado, and New Mexico) and the far southern records (Guatemala and Panama) are in error. Although Carvalho (1959) indicated that Knight (p. 717) in Blatchley (1926) synonymized *bipunctatus* under *annulicornis,* Blatchley did not agree with this opinion, noting that neither Reuter (1876) nor Distant (1883) mention the prominent pale spots on the corium which are distinctive in *bipunctatus.* Knight (1927b) added to Blatchley's discussion of *annulicornis,* stating that he had examined a co-type of *annulicornis* and that this specimen was the same as *bipunctatus,* but felt the final decision on synonymy should come only after all of Reuter's specimens were examined. We have examined the types of both species and can say, without a doubt, that *bipunctatus* is a junior synonym of *annulicornis.*

Blatchley (1926) redescribed and keyed *annulicornis.* Contrary to his key, *annulicornis* (couplet bb) has two white spots at the apex of the corium. His key should be modified accordingly.

Phytocoris antennalis Reuter

Phytocoris antennalis Reuter, 1909:32. Type data.—Lectotype male (here designated): Label 1, "Washington, D. C., 24-IX-04"; 2, "O. Heidemann Collector"; 3, "*Phytocoris antennalis* n. sp. [handwritten] O.M. Reuter det."; 4, "Mus. Zool. H:fors Spec. typ. No. 9685 *Phytocoris antennalis* O.M. Reut."; 5 (here added), "Lectotype: *Phytocoris antennalis* Reuter, by Henry and Stonedahl, 1983" [UZMH; good condition except the 4th antennal segments are missing and the wings are spread (pinned through right anterior region of abdomen). Measurements of lectotype: BL 6.10; BW not measured, wings spread; HW 0.90; V 0.44; RL 2.81; AI 1.60; AII 3.28; AIII 2.16; AIV missing; PL 0.79; PW 1.40. Paralectotypes: 4 females, same locality as for lectotype with dates 15-9, 4-7-1889, 4-7-1901, 19-VIII-1901, [3 females, UZMH; 1 female, USNM].

Remarks. Phytocoris antennalis has been redescribed and keyed by Knight (1923) and Blatchley (1926). This is a widespread species that occurs from Massachusetts, south to Florida, and west to Oklahoma (Carvalho, 1959).

Phytocoris barbatus Van Duzee

[See *roseus* (Uhler)]

Phytocoris bakeri Reuter

Phytocoris bakeri Reuter, 1909:28. Type data.—Lectotype male (here designated): Label 1, "Claremont, Cal., Baker"; 2, "1203"; 3, "*Phytocoris bakeri* n. sp. [handwritten] O. M. Reuter det."; 4, "Mus. Zool. H:fors, Spec. typ. No. 9681, *Phytocoris bakeri* O.M. Reut."; 5 (here added), "Lectotype: *Phytocoris bakeri* Reuter, by Henry and Stonedahl, 1983" [UZMH; good condition, except the 4th antennal segments are missing and the hemelytra are spread]. Measurements of lectotype: BL 5.25; BW ca. 1.67 (wings spread); HW 0.90; V 0.36; RL 2.02; AI 1.28; AII 2.08; AIII 1.28; AIV missing; PL 0.76; PW 1.40. Paralectotypes: 7 males and 2 females, same data as for lectotype [5 males and 2 females, CAS; 1 male, UZMH; 2 males, USNM].

Remarks. Phytocoris bakeri is known only from California. Knight (1968) included it in his key to the western species of *Phytocoris.*

Phytocoris bipunctatus Van Duzee

[See *annulicornis* (Reuter)]

Phytocoris breviusculus Reuter

Phytocoris breviusculus Reuter, 1876:68. Type data.—Lectotype male (here designated): Label 1, "Texas"; 2, "Paratypus"; 3, "417 82"; 4, "Riksmuseum Stockholm"; 5 (here added), "Lectotype: *Phytocoris breviusculus* Reuter, by Henry and Stonedahl, 1983" [NRS; good condition, except the right hindleg and left antenna are missing, and the specimen is pinned through the right hemelytron]. Measurements of lectotype: BL 4.05; BW 1.57; HW 0.90; V 0.30; RL 1.84; AI 0.59; AII 1.46; AIII 0.90; AIV missing; PL 0.79; PW 1.44. Paralectotypes: Same data as for lectotype [1 male and 2 females, NRS; 1 female, UZMH].

Remarks. Phytocoris breviusculus has been keyed and redescribed by Knight (1941). Froeschner (1949) included it in his key to the Missouri species. Wheeler and Henry (1977) described and figured the adult and 5th-instar nymph, studied biology, summarized the literature, and firmly associated this predatory species with *Juniperus* spp. and other conifers, as well as with apple, crabapple, and honeylocust. *Phytocoris breviusculus* is widespread from Pennsylvania, south to Alabama, and west to Colorado and Texas (Carvalho, 1959; Wheeler and Henry, 1977).

Phytocoris canadensis Van Duzee

Phytocoris inops Uhler, 1878:402 [preoccupied by *Phytocoris inops* Uhler, 1877]. Type data.—Lectotype [sex?] (here designated): Label 1, "53"; 2, "83"; 3, "M.C.Z. Type 26446"; 4 (here added) "Lectotype: *Phytocoris inops* Uhler [1878], by Henry and Stonedahl, 1983" [MCZ; condition very poor; pinned through scutellum; all legs and antennae, hemelytra (except for clavi), and abdomen missing]. Measurements of lectotype: HW 1.06; V 0.40; RL 2.76; PL 0.92; PW 1.76.

Phytocoris canadensis Van Duzee, 1920:346 [Kearney, Ontario, July 29, 1911; CAS type No. 2002].

Remarks. Phytocoris canadensis was described from a unique male. Knight (1941) redescribed and keyed this species and illustrated male genitalia.

Phytocoris inops Uhler (1878) has remained a mystery since its original description. Uhler (1877, 1878) used the name *Phytocoris inops* in two separate descriptions of new species. It has been assumed that both descriptions referred to the same species (Carvalho, 1959) or that the "eastern" *inops* (1878) was a species of *Neurocolpus* and the "western" *inops* (1877) was a true species of *Phytocoris* (Knight, *in* Blatchley, 1926:699). We have examined what we believe to be the original material studied by Uhler (1878), and find that the first description (1877) is based on a different species (see *Phytocoris inops* Uhler, 1877, listed in this paper) than the second (1878). Two specimens in the W. T. Harris collection (MCZ) bear the labels "53" just as Uhler (1878) cited. One specimen (also having "N.H." on the "53" label) is in relatively good condition, but is a female and pertinent markings are obscured by body oils. A second specimen (designated as the lectotype above) is badly broken, but distinct markings on the propleura and pronotum have enabled us to identify this specimen as what Van Duzee (1920) later described as *canadensis*. *Phytocoris canadensis*, thus, is a junior synonym of *inops* Uhler (1878), but *inops* (1878) is a junior primary homonym of *inops* Uhler (1877). *Phytocoris canadensis* is the next available name, as we recognize above.

Phytocoris canescens Reuter

Phytocoris canescens Reuter, 1909:30. Type data.—Lectotype male (here designated): Label 1, "Claremont, Cal., Baker"; 2, "*Phytocoris canescens* Reut." (handwritten); 3 (here added), "Lectotype: *Phytocoris canescens* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100387; good condition, except left 3rd and 4th antennal segments are missing, the right 2nd, 3rd, and 4th segments are curled, and the hemelytra are spread]. Measurements of lectotype: BL 6.42; BW 1.44; HW 0.88; V 0.36; RL 2.29; AI 1.46; AII 2.80; AIII 1.26; AIV ca. 0.84; PL 0.66; PW 1.24.

Paralectotypes: Same data as for lectotype [1 female, USNM; 1 male, LACM; 1 male (abdomen missing), UZMH; 3 males and 1 female, CAS].

Remarks. Phytocoris canescens, described and known only from California, can be keyed in Knight (1968).

Phytocoris confluens Reuter

Phytocoris confluens Reuter, 1909:20. Type data (Fig. 5).—Lectotype male (here designated): Label 1, "♂"; 2, "Wash[i]ngt[o]n, D.C., 10-7"; 3, "O. Heidemann Collector"; 4, "Spec. typ."; 5, "*Phytocoris puella* var. *confluens* n. [handwritten] O. M. Reuter det."; 6, "Mus. Zool. H:fors. Spec. typ. No. 9663, *Phytocoris puella* var. *confluens* O.M. Reut."; 7 (here added), "Lectotype: *Phytocoris confluens* Reuter, by Henry and Stonedahl, 1983" [UZMH; condition good, except left front tibia, left 2nd, 3rd, and 4th antennal segments, and right 4th antennal segment are missing, and the hemelytra are spread]. Measurements of lectotype: BL 5.17; BW ca. 1.50; HW 0.84; V 0.24; rostrum broken; AI 1.08; AII 2.88; AIII 1.40; AIV missing; PL 0.72; PW 1.28. Paralectotypes: 3 males, same data as for lectotype with dates June 23-05, 6-7-90, and 4-7-97 [CAS, UZMH, USNM].
Phytocoris confluens: Knight, 1923:650 (as species).

Remarks. Knight (1923, 1941) redescribed *confluens,* provided an identification key, and gave oak, *Quercus* sp., and red or river birch, *Betula nigra* L., as its hosts. Froeschner (1949) included *confluens* in his key to the *Phytocoris* of Missouri. This species is widely distributed in the eastern United States (Carvalho, 1959).

Phytocoris conspersipes Reuter

Phytocoris conspersipes Reuter, 1909:22. Type data.—Lectotype male (here designated): Label 1, "Wash[i]ngt[o]n, D. C., 16-7-97"; 2, "O. Heidemann Collector"; 3, "Mus. Zool. H:fors, Spec. typ. No. 9677, *Phytocoris conspersipes* O.M. Reut."; 4 (here added), "Lectotype: *Phytocoris conspersipes* Reuter, by Henry and Stonedahl, 1983" [UZMH; fair condition, with right antenna and left 4th antennal segment missing, and the left hindleg glued to point beside specimen]. Measurements of lectotype: BL 4.58; BW 1.83; HW 1.00; V 0.40; RL 1.96; AI 0.64; AII 1.68; AIII 1.00; AIV missing; PL 0.76; PW 1.44. Paralectotypes: Same data as for lectotype with dates 10-9, 7-10, 10-7, 26-7-95, 27-7-95, 5-10-96, 16-7-97, 20-7-97; 1-XI[1 male and 3 females, UZMH; 1 male and 2 females, CAS; 2 females, USNM].

Remarks. Knight (1923) redescribed this pine-inhabiting species, figured male genitalia (1941), and provided keys to separate it from other eastern species of *Phytocoris.*

Phytocoris covilleae Knight

[See *ramosus* Uhler]

Phytocoris cunealis Van Duzee

Phytocoris cunealis Van Duzee, 1914:16. Type data.—Lectotype male (here designated): Label 1, "San Diego Co., Cal., 6-5-13, EP Van Duzee"; 2, "Lectotype *cunealis*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris cunealis* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 2005; good condition; right hindleg glued to point beside specimen]. Measurements of lectotype: BL 6.75; BW 2.29; HW 1.02; V 0.45; RL 3.33; AI 1.71; AII 3.06; AIII 1.67; AIV 1.13; PL 1.03; PW 1.71. Paralectotypes: 10 males and 9 females, same locality data as for lectotype with dates 6 May–5 June 1913 and 13 April–6 June 1914 [CAS; 1 male, USNM].

Remarks. Phytocoris cunealis is known only from southern California (Van Duzee, 1914). Knight (1968) figured male genitalia and included this species in his key to the western *Phytocoris.*

Phytocoris eximius Reuter

Phytocoris eximius Reuter, 1876:67. Type data (Fig. 3).—Lectotype male (here designated): Label 1, "Texas"; 2, "Belfrage"; 3, "*eximius,* Typ., Reut." (handwritten); 4, "Typus" (red label); 5, "310, 82"; 6, "Riksmuseum Stockholm"; 7 (here added), "Lectotype: *Phytocoris eximius* Reuter, by Henry and Stonedahl, 1983" [NRS; good condition, except the right 3rd and 4th antennal segments are missing, and the specimen is pinned through the right hemelytron]. Measurements of lectotype: BL 6.25; BW ca. 1.83 (hemelytra slightly spread); HW 1.00; V 0.28; RL 2.36; AI 1.12; AII 2.72; AIII 1.48; AIV 1.08; PL 0.88; PW 1.64. Paralectotypes: No other syntypes located.

Phytocoris penepectus Knight, 1920:58. **NEW SYNONYMY** [described from East River, Connecticut; USNM type No. 100388].

Phytocoris penepecten: Knight, 1923:640; 1941:199 (unjustified emendation of *penepectus*—see Steyskal, 1973:208).

Remarks. There is a large amount of literature using the name *eximius* (Carvalho, 1959). Most or all of these records, however, are in error. Typical of many early descriptions of *Phytocoris,* Reuter's description probably was based on a composite of species. *Phytocoris eximius* belongs to group II of Knight's (1941) treatment of *Phytocoris.* Apparently no one before us examined the above lectotype that clearly belongs to Reuter's "type" series. Knight (1920) redescribed *eximius* in detail and figured male genitalia, stating that his redescription was based on a specimen returned by Reuter to Heidemann at the USNM. We searched the USNM, but could not find the specimen studied by Knight. Knight apparently reconsidered his definition of *eximius,* for later (1941), he recognized *canadensis* Van Duzee for the species he called *eximius* in 1920 (using the same figures and description). Knight did not attempt to further clarify the identity of *eximius* after his reversed decision.

Male genitalia of the "Belfrage" specimen clearly show that *eximius* is the senior synonym of *penepectus* Knight (1920). Most early records of *eximius* are confused and should be disregarded. *Phytocoris eximius* can be recognized using Knight's (1923, 1941) keys and descriptions of *penepectus.* This species is widespread in the eastern U.S. west to Texas (Carvalho, 1959).

Phytocoris fenestratus Reuter

Phytocoris fenestratus Reuter, 1909:24. Type data.—Lectotype female (here designated): Label 1, "Retreat, NC, 1-6"; 2, "O. Heidemann Collector"; 3, "Spec. typ."; 4, "*Phytocoris fenestratus* n. sp. [handwritten] O. M. Reuter det."; 5 (here added), "Lectotype: *Phytocoris fenestratus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100389; fair condition, with right middle and hindlegs and left antenna missing]. Measurements of lectotype: BL 7.75; BW 2.33; HW 1.16; V 0.44; RL 3.20; AI 1.20; AII 3.08; AIII 1.64; AIV 0.92; PL 1.04; PW 2.00. Paralectotypes: 2 females, Wash., D.C., dates 16-V-02 and 27-6-95, Heidemann coll. [UZMH]; 1 female, same data as for lectotype [CAS].

Remarks. This pine-inhabiting species, known from Connecticut, Georgia, North Carolina, and Washington, D.C., has been redescribed and keyed by Blatchley (1926). Henry (1979) figured male genitalia and separated *fenestratus* from two closely related species, *discoidalis* Henry (now a junior synonym of *dreisbachi* Knight (Henry, 1982a)) and *intermedius* Henry.

Phytocoris formosus Van Duzee

Phytocoris reuteri Van Duzee, 1914:18 (name preoccupied by *P. reuteri* Saunders, 1875. Type data.—Lectotype male (here designated): Label 1, "San Diego Co., Cal., 7-4-13, EP Van Duzee"; 2, "Lectotype *reuteri*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris reuteri* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 2000; good condition; antennal segment IV on right side missing]. Measurements of lectotype: BL 6.00; BW 1.69; HW 0.92; V 0.30; RL ca. 2.88 (apex obscured by point and glue); AI 1.40; AII 2.57; AIII 1.87; AIV 1.24; PL 0.81; PW 1.35. Paralectotypes: 6 males and 10 females, same locality data as for lectotype with dates 4 July 1913 and 5 August 1913 [14, CAS; 2 USNM].

Phytocoris formosus Van Duzee, 1916:37 (new name for *P. reuteri* Van Duzee).

Remarks. Phytocoris formosus is known only from Southern California (Van Duzee, 1914). Knight (1968) recorded *Cordylanthus filifolius* Nutt. (as *Adenostegia filifolia*) as the host and included *formosus* in his key to the western species of *Phytocoris.*

Phytocoris fumatus Reuter

Phytocoris fumatus Reuter, 1909:25. Type data.—Lectotype female (here designated): Label 1, "Wash[i]ngt[o]n, D. C. 20-6"; 2, "Heidemann Collector"; 3, "7"; 4, "Spec. typ."; 5, "*Phytocoris fumatus* n. sp. [handwritten] O. M. Reuter det."; 6 (here added), "Lectotype: *Phytocoris fumatus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100391; fair condition, with antennae and legs on left side missing]. Measurements of lectotype: BL 7.58; BW 2.58; HW 1.16; V 0.48; RL 4.83; antennae missing; PL 1.24; PW 2.00. Paralectotypes: No other syntypes located.

Phytocoris subnitidulus Reuter, 1909:26 (synonymized by Knight, 1920:63). Type data.—Lectotype female (here designated): Label 1, "Plummer's [sic] I[sland]., Md. [date obscured by glue]"; 2, "O. Heidemann Collector"; 3, "*Phytocoris subnitidulus* n. sp. [handwritten] O. M. Reuter det."; 4 (here added), "Lectotype: *Phytocoris subnitidulus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100390; good condition, except the 3rd and 4th antennal segments are missing and a pin has been inserted into and removed from the right hemelytron; the left hindleg is glued to the locality label below the specimen]. Measurements of lectotype: BL 7.25; BW ca. 2.50 (hemelytra slightly spread); HW 1.16; V 0.44; RL 4.83; AI 1.92; AII 3.75; AIII and AIV missing; PL 1.12; PW 1.92. Paralectotype: 1 male, Wash., D.C., 10-6, Heidemann [UZMH].

Remarks. This widespread eastern U.S. species (Carvalho, 1959) has been redescribed and keyed by Knight (1923, 1941). Knight (1920, 1941) figured male genitalia and correctly placed *subnitidulus* as a junior synonym of *fumatus.* Froeschner (1949) included *fumatus* in his key to the *Phytocoris* of Missouri. We have chosen the female from Plummers Island as the lectotype because of the very poor condition of the male from Washington, D.C.

Phytocoris heidemanni Reuter

Phytocoris heidemanni Reuter, 1909:27. Type data (Fig. 4).—Lectotype female (here designated): Label 1, "Pecos, N. M., June 23 (C[oc]k[ere]ll)" (handwritten); 2, "O. Heidemann Collector"; 3, "*Phytocoris heidemanni* n. sp. [handwritten] O. M. Reuter det."; 4 (here added), "Lectotype: *Phy-*

tocoris heidemanni Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100401; good condition, except the right middle and right hindlegs are missing, and a pin has been inserted through and removed from the scutellum; right foreleg glued to point beside specimen]. Measurements of lectotype: BL 7.92; BW 2.75; HW 1.32; V 0.52; RL 3.96; AI 1.84; AII 3.68; AIII 1.68; AIV 1.24; PL 1.16; PW 2.12. Paralectotypes: No other syntypes located.

Remarks. This western pine-inhabiting species, recorded from Arizona, Colorado, New Mexico, and Nevada (Carvalho, 1959), is included in Knight's (1968) key to the western species of *Phytocoris.*

Phytocoris hesperellus Knight

[See *inops* Uhler]

Phytocoris hesperius Knight

[See *inops* Uhler]

Phytocoris infuscatus Reuter

Phytocoris puella var. *infuscatus* Reuter, 1909:20. Type data.—Lectotype male (here designated): Label 1, "♂"; 2, "Wash[i]ngt[o]n, D. C., June 23, 04"; 3, "Heidemann Collector"; 4, "Mus. Zool. H:fors, Spec. typ. No. 9664, *Phyt. puella* var. *infuscata*, O. M. Reuter" (handwritten); 5 (here added), "Lectotype: *Phytocoris infuscatus* Reuter, by Henry and Stonedahl, 1983" [UZMH; good condition, except the right hindleg is missing and specimen is pinned through left clavus]. Measurements of lectotype: BL 5.92; BW 2.17; HW 0.96; V 0.48; RL 2.76; AI 1.08; AII 2.76; AIII 1.40; AIV 1.00; PL 0.84; PW 1.64. Paralectotypes: 1 female, Wash., D.C., 27-7-91, Heidemann [UZMH]; 2 males, 2 females, Rock Creek, 17-6-93 and 24-6-93, Heidemann [1 CAS; 1 UZMH; 2 USNM].

Phytocoris infuscatus: Van Duzee, 1914:16 (as species).

Remarks. Phytocoris infuscatus, an eastern U.S. species (Carvalho, 1959), has been redescribed and keyed (Knight, 1923, 1941; Blatchley, 1926). Knight (1923, 1941) figured male genitalia. Froeschner (1949) included *infuscatus* in his key to the species of *Phytocoris* from Missouri.

Phytocoris inops Uhler

Phytocoris inops Uhler, 1877:413. Type data.—Lectotype female (here designated): Label 1, "Clear Cr[eek]. Canon" (handwritten); 2, "PR Uhler Collection"; 3 (here added), "Lectotype: *Phytocoris inops* Uhler [1877], by Henry and Stonedahl, 1983" [USNM type No. 100392; condition fair;

left 3rd and 4th and right 4th antennal segments and middle left and both hindlegs missing, and specimen is pinned between hemelytra just below apex of scutellum]. Measurements of lectotype: BL 7.58; BW ca. 2.50; HW 1.05; V 0.48; RL 3.28; AI 1.80; AII 3.48; AIII 1.68; AIV missing; PL 1.00; PW 1.84. Paralectotypes: No other syntypes located.

Phytocoris vittatus Reuter, 1909:28. **NEW SYNONYMY.** Type data.—Lectotype female (here designated): Label 1, "Lake Placid, NY, 8-12-04"; 2, "Van Duzee Collector"; 3, "*Phytocoris vittatus* n. sp. [handwritten] O. M. Reuter det."; 4 (here added), "Lectotype: *Phytocoris vittatus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100395; good condition, except the right middle leg, left antenna, and right 4th antennal segment are missing; the left hindleg is detached and glued to point]. Measurements of lectotype: BL 7.42; BW 2.33; HW 1.04; V 0.44; RL 3.24; AI 1.72; AII 3.44; AIII 1.72; AIV missing; PL 0.96; PW 1.76. Paralectotypes: No other syntypes located.

Phytocoris palmeri Reuter, 1909:32. **NEW SYNONYMY.** Type data.—Lectotype male (here designated): Label 1, "Quinze L[a]k[e]., P[rovince]. Q[uebec]., 8-14-07, W.J. Palmer"; 2, "Holotype *palmeri*" (handwritten); 3, "E. P. Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris palmeri* Reuter, by Henry and Stonedahl, 1983" [CAS type No. 1994; poor condition, with right 2nd, 3rd, and 4th antennal segments missing, the right hemelytron broken on the basal ½ of corium, and the wing membrane folded downward]. Measurements of lectotype: BL ca. 6.83 (head turned up and wing membrane folded down); BW 1.08; HW 1.05; V 0.36; RL ca. 3.00 (slightly bent); AI 1.40; AII 3.08; AIII 1.52; AIV 1.20; PL 0.92; PW 1.76. Paralectotypes: 1 female, Quinze Lake, PQ, 8-14-07 [USNM].

Phytocoris hesperius Knight, 1928:44. **NEW SYNONYMY** [described from Stonewall, Las Animas County, Colorado; USNM type No. 100393].

Phytocoris hesperellus Knight, 1968:232. **NEW SYNONYMY** [described from Salt Lake City, Salt Lake County, Utah; USNM type No. 100394].

Remarks. Phytocoris inops, like *eximius* Reuter, has been an enigma to mirid workers since its original description. Uhler (1877) probably had a composite of species when he considered the range of *inops* to be Colorado, Maryland, Massachusetts, New Jersey, Rhode Island, and "lower Canada." His remarks that this species resembled Say's species *Phytocoris nubilus* (now in the genus *Neurocolpus*), that it could be confused in the field with the genus *Psocus* (Psocidae), and that some specimens in the "south" had lead-colored or bluish markings at the apex of the corium further confused the identity of *inops*. Additionally, Uhler (1878) published a second description of *inops* as a new species based on another species of *Phytocoris* (See *Phytocoris canadensis* listed in this paper).

Only one of Uhler's (1877) localities, "Beaver Brook Gulch, next to Clear Creek Canon," can be associated with the species *inops*. We have found a single female in with undetermined material at the USNM that bears the single label "Clear Cr. Canon." This specimen exactly fits Uhler's (1877) description, making us certain that this specimen belongs to his syntype series.

Because of past confusion, early distribution records of *inops* cannot be trusted. Based on the above synonyms, its distribution can be confirmed for Arizona, Colorado, Nevada, New Mexico, New York, Oregon, Wyoming, and Quebec. Knight (1923) redescribed (as *palmeri*) and keyed (1923, 1941) (as *palmeri* and *vittatus*, respectively) *inops*.

Phytocoris interspersus Uhler

Phytocoris interspersus Uhler, 1895:32. Type data.—Neotype male (here designated): Label 1, "F[or]t. Garland, Colo., Ute Creek Ranch, Aug. 11, 1925, H. H. Knight"; 2, "H. H. Knight Collection"; 3 (here added), "Neotype: *Phytocoris interspersus* Uhler, by Henry and Stonedahl, 1983" [USNM type No. 100396; excellent condition]. Measurements of neotype: BL 6.92; BW 2.25; HW 1.04; V 0.28; RL 2.48; AI 1.12; AII 2.64; AIII 1.48; AIV 1.16; PL 0.88; PW 1.60.

Remarks. We could not find the original female described from "Cheyenne Canon, Colorado Springs, July (Tucker)"; therefore, we have designated the above specimen from the same general type locality as the neotype to represent this species. This specimen agrees with Uhler's description and subsequently identified material of the species.

Knight (1968) recorded *Phytocoris interspersus* from Arizona, California, Colorado, Idaho, New Mexico, Utah, and British Columbia, and included it in his key to the western species of *Phytocoris*.

Phytocoris jucundus Van Duzee

Phytocoris jucundus Van Duzee, 1914:17. Type data.—Lectotype male (here designated): Label 1, "San Diego Co., Cal., 10-19-13, EP Van Duzee"; 2, "Lectotype *jucundus*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris jucundus* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 1998; fair condition; left foreleg and hindleg missing; antennal segments II–IV on right side missing; hemelytra slightly spread]. Measurements of lectotype: BL 6.59; BW ca. 2.34; HW 1.09; V 0.34; RL ca. 2.41; AI 1.31; AII 2.95; AIII 1.48; AIV 0.97; PL 0.95; PW 1.64. Paralectotypes: 8 females, same label data as for lectotype [7, CAS; 1, USNM].

Remarks. Phytocoris jucundus is known from California, Idaho, Oregon, and Washington where it occurs commonly on *Pinus* spp. Knight (1968) included it in his key to the western species of *Phytocoris.*

Phytocoris laevis (Uhler)

Callodemas laevis Uhler, 1895:33. Type data.—Lectotype male (here designated): Label 1, "Albuq[uerque], N. M., 9-19-88 [handwritten, printing unclear for year]"; 2, "PR Uhler Collection"; 3, "*Callodemas laevis* Uhler, N. M., Osborn" (handwritten); 4, "*Callodemas laevis,* N. M., det. Uhler" (handwritten); 5 (here added), "Lectotype: *Callodemas laevis* Uhler, by Henry and Stonedahl, 1983" [USNM type No. 100397; condition poor, specimen glued to card, abdomen partially eaten by dermestids, and many appendages broken but glued to card]. Measurements of lectotype: BL 9.00; BW 2.17; HW 1.12; V 0.36; RL ca. 2.48 (obscured under body); AI 1.76; AII 3.04; AIII and AIV missing; PL 1.12; PW 2.04. Paralectotypes: 1 female, Colorado [USNM].

Phytocoris laevis: Reuter, 1909:14 (new combination).

Remarks. Phytocoris laevis is known from Arizona and New Mexico, north to Alberta, Canada (Knight, 1968). Knight (1968) included *laevis* in his key to the western species of *Phytocoris.*

Phytocoris lasiomerus Reuter

Phytocoris lasiomerus Reuter, 1909:34. Lectotype male (here designated): Label 1, "Long Lake [New York]"; 2, "typus"; 3 (here added), "Lectotype: *Phytocoris lasiomerus* Reuter, by Henry and Stonedahl, 1983" [TMB; good condition, except 3rd and 4th segments on both antennae missing]. Measurements of lectotype: BL 7.67; BW 2.25; HW 1.04; V 0.44; RL 3.40; AI 1.68; AII 3.32; AIII and IV missing. Paralectotypes: 1 female, Cold River [New York]; 1 male, Huckleberry [New York] (both TMB).

Remarks. Phytocoris lasiomerus is known from Quebec south to Massachusetts and New York, west to Colorado, Washington, and Wyoming (Knight, 1941). Knight (1923) correctly redescribed and keyed this northern species.

Phytocoris lineatus Reuter

Phytocoris lineatus Reuter, 1909:30. Type data (Fig. 2).—Lectotype male (here designated): Label 1, "Rifle, Oil, 7-25-00"; 2, "Holotype *lineatus*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris lineatus* Reuter, by Henry and Stonedahl, 1983" [CAS type No. 1993; fair condition, except all of the right legs and antennal segments III and IV (left) and II, III, IV (right) are missing]. Measurements of lectotype: BL 6.00; BW 1.67; HW 0.92; V 0.44; RL 3.04; AI 1.64; AII 3.28; AIII broken at apex; AIV missing; PL 0.80; PW 1.40. Paralectotypes: No other syntypes located.

Remarks. Phytocoris lineatus has not been treated since its original description and is known only from Colorado.

Phytocoris marmoratus (Van Duzee)

[See *vanduzeei* Reuter]

Phytocoris minutulus Reuter

Phytocoris minutulus Reuter, 1909:24. Type data.—Neotype male (here designated): Label 1, "Plummers I[sland], 6-7-06, Md."; 2, "D. H. Clemons Collector"; 3, "*Phytocoris minutulus* Reut., Det. H. H. Knight"; 4 (here added), "Neotype: *Phytocoris minutulus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100398; excellent condition except the left 4th antennal segment is missing]. Measurements of neotype: BL 4.48; BW 1.60; HW 0.88; V 0.26; RL 2.22; AI 1.04; AII 2.22; AIII 1.44; AIV 0.90; PL 0.62; PW 1.14.

Remarks. Phytocoris minutulus was described from a single female taken on Plummers Island, Md., 26 July 1903, by O. Heidemann. We have been unable to locate this specimen which should be in the USNM; therefore, we have chosen the above specimen from the same type locality as the neotype.

This species is recorded from Maryland, Massachusetts, New Hampshire, NewYork, North Carolina, Pennsylvania, and Virginia (Knight, 1941). Knight (1923) and Blatchley (1926) redescribed and keyed it with other eastern U.S. species of *Phytocoris.*

Phytocoris mundus Reuter

Phytocoris mundus Reuter, 1909:18. Type data.—Lectotype male (here designated): Label 1, "Wash[i]ngt[o]n, D. C., 19-IV-02"; 2, "10"; 3, "O. Heidemann Collector"; 4, "*Phytocoris* sp.[2] near *breviusculus* Reut." (handwritten); 5, "*Phytocoris mundus* Uhl. [handwritten] O. M. Reuter det."; 6 (here added), "Lectotype: *Phytocoris mundus* Reuter, by Henry and Stonedahl, 1983" [USNM type No. 100399; good condition, except the right middle leg and segments III and IV are missing on both antennae]. Measurements of lectotype: BL 4.83; BW 1.75; HW 0.92; V 0.40; RL 2.00; AI 0.64; AII 1.80; AIII and AIV missing; PL 0.72; PW 1.36. Paralectotypes: 1 female, Wash., D.C. 1-7-97, Heidemann [USNM]; 1 female, Rock Crk., D.C., 6-7-97, Heidemann [CAS]; 1 female, Bladnsbg., Md., 20-7-92, Heidemann [CAS].

Remarks. Phytocoris mundus, a common eastern, pine-inhabiting species, has been redescribed and keyed (Knight, 1923, 1941). Knight (1941) figured male genitalia.

Phytocoris nigripubescens Knight

[See *vanduzeei* Reuter]

Phytocoris pallidicornis Reuter

Phytocoris pallidicornis Reuter, 1876:69. Type data.—Holotype female: Label 1, "Wisconsin"; 2, "Kumlien."; 3, "Typus"; 4, "*pallidocornis* Reut." (folded, handwritten); 5, "311, 82"; 6, "Riksmuseum Stockholm"; 7 (here added), "Holotype: *Phytocoris pallidicornis* Reuter, by Henry and Stonedahl, 1983" [NRS; condition poor, with the antennae and all but 3 legs missing, the wing membrane badly folded, and the right clavus forced up because the specimen is pinned through the middle of the body]. Measurements of holotype: BL ca. 6.67 (wing membrane folded under); BW 2.33; HW 1.00; V 0.44; RL 3.24; antennae missing; PL 0.92; PW 1.64.
Phytocoris pallicornis: Reuter, 1909:33 (misspelling).

Remarks. Reuter (1876) described this species from a unique female (Reuter, 1909). *Phytocoris pallidicornis* is a widespread northern species that occurs over much of northeastern U.S., west to Colorado and British Columbia. It has been redescribed and keyed by Knight (1923, 1941), Blatchley (1926), and Kelton (1980); Kelton also figured male genitalia.

Phytocoris palmeri Reuter

[See *inops* Uhler]

Phytocoris penepectus Knight

[See *eximius* Reuter]

Phytocoris politus Reuter

Phytocoris politus Reuter, 1909:21. Type data.—Lectotype male (here designated): Label 1, "Ormsby Co., Nev., July, Baker"; 2, "Mus. Zool. H: fors, Spec. typ. No. 9672, *Phytocoris politus* O.M. Reut."; 3 (here added), "Lectotype: *Phytocoris politus* Reuter, by Henry and Stonedahl, 1983" [UZMH; poor condition with one segment III and both 4th antennal segments, and all but three legs missing, the hemelytra spread apart, and the apical parts of the wing membrane broken]. Measurements of lectotype: BL 6.17; BW ca. 2.00; HW 1.12; V 0.36; RL ca. 2.28 (broken and imbedded in glue); AI 1.12; AII 2.76; AIII 1.24; AIV missing; PL 0.96; PW 1.80.

Paralectotypes: 3 females, same locality data as for lectotype [1, UZMH; 2, USNM].

Phytocoris rusticus Van Duzee, 1920:348. **NEW SYNONYMY** [described from Mt. St. Helena, Napa County, California; CAS type No. 699].

Remarks. Phytocoris politus is known from California, Idaho, Oregon, and Washington. Knight (1968) included it in his key to the western species of *Phytocoris.*

Phytocoris puella Reuter

Phytocoris puella Reuter, 1876:69. Type data.—Lectotype male (here designated): Label 1, "N[ew]. York"; 2, "Belfrage"; 3, "*puella* Reut." (folded, handwritten); 4, "Typus"; 5, "312, 82"; 6, "Riksmuseum Stockholm"; 7 (here added), "Lectotype: *Phytocoris puella* Reuter, by Henry and Stonedahl, 1983" [NRS; condition poor (slightly teneral). The specimen is pinned through the right hemelytron and mounted on a hollow plastic tube that is attached to the label pin; the left 2nd, 3rd, and 4th antennal segments are missing; the hemelytra are folded up; and the base of the abdomen has been eaten by dermestids]. Measurements of lectotype: BL 4.67; BW (not measured; body distorted); HW 0.80; V 0.24; RL 1.96; AI 0.96; AII 2.04; AIII 1.24; AIV 1.16; PL 0.64; PW 1.20. Paralectotypes: No other syntypes located.

Remarks. Phytocoris puella is a widespread eastern U.S. species (Carvalho, 1959) found on numerous deciduous trees, including *Carya* and *Quercus* spp. Knight (1923, 1941) and Blatchley (1926) redescribed and keyed this species. Froeschner (1949) included *puella* in his key to the *Phytocoris* of Missouri.

Phytocoris ramosus Uhler

Phytocoris ramosus Uhler, 1894:252. Type data.—Lectotype female (here designated): Label 1, "S[an]. Berna[r]dino Co., Cal."; 2, "Uhler Type"; 3, "♀"; 4, "Lectotype *ramosus*" (in red, handwritten); 5, "*Phytocoris ramosus* Uhl." (handwritten); 6 (here added), "Lectotype: *Phytocoris ramosus* Uhler, by Henry and Stonedahl, 1983" [CAS type No. 555; poor condition, with right middle and forelegs, left middle and hindlegs, and antennae missing; wing membrane curled]. Measurements of lectotype: BL 5.56; BW 2.16; HW 1.01; V 0.40; RL ca. 2.07; antennae missing; PL 1.01; PW 1.87. Paralectotypes: 2 females, same data as for lectotype except with additional CAS type identification label [CAS].

Phytocoris covilleae Knight, 1925:54 (synonymized by Carvalho, 1959:214).

Remarks. Knight (1968) recorded this species from Arizona, California, Nevada, and Utah, and included it in his key to the western species of *Phytocoris.*

Phytocoris reuteri Van Duzee

[See *formosus* Van Duzee]

Phytocoris roseus (Uhler)

Compsocerocoris roseus Uhler, 1894:253. Type data.—Lectotype male (here designated): Label 1, "San Borja, Lower Cal., Mex., Chas D. Haines, May 1889"; 2, "778"; 3, "♂"; 4, "Lectotype *roseus*" (in red, handwritten); 5 (here added), "Lectotype: *Compsocerocoris roseus* Uhler, by Henry and Stonedahl, 1983" [CAS type No. 557; poor condition with hindlegs, left antenna, and 3rd and 4th segments of right antenna missing; pinned through scutellum and hemelytra slightly spread; abdomen partially eaten by dermestids but leaving genital segment intact]. Measurements of lectotype: BL 7.34; BW ca. 2.20; HW 1.07; V 0.34; RL 3.19; AI 1.67; AII 3.11; AIII and AIV missing; PL 0.95; PW 1.76. Paralectotypes: 2 females, Los Angeles, no other data [USNM].

Phytocoris roseus: Reuter, 1909:27 (new combination).

Phytocoris barbatus Van Duzee, 1920:353 (synonymized by Carvalho, 1959: 214).

Remarks. Phytocoris roseus is known only from southern California and Mexico (Carvalho, 1959). Knight (1968) included it in his key to the western species of *Phytocoris.*

Phytocoris rufoscriptus Van Duzee

Phytocoris rufoscriptus Van Duzee, 1914:15. Type data.—Lectotype male (here designated): Label 1, "San Diego Co., Cal., 6-8-13, EP Van Duzee"; 2, "Lectotype *rufoscriptus*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris rufoscriptus* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 2007; good condition except the left hindleg is missing]. Measurements of lectotype: BL 7.78; BW 2.45; HW 1.04; V 0.44; RL (not measured; tip obscured by point and glue); AI 1.94; AII 3.53; AIII 1.87; AIV 1.26; PL 1.13; PW 1.85. Paralectotypes: 2 males and 1 female, same data as for lectotype except dates 6-6-14 and IV-13-1913 [CAS]; 1 male, same data as for lectotype except 4-13-14 [USNM].

Remarks. Phytocoris rufoscriptus is known only from southern California (Van Duzee, 1914). Knight (1968) included it in his key to the western species of *Phytocoris.*

Phytocoris rufus Van Duzee

Phytocoris rufus Van Duzee, 1912:477. Type data.—Lectotype male (here designated): Label 1, "7-Oaks, Fla., May 1, '08, Van Duzee"; 2, "Lectotype *rufus*" (in red, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Phytocoris rufus* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 2009; fair condition; the right 3rd and 4th antennal segments are missing; hemelytra spread, outer margins raised]. Measurements of lectotype: BL 4.54; BW ca. 1.62; HW 0.77; V 0.25; RL ca. 1.62, tip obscured by point and glue; AI 0.59; AII 1.62; AIII 0.90; AIV 0.79; PL 0.59; PW 1.17. Paralectotypes: 3 females, same data as for lectotype [2, CAS; 1, USNM].

Remarks. *Phytocoris rufus* is known from Florida (Van Duzee, 1912), Louisiana, and Mississippi (Knight, 1927a). Blatchley (1926) included this species in his key to the eastern species of *Phytocoris.* Henry (1982b) recorded *Hypericum* spp. as the hosts.

Phytocoris rusticus Van Duzee

[See *politus* Reuter]

Phytocoris subnitidulus Reuter

[See *fumatus* Reuter]

Phytocoris tibialis Reuter

Phytocoris tibialis Reuter, 1876:68. Type data.—Lectotype female (here designated): Label 1, "Wisconsin"; 2, "Kumlien"; 3, "Allotypus"; 4, "414 82"; 5, "Riksmuseum Stockholm"; 6 (here added), "Lectotype: *Phytocoris tibialis* Reuter, by Henry and Stonedahl, 1983" [NRS; poor condition with legs and left antenna missing; abdomen somewhat shriveled]. Measurements of lectotype: BL 5.02; BW 1.78; HW 0.82; V 0.32; RL ca. 2.07; AI 0.92; AII 2.03; AIII 1.33; AIV 0.70; PL 0.72; PW 1.40. Paralectotypes: No other syntypes could be recognized with certainty.

Compsocerocoris vilis Distant, 1883:260 [described from San Deronimo, Guatemala and Bugaba, Panama; lectotype from Bugaba designated by Carvalho and Dolling, 1976:809] (synonymized by Reuter, 1909:20.)

Remarks. Two male specimens of this species also were examined from the collection of the NRS. Both of these were collected in New York by Belfrage; one bears Reuter's handwritten determination label reading: "*tibialis,* Typ., Reut." Although these specimens are not included in the original description of *P. tibialis,* their association with the Wisconsin specimen in the NRS and Reuter's det. label on the one specimen suggests that they may be syntypes. In the original description, "Texas (Belfrage)" is given as the label data for at least part of the syntypes, but it is possible that "Texas" was recorded in error, or less likely, that the specimens were mislabeled (see label data for lectotype of *puella* Reuter).

Phytocoris tibialis is a widespread species occurring from eastern Canada, west to Minnesota, and south to Panama and Venezuela (Carvalho, 1959). Knight (1923, 1941) keyed this species, figured genitalia, and indicated that it could be found among weedy herbaceous plants, including mountain mint *Pycnanthemum* sp., in damp situations.

Phytocoris validus Reuter

Phytocoris validus Reuter, 1909:31. Type data (Fig. 6).—Lectotype male (here designated): Label 1, "F[or]t. Collins, Colo., 7-16-03"; 2, "Van Duzee Collector"; 3, "E P Van Duzee Collection"; 4, "*Phytocoris validus* (Uhl.) [handwritten] O. M. Reuter det."; 5 (here added), "Lectotype: *Phytocoris validus* Reuter, by Henry and Stonedahl, 1983" [CAS type No. 14257; condition fair; the left antenna, left foreleg, and right hindleg are missing; abdomen removed for dissection of genitalia and 9th segment retained in microvial which is attached below specimen on pin]. Measurements of lectotype: BL ca. 6.83 (wing membrane folded under); BW 2.17; HW 0.96; V 0.42; RL 2.80; AI 1.24; AII 2.68; AIII 1.64; AIV 0.88; PL 1.00; PW 1.68. Paralectotypes: No other syntypes could be recognized with certainty.

Remarks. Knight (1968) recorded *validus* from Colorado and North Dakota, and included it in his key to the western species of *Phytocoris.* Kelton (1980) figured male genitalia, recorded Alberta, Manitoba, and Saskatchewan, and keyed it with the *Phytocoris* of the Prairie Provinces.

Phytocoris vanduzeei Reuter

Lygus vividus Uhler, 1894:260. Type data.—Lectotype male (here designated): Label 1, "Comondu"; 2, "Uhler Type"; 3, "318"; 4, "♂"; 5, "Lectotype *vividus*" (in red, handwritten); 6, "*Lygus vividus* Uhler" (handwritten); 7 (here added), "Lectotype: *Lygus vividus* Uhler, by Henry and Stonedahl, 1983" [CAS type No. 561; fair condition, with left hindleg, left antenna, and right 2nd–4th antennal segments missing; wing membrane curled upward]. Measurements of lectotype: BL ca. 5.40; BW 1.75; HW 0.97; V 0.28; RL 1.66; AI 0.54; AII–AIV missing; PL 0.90; PW 1.58. Paralectotypes: No other syntypes located.

Dichrooscytus marmoratus Van Duzee, 1910:78. Type data.—Lectotype male (here designated): Label 1, "Alamogordo, NM, V-7-'02"; 2, "Paratype *marmoratus*" (in orange, handwritten); 3, "EP Van Duzee Collection"; 4 (here added), "Lectotype: *Dichrooscytus marmoratus* Van Duzee, by Henry and Stonedahl, 1983" [CAS type No. 2015; good condition except left middle leg, left antennal segments II–IV, and right antennal segment IV missing]. Measurements of lectotype: BL 4.86; BW 1.64; HW 0.98; V 0.30; RL (not measured, obscured by point and glue); AI 0.45; AII 1.86; AIII 0.86; AIV missing; PL 0.77; PW 1.44. Paralectotypes: 1 male and 1 female [USNM]; 8 males and 5 females [CAS]; all having same locality data as for lectotype with dates ranging from 8 March to 10 May 1902.

Phytocoris vanduzeei Reuter, 1912:30 [new name for *Dichrooscytus marmoratus* Van Duzee (combination *Phytocoris marmoratus* preoccupied by Palearctic species of Douglas and Scott, 1869)]; Knight, 1917:640 (synonymy of *P. vanduzeei* with secondary junior homonym *Phytocoris vividus* (Uhler)).

Phytocoris vividus: Knight, 1917: 640 (new combination) (preoccupied by *Lygaeus vividus* Fabricius, 1803).

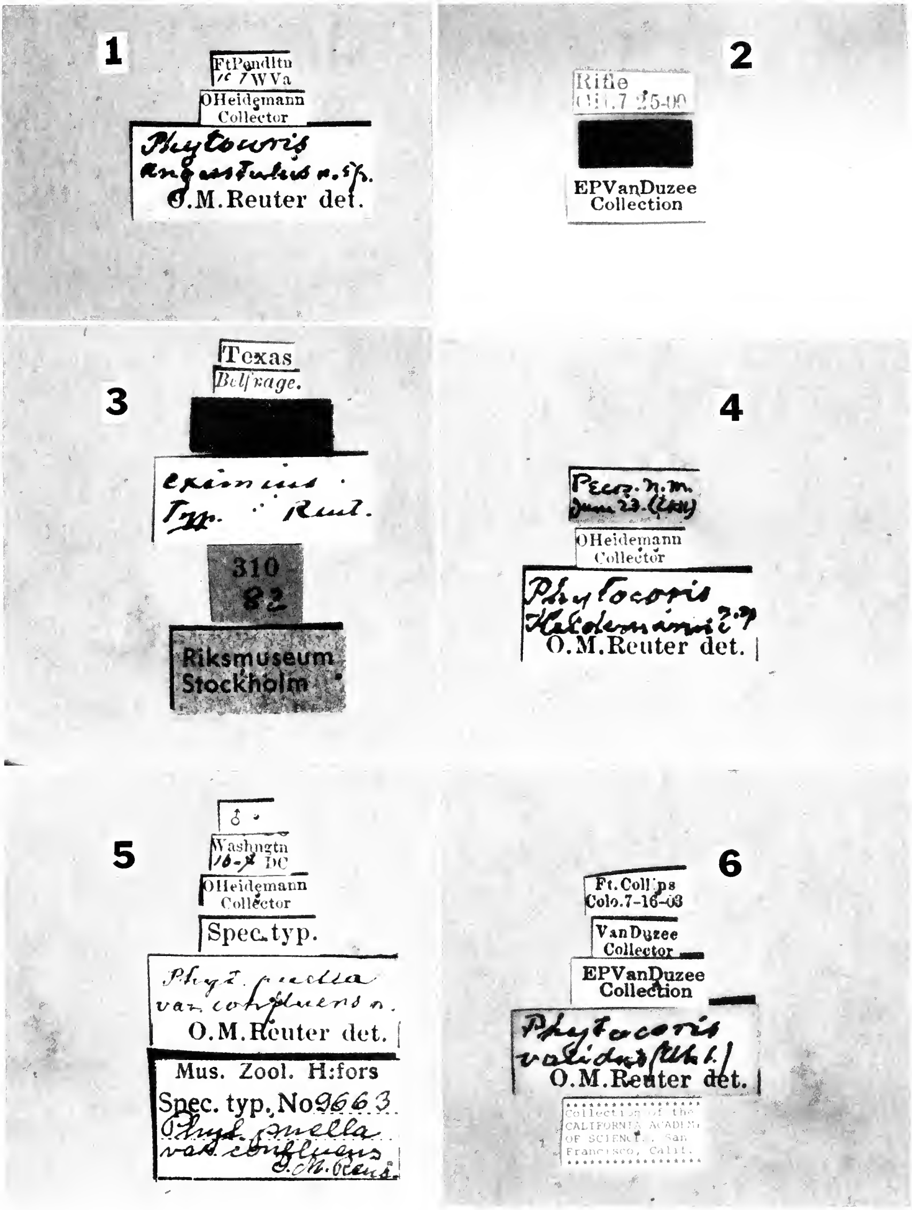
Phytocoris nigripubescens Knight, 1925:55. **NEW SYNONYMY** [described from Tucson, Pima County, Arizona; USNM type No. 100400].

Remarks. Reuter (1912) first recognized that *Dichrooscytus marmoratus* Van Duzee belonged in the genus *Phytocoris* and that it was preoccupied by the Palearctic species *Phytocoris marmoratus* Douglas and Scott. He renamed Van Duzee's species *vanduzeei.* Knight (1917) considered *vanduzeei* a junior synonym of *Lygus vividus* Uhler, but later (1968), in treating the western species of *Phytocoris* he apparently overlooked his earlier decision and again recognized both *vividus* and *vanduzeei.* We agree with Knight's earlier work that *Dichrooscytus marmoratus* is a junior synonym of *Lygus vividus.* This situation should allow for the recognition of *Phytocoris vividus* (Uhler) as the acceptable name; however, *Phytocoris vividus* is a secondary junior homonym of *Lygaeus vividus* Fabricius. *Phytocoris vanduzeei* is the next available name, as we recognize above.

Phytocoris vanduzeei is known from Arizona, California, New Mexico, and Nevada (Knight, 1968).

Phytocoris vigens (Uhler)

Calocoris vigens Uhler, 1894:255. Type data.—Lectotype male (here designated): Label 1, "San Jose del Cabo"; 2, "Uhler Type"; 3, "♂"; 4, "Lectotype *vigens*" (in red, handwritten); 5, "*Calocoris vigens* Uhl., San Jose del Cabo" (handwritten); 6 (here added), "Lectotype: *Calocoris vigens* Uhler, by Henry and Stonedahl, 1983" [CAS type No. 558; poor condition with legs, right 3rd and 4th antennal segments, and left 4th antennal segment missing; hemelytra spread, membrane tattered; originally pinned through scutellum and later transferred to a point]. Measurements of lectotype: BL ca. 6.59; BW (not measured; hemelytra spread); HW 1.00; V



Figs. 1–6. Labels for lectotypes of *Phytocoris* species described by Reuter. 1. *angustulus.* 2. *lineatus* (dark-red 2nd label reads "Holotype *lineatus.*" 3. *eximius* (dark-red 3rd label reads "Typus"). 4. *heidemanni.* 5. *confluens.* 6. *validus* (last collection label not in type data; added by authors).

0.39; RL 2.90; AI 1.57; AII 3.11; AIII broken or missing; AIV missing; PL 1.08; PW 2.00. Paralectotypes: 1 male, same locality data as for lectotype [CAS].

Phytocoris vigens: Carvalho, 1959:221 (new combination).

Remarks. Phytocoris vigens is known only from Baja California, Mexico (Uhler, 1894).

Phytocoris vilis (Distant)

[See *tibialis* Reuter]

Phytocoris vittatus Reuter

[See *inops* Uhler]

Phytocoris vividus (Uhler)

[See *vanduzeei* Reuter]

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AN ANNOTATED SYNONYMIC LIST OF NORTH AMERICAN AND CARIBBEAN WASPS OF THE GENUS *CERCERIS* (HYMENOPTERA: PHILANTHIDAE)[1]

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Abstract.—Results of a study of primary types representing 258 species-group names in the genus *Cerceris* are presented: 43 new synonyms are proposed; 14 names are removed from synonymy and given species status; 10 names previously recognized as subspecies are elevated to species status; one name is removed from synonymy and given subspecies status; three names are reduced from species to subspecies status; and eight names are transferred from the synonymy of one species to that of another. *Cerceris nitidoides* Ferguson is proposed as a *New Name* for the preoccupied *Cerceris nitida* Banks.

As part of a study of North American and Caribbean wasps of the genus *Cerceris* I have examined primary types representing 258 species-group names. The resulting new and revised synonymy is presented as an annotated list. Included species are those known to occur in North America, south to and including Panama, and the islands of the Caribbean other than Trinidad. Exclusive of new names, emendations, and misspellings, some 294 species-group names have been applied to *Cerceris* occurring within the geographic limits indicated. Ferguson and Vardy (1983) removed *Cerceris serripes* (Fabricius) from the North American faunal list, showing that it was a junior subjective synonym of the palaearctic *Cerceris arenaria* (Linnaeus).

Of the remaining 293 species-group names, 137 are recognized as valid species and four as subspecies. Ten names previously treated as subspecies

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are elevated to species rank, and 15 species-group names are removed from synonymy and recognized as valid species or subspecies. Three taxa are here reduced from species to subspecies status. Seven species-group names are transferred from the synonymy of one species to that of another. Twenty-seven species-group names are synonymized because of conspecificity of types (10 of these by sex association); and 16 species-group names previously treated as subspecies are synonymized under the nominate species. One new name, *C. nitidoides* Ferguson, is proposed for the preoccupied *C. nitida* Banks, here elevated to species status.

Color variation. Sexual dimorphism has led to the description of the opposite sexes as different species in many cases. However, the plethora of names is due largely to extensive color variation in widely distributed species with many color variants having been described as species or as infraspecific taxa. Bohart and Grissell (1975) synonymized many of the color variants which had been recognized as subspecies by Scullen (1965a, 1972). Color variation in most cases is clinal, and species with similar distributions often show similar geographic patterns of color variation. I attribute this to convergent responses to extrinsic environmental conditions and do not consider such variants as worthy of subspecies recognition. These color variants have been given names by previous authors in some cases but not in others. If one were to be consistent in naming color forms, a large number of additional names would have to be created. In their Philanthinae of California, Bohart and Grissell (1975) consistently ignored these variations in shade and extent of pale maculations as criteria for establishing taxonomic entities. As a general rule I have followed the same policy in this paper.

One common pattern of variation is the gradual transition in shade of pale markings from yellow to white in a south to north cline among several western species (e.g., *C. aequalis, C. calochorti, C. nigrescens, C. vanduzeei*). Another pattern (e.g., *C. californica, C. sexta*) is the development of broad pale bands on the terga in the southwestern deserts with a gradually increasing amount of melanism exhibited in both northerly and southerly directions. Several species widely distributed in eastern North America exhibit a tendency toward a red instead of black background color in Florida and adjacent southeastern states (e.g., *C. blakei, C. flavofasciata, C. compar,C. rufopicta* and *Philanthus sanbornii*). Some widely distributed eastern species have extended their ranges into the southwestern states where they exhibit a clinal change from yellowish to whitish pale markings and a gradually increasing amount of pale color on the body (e.g., *C. compar, C. compacta, C. insolita*). I do not consider it useful to designate these kinds of variation as subspecies.

Other cases of color convergence are apparently due to mimicry. Saussure (1867) pointed out the resemblance of color pattern of *C. simulans* to that of *Polybia emaciata* Lucas (misidentified by Saussure as *Polybia fasciata* according to Richards, 1978). *C. militaris* and *C. scapularis* have similar patterns of pale markings. In the northern part of their ranges *C. azteca, C. bakeri, C. dilatata,* and *C. tolteca,* each belonging to a different species group, exhibit broad pale bands on the posterior terga similar to the color pattern of some social wasps of the genus *Brachygastra.* In Costa Rica and adjacent areas *C. bakeri, C. kennicottii,* and *C. mexicana* exhibit a color pattern similar to that of *Polybia occidentalis bohemani* Holmgren, having an almost completely yellow propodeum with posterior tergal markings reduced. I divide *C. bakeri, C. kennicottii* and *C. mexicana* into subspecies based on this pattern of mimicry, which may have biological significance.

Differences in color pattern, as opposed to differences in shade of color or size of maculations within the same pattern, are important taxonomic characters, but such differences in pattern are almost always associated with differences in structural morphology.

Format. All species-group names are listed alphabetically whether originally described as specific or infraspecific taxa. Synonyms are italicized and placed in parentheses with the name of the valid species under which each is cited. A generalized summary of geographic distribution is given after each name. [Abbreviations used are n., s., e., w. and c. for north, south, east, west and central respectively]. Under each valid name is placed the bibliographic citation to the original description or emendation for each name included in the synonymy. The original orthography is used in the literature citation.

An asterisk (*) following the species-group name in the bibliographic citation indicates that I have studied the type. A double asterisk (**) indicates that a type comparison has been made by C. R. Vardy of the British Museum (Natural History) using specimens supplied by me. Insofar as possible I have placed in brackets the sex, type locality, and location of the type specimen(s) following each bibliographic citation. If a neotype or lectotype has been designated, the reference to such designation is given. Immediately following the brackets I have attempted to give the first author and citation for the synonymy.

Type repositories. The following abbreviations for type repositories are used in the text:

AMNH—American Museum of Natural History, New York
ANSP—Academy of Natural Sciences of Philadelphia
Berlin—Zoologisches Museum, Humboldt Universität, Berlin (DDR)
BMNH—British Museum (Natural History), London
BPBM—Bishop Museum, Honolulu, Hawaii
CAS—California Academy of Sciences, San Francisco
Geneva—Museum d'Histoire Naturelle, Geneva

Genoa—Museo Civico di Storia Naturale, Genoa, Italy
Halle—Zoologisches Institut, Martin Luther Universität, Halle am Saale, DDR
Havana—Academia de Ciencias de Cuba, Havana
KANS—University of Kansas, Lawrence
Lund—Universitets Zoologiska Institut, Lund, Sweden
MACN—Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires
Madrid—Museo Nacional de Ciencias Naturales de Madrid
MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts
NCDA—North Carolina State Department of Agriculture, Raleigh
NEB—University of Nebraska State Museum, Lincoln
Torino—Museo ed Istituto Zoologia Sistematica, Torino, Italy
UCD—University of California, Davis
USNM—United States National Museum of Natural History, Washington
Vienna—Naturhistorisches Museum Wien, Vienna

LIST OF NORTH AMERICAN AND CARIBBEAN *Cerceris*

(*abbreviata* Banks = *nigrescens* F. Smith)

acanthophila Cockerell sw. U.S., n. Mexico

*Cerceris acanthophilus** Cockerell, 1897:135. [Male lectotype, Deming, New Mexico, designated by Cresson (1928); ANSP No. 10038].

*Cerceris chilopsidis** Viereck and Cockerell, 1904:136. [Female holotype, Rincon, New Mexico; ANSP No. 10375]. Synonymy by Banks (1947), Ferguson (1983b).

Ferguson (1983b) reviewed previous misapplications of the name *acanthophila.*

acolhua Saussure Mexico

*Cerceris acolhua** Saussure, 1867:90. [Male lectotype, Mexico, designated by Ferguson (1984); Geneva]

Scullen (1972) left *C. acolhua* as an unrecognized species. It is allied to, but distinct from, *C. occipitomaculata* Packard. The female is unknown.

aequalis Provancher sw. Canada to nw. Mexico

*Cerceris aequalis** Provancher, 1888:417. [Female lectotype, California, designated by Gahan and Rohwer (1917); USNM].

*Cerceris aequalis idahoensis** Scullen, 1965a:454. [Female holotype, Craig's Mountain, Idaho; ANSP No. 5040]. **New Synonymy**.

Scullen (1965a) separated *idahoensis* from the nominate subspecies by its creamy white versus yellow pale markings. As in some other western species, these markings vary from yellow to whitish in a south to north cline.

(*affumata* Schletterer = *intricata* F. Smith)

alacris Mickel (Revised Status) sc. U.S.

*Cerceris alacris** Mickel, 1918:334. [Female holotype, Mitchell, Nebraska; NEB].

Scullen (1965a) incorrectly synonymized *alacris* under *C. halone* Banks. They are distinct species.

alamos Scullen w. Mexico

*Cerceris alamos** Scullen, 1972:18. [Female holotype, 10 mi. se. Alamos, Sonora, Mexico; CAS].

alaope Banks (Revised Status) e. U.S.

*Cerceris alaope** Banks, 1912:22. [Male lectotype, Falls Church, Virginia, designated by Ferguson (1983a); MCZ No. 13784].

*Cerceris banksi** Scullen, 1965a:461. [Female holotype, Falls Church, Virginia; MCZ No. 30477]. **New Synonymy**.

Synonymy is by sex association. Scullen (1942) incorrectly synonymized *alaope* under *C. prominens* Banks.

(*albida* Scullen = *insolita* Cresson)

(*albimana* Taschenberg = *cribrosa* Spinola)

(*albinota* Scullen = *compar* Cresson)

(*alceste* Mickel = *sexta* Say)

(*ampla* Banks = *intricata* F. Smith)

(*arbuscula* Mickel = *atramontensis* Banks)

(*architis* Mickel = *halone* Banks)

arelate Banks (Revised Status) se. Canada, ne. U.S.

*Cerceris arelate** Banks, 1912:18. [Female holotype, Great Falls, Virginia; MCZ No. 13779].

*Cerceris nigritulus** Banks, 1915:402. [Male holotype, Colden, New York; MCZ No. 13782]. Synonymy by Scullen (1965a).

*Cerceris crawfordi** Brimley, 1928:199. [Male holotype, Raleigh, North Carolina; NCDA]. Synonymy by Scullen (1965a).

Scullen (1965a) treated *arelate* as a yellow marked subspecies of *C. nigrescens* F. Smith, and Bohart and Grissell (1975) synonymized the two forms. *C. arelate* is distinct from *C. nigrescens* in having a triangular median tooth on the apical margin of the clypeal midsection, whereas in *nigrescens* this tooth is rectangular.

(*argia* Mickel = *rufinoda* Cresson)

(*argyrotricha* Rohwer = *californica* Cresson)

(*arizonella* Banks = *vierecki* Banks)

(*arno* Banks = *californica* Cresson)

astarte Banks se. Canada, e. U.S.

*Cerceris astarte** Banks, 1913b:424. [Female lectotype, Falls Church, Virginia, designated by Ferguson (1983a); MCZ No. 13788].

(*athene* Banks = *femurrubrum* Viereck and Cockerell)

(*atlacomulca* Scullen = *flavida* Cameron)

(*atrafemori* Scullen = *insolita* Cresson)

atramontensis Banks se. Canada, e. U.S.

*Cerceris atramontensis** Banks, 1913b:425. [Female holotype, Valley of Black Mountains, North Carolina; AMNH].

*Cerceris arbuscula** Mickel, 1916:410. [Female holotype, Omaha, Nebraska; NEB]. Synonymy by Scullen (1951).

Scullen (1965a) incorrectly stated that the type of *atramontensis* was at the MCZ.

(*atrata* Scullen = *echo* Mickel)

(*aureofacialis* Cameron = *compacta* Cresson)

(*austrina* Fox = *rufopicta* F. Smith)

azteca Saussure sw. U.S. to Nicaragua

*Cerceris azteca** Saussure, 1867:97. [Female lectotype, Cuantla, Mexico, designated by Ferguson (1984); Vienna].

Cerceris (*Apiratirx*) [sic] *seminigra** Banks, 1947:33, nec Taschenberg 1875. [Male holotype, Patagonia, Arizona; MCZ No. 27621]. Synonymy by Scullen (1961).

bakeri bakeri Cameron (Revised Status) El Salvador to Costa Rica

*Cerceris bakeri** Cameron, 1904:67. [Female lectotype, Chinandega, Nicaragua, designated by Ferguson (1984); BMNH].

bakeri parkeri Scullen (Revised Status) sw. U.S. to Guatemala

*Cerceris parkeri** Scullen, 1972:35. [Female holotype, 48 mi. nw. Tehuantepec, Oaxaca, Mexico; USNM].

Scullen (1972) misidentified *bakeri* and used the name as a subspecies of *C. kennicottii* Cresson. However, the type of *C. bakeri* is conspecific with *C. parkeri.* The nominate subspecies has a yellow tergum I and yellow propodeum with reduced pale markings on the terga. It is apparently a mimic of *Polybia occidentalis bohemani* Holmgren. The subspecies *parkeri* has tergum I and the propodeum mostly or entirely black and terga III–V are broadly banded with yellow apparently mimicking *Brachygastra azteca* (Saussure), another common polybiine wasp.

(*banksi* Scullen = *alaope* Banks)

(*beali* Scullen = *kennicottii* Cresson)

(*belfragei* Banks = *compacta* Cresson)

(*bicornis* Ashmead = *bicornuta* Guerin)

bicornuta Guerin U.S., n. Mexico

Cerceris bicornuta Guerin, 1844:443. [Female holotype, New Oreleans, Louisiana; Genoa].

Cerceris dufourii Guerin, 1844:443. [Male holotype, New Orleans, Louisiana; Genoa]. Synonymy by Cresson (1875).

*Cerceris venator** Cresson, 1865:116. [Male lectotype, Illinois, designated by Cresson (1916); ANSP No. 1937]. Synonymy by Cresson (1875).

*Cerceris curvicornis*** Cameron, 1890:124. [Male holotype, Mazatlan, Mexico; BMNH]. Synonymy by Scullen (1961).

Cerceris bicornis Ashmead, 1899:295. *Lapsus.*

*Cerceris fidelis** Viereck and Cockerell, 1904:132. [Female holotype, Santa Fe, New Mexico; ANSP No. 10379]. Synonymy by Bohart and Grissell (1975).

Cerceris venatrix Schulz, 1906:195. Emendation.

(*bifida* Scullen = *rufopicta* F. Smith)

(*bilinieata* Schletterer = *triangulata* Cresson)

(*bilunata* Cresson = *triangulata* Cresson)

binodis Spinola s. Mexico to Argentina

*Cerceris binodis** Spinola, 1841:117. [Male lectotype, Cayenne, French Guiana, designated by Ferguson (1984); Torino].

Diamma spinolae Dahlbom, 1844:225. Described in synonymy.

*Cerceris viduata*** F. Smith, 1856:463. [Female holotype, Para, Brasil; BMNH]. Synonymy by Fritz (1971).

Cerceris singularis Brethes, 1910:265. [Female holotype, Cordoba, Argentina; MACN]. Synonymy by Fritz (1971).

(*biungulata* Cresson = *sexta* Say)

(*blackii* Schletterer = *blakei* Cresson)

blakei Cresson e. U.S.

*Cerceris elegans** F. Smith, 1856:467, nec Eversmann 1849. [Male lectotype, St. John's Bluff, E. Florida, designated by Ferguson (1984); BMNH].

*Cerceris blakei** Cresson, 1865b:121. [Female holotype, Georgia; ANSP No. 1947]. Synonymy by Scullen (1961).

Cerceris blackii Schletterer, 1887:487. *Lapsus.*

Cerceris elegantissima Schletterer, 1887:490. New name for *Cerceris elegans* F. Smith.

Scullen (1961) was correct in stating that *elegantissima* was proposed as a new name for *Cerceris elegans* F. Smith, but he was later (Scullen 1965a) incorrect in stating that it was proposed as a new name for *Eucerceris elegans* Cresson.

boharti Scullen sw. U.S., n. Mexico

*Cerceris boharti** Scullen, 1965a:466. [Female holotype, Mount Lemmon Lodge, Santa Catalina Mountains, Arizona; UCD].

bolingeri Scullen (New Status) nw. U.S.

*Cerceris aequalis bolingeri** Scullen, 1965a:453. [Female holotype, Hart Mountain, Jacob's Cabin, Lake County, Oregon; USNM].

Although described as a subspecies of *aequalis,* this taxon is a morphologically distinct species.

(*bolingeri* Scullen, 1972 = *bolingeriana* Krombein)

bolingeriana Krombein sw. U.S. to c. Mexico

*Cerceris bolingeri** Scullen, 1972:72, nec Scullen 1965a. [Female holotype, 40 mi. nw. Gomez Palacio, Durango, Mexico; USNM].

Cerceris bolingeriana Krombein, 1979:1730. New name for *Cerceris bolingeri* Scullen, 1972.

bothriophora Schletterer sw. U.S. to El Salvador

*Cerceris bothriophora** Schletterer, 1887:456. [Male lectotype, Mexico, designated by Ferguson (1984); Vienna].

*Cerceris geniculata** Cameron, 1890:113. [Female lectotype, Cuantla, Mexico, designated by Ferguson (1984); BMNH]. **New Synonymy.**

*Cerceris feralis** Cameron, 1890:113. [Male lectotype, Cuantla, Mexico, designated by Ferguson (1984); BMNH]. **Revised Synonymy**. Synonym of *C. geniculata* by Scullen (1962).

*Cerceris orestes** Banks, 1947:13. [Female lectotype, Patagonia, Arizona, designated by Ferguson (1983a); MCZ No. 27673]. **New Synonymy.**

Scullen (1972) left *bothriophora* as an unrecognized species, and he treated *geniculata* (=*feralis*) and *orestes* each as a subspecies of *C. compar* Cresson.

bradleyi Scullen s. Mexico to Nicaragua

*Cerceris bradleyi** Scullen, 1972:73. [Female holotype, La Calera (?), Nicaragua; USNM].

bridwelli Scullen sw. U.S., nw. Mexico

*Cerceris bridwelli** Scullen, 1965a:361. [Female holotype, Imperial County, California; USNM].

butleri Scullen sw. U.S., n. Mexico

*Cerceris butleri** Scullen, 1965a:363. [Female holotype, 30 mi. s. Stafford, Arizona; USNM].

cacaloapana Scullen se. Mexico

*Cerceris cacaloapana** Scullen, 1972:74. [Female holotype, Cacaloapan, Puebla, Mexico; UCD].

californica Cresson sw. Canada to c. Mexico

*Cerceris californica** Cresson, 1865b:128. [Male holotype, California; ANSP No. 1953].

?*Cerceris texensis* Saussure, 1867:89. [Female holotype, Texas; type not located]. **Revised Tentative Synonymy**.

*Cerceris ferruginior** Viereck and Cockerell, 1904:134. [Male holotype, Deming, New Mexico; ANSP No. 10378]. Synonymy by Scullen (1960).

*Cerceris garciana** Viereck and Cockerell, 1904:135. [Male holotype, Las Cruces, New Mexico; ANSP No. 10380]. Synonymy by Scullen (1960).

*Cerceris populorum** Viereck and Cockerell, 1904:135. [Male lectotype, Albuquerque, New Mexico, designated by Cresson (1928); ANSP No. 10385]. Synonymy by Scullen (1960).

*Cerceris argyrotricha** Rohwer, 1908:324. [Female holotype, Las Cruces, New Mexico; USNM]. Synonymy by Bohart and Grissell (1975).

*Cerceris cognata** Mickel, 1916:408. [Female holotype, Worland, Wyoming; NEB]. Synonymy by Scullen (1960).

*Cerceris denticularis** Banks, 1917:113. [Female lectotype, Umatilla, Oregon, designated by Ferguson (1983a); MCZ No. 10028]. Synonymy by Scullen (1960).

*Cerceris interjecta** Banks, 1919:84. [Male holotype, Lake Point, Utah; MCZ No. 13766]. Synonymy by Scullen (1960).

*Cerceris arno** Banks, 1947:19. [Female lectotype, Mountains near Claremont, California, designated by Ferguson (1983a); MCZ No. 23542]. Synonymy by Bohart and Grissell (1975), synonym of *argyrotricha* by Scullen (1972).

*Cerceris calodera** Banks, 1947:22. [Male holotype, Jacumba, California; MCZ No. 27622]. Synonymy by Scullen (1961).

*Cerceris illota** Banks, 1947:23. [Male lectotype, Tucson, Arizona, designated by Ferguson (1983a); MCZ No. 23541]. Synonymy by Scullen (1960).

C. texensis Saussure was described from a headless female which has not been located. Scullen (1961) synonymized it under *C. frontata* Say, but the original description does not support this placement. The wing length of 10 mm, red scutum, and mostly polished propodeal enclosure make it much more likely that Saussure had a specimen of *C. californica* Cresson, and I provisionally place it in the above synonymy rather than under *C. frontata.*

calochorti Rohwer sw. Canada, w. U.S.

*Cerceris calochorti** Rohwer, 1908:322. [Female holotype, Boulder, Colorado; USNM].

*Cerceris varians** Mickel, 1918:336. [Female holotype, Donner Lake, Placer County, California; NEB]. **New Synonymy**.

Scullen (1965a) separated *calochorti* and *varians* by their whitish and yellowish pale markings respectively. As in several other western species the pale markings vary from yellow to white in a south to north cline. The types of both *calochorti* and *varians* are the yellow form. I do not consider the whitish form worthy of subspecies recognition.

(*calodera* Banks = *californica* Cresson)

(*caridei* Holmberg = *dilatata* Spinola)

(*carolina* Banks = *compar* Cresson)

carrizonensis Banks sw. U.S.

*Cerceris carrizonensis** Banks, 1915:403. [Male holotype, Uvalde, Texas; MCZ No. 13772].

*Cerceris poculum** Scullen, 1965a:391. [Female holotype, 23 mi. ne. Douglas, Arizona; USNM]. **New Synonymy**.

Synonymy is by sex association. Scullen (1965a) left *carrizonensis* as an unrecognized species.

(*catamarcensis* Schrottky = *intricata* F. Smith)

(*catawba* Banks = *compar* Cresson)

cavagnaroi Scullen El Salvador to Brasil

*Cerceris cavagnaroi** Scullen, 1972:75. [Female holotype, Quezaltepeque, El Salvador; UCD].

cerverae Giner Marí Cuba

Cerceris cerverae Giner Mari, 1941:333. [Male holotype, Havana, Cuba; Madrid ?].

(*chilopsidis* Viereck and Cockerell = *acanthophila* Cockerell)

(*chinandegaensis* Cameron = kennicottii Cresson)

chiriquensis Cameron (Revised Status) sw. U.S. to Colombia

*Cerceris chiriquensis** Cameron, 1890:114. [Female holotype, Volcan de Chiriqui, Panama; BMNH].

Scullen (1972) treated this taxon as a subspecies of *insolita* Cresson, but it is morphologically distinct.

(*chisosensis* Scullen = *dilatata* Spinola)

(*chrysogastra* Schletterer = *simulans* Saussure)

(*chryssipe* Banks = *clypeata* Dahlbom)

(*cincta* Dahlbom = *fumipennis* Say)

(*cisandina* Brethes = *intricata* F. Smith

(*citrina* Scullen = *finitima* Cresson)

(*cleomae* Rohwer = *crucis* Viereck and Cockerell)

(*clymene* Banks = *clypeata* Dahlbom)

clypeata Dahlbom se. Canada, e. U.S.

*Cerceris clypeata** Dahlbom, 1844:221. [Female lectotype, e. South Carolina, designated by Ferguson (1984); Lund].

*Cerceris imitator** Cresson, 1865b:125, nec F. Smith 1856. [Male lectotype, Illinois, designated by Cresson (1916); ANSP No. 1951]. Synonymy by Scullen (1960).

Cerceris imitatoria Schletterer, 1887:494. New name for *Cerceris imitator* Cresson.

*Cerceris chryssipe** Banks, 1912:18. [Female lectotype, Falls Church, Virginia, designated by Ferguson (1983a); MCZ No. 13791]. Synonymy by Scullen (1951).

*Cerceris clymene** Banks, 1912:20. [Female lectotype, Falls Church, Virginia, designated by Ferguson (1983a); MCZ No. 13789]. Synonymy by Scullen (1951).

*Cerceris zobeide** Brimley, 1929:194. [Male holotype, Raleigh, North Carolina; NCDA]. Synonymy by Scullen (1960).

*Cerceris zosma** Brimley, 1929:195. [Female holotype, Raleigh, North Carolina; NCDA]. Synonymy by Scullen (1960).

(*cochise* Scullen = *cochisi* Scullen)

cochisi Scullen sw. U.S., n. Mexico

*Cerceris cochisi** Scullen, 1965a:416. [Female holotype, Lordsburg to Silver City, New Mexico; USNM].

Cerceris cochise Scullen, 1972:42. *Lapsus.*

cockerelli Viereck sw. Canada, w. U.S.

*Cerceris cockerelli** Viereck, 1902:731. [Male lectotype, La Jolla, California, designated by Cresson (1928); ANSP No. 10037].

*Cerceris minax** Mickel, 1918:339. [Female holotype, Sacramento, California; NEB]. Synonymy by Ferguson (1983b).

(*cognata* Mickel = *californica* Cresson)

compacta Cresson e. and sw. U.S. to Costa Rica

*Cerceris compacta** Cresson, 1865b:127. [Female lectotype, Illinois, designated by Cresson (1916); ANSP No. 1940].

Cerceris huastecae Saussure, 1867:102. [Female, male syntypes, Tampico, Mexico; type specimens not located]. **New Synonymy**.

*Cerceris aureo-facialis*** Cameron, 1890:112. [Male holotype, Orizaba, Mexico; BMNH]. Synonymy by Scullen (1972).

*Cerceris solidaginis** Rohwer, 1908:323. [Male holotype, Las Cruces, New Mexico; USNM]. Synonymy by Scullen (1960).

*Cerceris belfragei** Banks, 1917:114. [Female lectotype, Texas, designated by Ferguson (1983a); MCZ No. 10029]. Synonymy by Scullen (1960).

*Cerceris costarica costarica** Scullen, 1972:44. [Female holotype, 3 mi. nw. Liberia, Costa Rica; USNM]. **New Synonymy**.

*Cerceris costarica mitla** Scullen, 1972:46. [Female holotype, Mitla, Oaxaca, Mexico; USNM]. **New Synonymy**.

C. huastecae is identifiable from the original description and figures. The color forms on which Scullen (1972) based his two subspecies of *costarica* are part of a clinal north to south variation, and both *huastecae* and *aureofacialis* are older names for the same color form.

compar Cresson e. and sw. U.S., n. Mexico

*Cerceris compar** Cresson, 1865b:126. [Male lectotype, Illinois, designated by Cresson (1916); ANSP No. 1949].

*Cerceris catawba** Banks, 1912:25. [Female lectotype, Southern Pines, North Carolina, designated by Ferguson (1983a); MCZ No. 13787]. Synonymy by Scullen (1960).

*Cerceris jucunda carolina** Banks, 1912:26. [Male lectotype, Southern Pines, North Carolina, designated by Ferguson (1983a); MCZ No. 13785]. Synonymy by Scullen (1951).

*Cerceris rufa** Scullen, 1965a:449, nec Taschenberg 1875. [Female holotype, South Miami, Florida; USNM]. **New Synonymy**.

*Cerceris compar albinota** Scullen, 1972:60. [Female holotype, 2 mi. ne. Portal, Cochise County, Arizona; USNM]. **New Synonymy**.

Cerceris rubrata Bohart and Menke, 1976:586. New name for *Cerceris rufa* Scullen.

C. compar varies clinally from yellow markings on a partially red background in Florida to whitish markings on a black background in southwestern U.S. and northern Mexico. The color variation is similar to that of several other species, and I do not consider these minor color forms worthy of subspecific names.

(*complanata* Mickel = *vanduzeei* Banks)

completa Banks California

*Cerceris completa** Banks, 1919:83. [Male holotype, Claremont, California; MCZ No. 13767].

*Cerceris grandis percna** Scullen, 1965a:415. [Female holotype, Mokelumne Hill, Calaveras County, California; USNM]. Synonymy by Bohart and Grissell (1975).

conifrons Mickel w. U.S., n. Mexico

*Cerceris conifrons** Mickel, 1916:410. [Female holotype, Harrison, Nebraska; NEB].

(*contracta* Taschenberg = *dilatata* Spinola)

convergens Viereck and Cockerell w. U.S., n. Mexico

*Cerceris convergens** Viereck and Cockerell, 1904:136. [Female holotype, Alamogordo, New Mexico; ANSP No. 10376].

*Cerceris rinconis** Viereck and Cockerell, 1904:137. [Female holotype, Rincon, New Mexico; ANSP No. 10386]. Synonymy by Scullen (1942).

*Cerceris hesperina** Banks, 1917:115. [Female lectotype, Ainsworth, Washington, designated by Ferguson (1983a); MCZ No. 10031]. Synonymy by Scullen (1951).

*Cerceris pudorosa** Mickel, 1918:338. [Female holotype, Auburn, California; NEB]. Synonymy by Scullen (1942).

*Cerceris snowi** Banks, 1919:84. [Male lectotype, Tucson, Arizona, designated by Ferguson (1983a); MCZ No. 13764]. Synonymy by Scullen (1951).

cooperi Scullen s. Mexico to Costa Rica

*Cerceris cooperi** Scullen, 1972:43. [Female holotype, 6 mi. w. Turrialba, Costa Rica; USNM].

The holotype female bears the label "NEOTYPE—*Eucerceris cooperi* Scullen," an obvious lapsus in labelling.

cortezi Scullen (New Status) s. Mexico

*Cerceris insolita cortezi** Scullen, 1972:64. [Female holotype, Cuernavaca, Morelos, Mexico; USNM].

Although described as a subspecies, this taxon is a morphologically distinct species.

(*cosmiocephala* Cameron = *tolteca* Saussure)

(*costarica* Scullen = *compacta* Cresson)

crandalli Scullen sw. U.S., nw. Mexico

*Cerceris crandalli** Scullen, 1965a:372. [Female holotype, Tucson, Arizona; USNM].

(*crawfordi* Brimley = *arelate* Banks)

cribrosa Spinola s. Mexico to Brazil

*Cerceris cribrosa** Spinola, 1841:119. [Female lectotype, Cayenne, French Guiana, designated by Ferguson (1984); Torino].

*Cerceris subpetiolata** Saussure, 1867:95. [Female lectotype, Cordova, Mexico, designated by Ferguson (1984); Vienna]. Synonymy by Scullen (1961).

*Cerceris pullatus** F. Smith, 1873:105. [Female lectotype, Sao Paulo, Brasil, designated by Ferguson (1984); BMNH]. Synonymy by Scullen (1962).

Cerceris albimana Taschenberg, 1875:395. [Female lectotype, Venezuela, designated by Scullen (1962); Halle]. Synonymy by Scullen (1962).

crotonella Viereck and Cockerell sw. U.S., n. Mexico

*Cerceris crotonella** Viereck and Cockerell 1904:139. [Female holotype, Las Cruces, New Mexico; ANSP].

crucis Viereck and Cockerell (New Status) s. Canada to n. Mexico

Cerceris rufinoda var. *crucis** Viereck and Cockerell, 1904:139. [Female lectotype, Las Cruces, New Mexico, designated by Ferguson (1984); ANSP].

*Cerceris cleomae** Rohwer, 1908:325. [Male holotype, Denver, Colorado; USNM]. **New Synonymy**.

*Cerceris finitima nigroris** Banks, 1912:27. [Male lectotype, Falls Church, Virginia, designated by Ferguson (1983a); MCZ No. 13786]. **Revised Synonymy**. Synonym of *C. finitima* Cresson by Scullen (1965a).

Viereck and Cockerell (1904) and subsequent authors have used the name *C. rufinoda* for this species. However, the male holotype of *C. rufinoda* Cresson is a specimen of the species which has gone under the name *C. argia* Mickel. *C. crucis* is the oldest available name for the *rufinoda* of authors. *C. cleomae* and *C. nigroris* are both males with a black tergum I. This color form occurs sporadically over most of the range of the species. Scullen (1965a) had left *cleomae* as an unrecognized species.

cubensis Cresson (Revised Status) Cuba; Jamaica

*Cerceris zonata** Cresson, 1865a:156, nec Say 1823. [Female lectotype, Cuba, designated by Cresson (1916); ANSP No. 1958].

Cerceris cubensis Cresson, 1865b:123. Created in synonymy as a new name for *C. zonata* Cresson.

Cresson (1865b) proposed *C. cubensis* as a new name for *C. zonata* Cresson because of the similarity of the latter name to *C. zonalis* (!) F. Smith 1856. The name *cubensis* was created in synonymy since *zonalis* is not a homonym of *zonata*. However, when *Philanthus zonatus* Say was transferred by Schletterer (1887) from *Eucerceris* to *Cerceris, C. zonata* Cresson became a junior secondary homonym of *C. zonata* (Say). Dalla Torre (1890, 1897) rejected *zonata* Cresson and used *cubensis* Cresson as the next available name. *C. zonata* Cresson was thereby permanently rejected, and *cubensis* is available even though it was created in synonymy.

cuernavaca Scullen s. Mexico

*Cerceris cuernavaca** Scullen, 1972:46. [Female holotype, Cuernavaca, Morelos, Mexico; USNM].

(*curvicornis* Cameron = *bicornuta* Guerin)

(*dakotensis* Banks = *vicina* Cresson)

(*denticularis* Banks = *californica* Cresson)

dentifrons Cresson se. Canada, e. U.S.

*Cerceris dentifrons** Cresson, 1865b:124. [Female lectotype, Illinois, designated by Cresson (1916); ANSP No. 1942].

deserta Say se. Canada, ne. U.S.

*Cerceris deserta** Say, 1824:343. [Male neotype, South Dakota, designated by Scullen (1965a); MCZ No. 31113].

*Cerceris fulvipes** Cresson, 1865b:126, nec Eversmann 1849. [Female lectotype, Delaware, designated by Cresson (1916); ANSP No. 1941]. Synonymy by Scullen (1942).

Cerceris fulvipediculata Schletterer, 1887:492. New name for *Cerceris fulvipes* Cresson.

dilatata Spinola sw. U.S. to Argentina

*Cerceris dilatata** Spinola, 1841:118. [Female lectotype, Cayenne, French Guiana, designated by Ferguson (1984); Torino].

*Cerceris atriceps** F. Smith, 1856:458. [Female holotype, Para, Brasil; BMNH]. **New Synonymy**.

*Cerceris maximiliani** Saussure, 1867:94. [Female lectotype, Mexico, designated by Scullen (1961); Geneva]. Synonymy by Scullen (1961).

Cerceris contracta Taschenberg, 1875:396. [Female lectotype, Brasil, designated by Scullen (1962); Halle]. Synonymy by Scullen (1962).

Cerceris caridei Holmberg, 1903:478. [Female holotype, Territorium Pampa Centralis, Argentina; MACN]. Synonymy by Fritz (1971).

Cerceris vigilii Brethes, 1910:270. [Male lectotype, Alta Gracia, Cordoba, Argentina, designated by Fritz (1970); MACN]. Synonymy by Fritz (1971).

Cerceris divisa Brethes, 1910:270. [Female holotype, Las Mercedes, Chaco, Argentina; MACN]. Synonymy by Fritz (1971).

*Cerceris olymponis** Strand, 1910:140. [Female holotype, Asuncion, Paraguay; Berlin]. Synonymy by Scullen (1962).

*Cerceris semiatra** Banks, 1947:25. [Male holotype, Patagonia, Arizona; MCZ No. 27620]. Synonymy by Scullen (1961).

*Cerceris dilatata chisosensis** Scullen, 1965a:409. [Female holotype, Chisos Mountains, Big Bend National Park, Texas; USNM]. **New Synonymy.**

The subspecies *chisosensis* was based on specimens with a partially red background color on the propodeum and tergum I. These forms occur with normally colored specimens in the southwestern U.S. and northern Mexico.

A dark form in eastern Brasil and Argentina having a pale band on tergum III with the markings on the posterior terga absent or evanescent may be worthy of subspecies status. *C. atriceps* F. Smith is the oldest name applicable to this form, but I have not seen sufficient material to recognize a subspecies at this time.

(*dissita* Holmberg = *intricata* F. Smith)

(*divisa* Brethes = *dilatata* Spinola)

dreisbachi Scullen s. Mexico

*Cerceris dreisbachi** Scullen, 1972:77. [Female holotype, Cuernavaca, Morelos, Mexico; USNM].

(*dufourii* Guerin = *bicornuta* Guerin)

(*duisi* Scullen = *flavotrochanterica* Rohwer)

durango Scullen c. Mexico

*Cerceris durango** Scullen, 1972:78. [Female holotype, 15 mi. n. Durango, Durango, Mexico; USNM].

(*eburnea* Scullen = *vanduzeei* Banks)

echo Mickel s. Canada to n. Mexico

*Cerceris echo** Mickel, 1916:412. [Female holotype, Monroe Canyon, Sioux County, Nebraska; NEB].

*Cerceris echo atrata** Scullen, 1965a:377. [Female holotype, Camden County, New Jersey; ANSP No. 5039]. **New Synonymy.**

The subspecies *atrata* was based on the color form with a black tergum I. This color form occurs sporadically throughout the range of the species, and I do not consider it worthy of subspecies recognition.

(*elegans* F. Smith = *blakei* Cresson)

(*elegantissima* Schletterer = *blakei* Cresson)

(*elephantinops* Holmberg = *intricata* F. Smith)

(*emmiltosa* Scullen = *rufopicta* F. Smith)

(*englehardti* Banks = *mimica* Cresson)

(*eriogoni* Viereck and Cockerell = *kennicottii* Cresson)

erythropoda Cameron s. Mexico

*Cerceris erythropoda** Cameron, 1890:126. [Female holotype, Cordova, Mexico; BMNH].

(*esau* Schletterer = *mimica* Cresson)

(*eurymele* Banks = *sextoides* Banks)

(*eustylicida* Williams = *nigra* Ashmead)

evansi Scullen c. Mexico

*Cerceris evansi** Scullen, 1972:80. [Female holotype, 3 mi. nw. Cuernavaca, Morelos, Mexico; USNM].

(*exsecta* F. Smith = *imperialis* Saussure)

farri Scullen Jamaica

*Cerceris farri** Scullen, 1970:199. [Female holotype, 3.5 mi. sw. Mandeville, Manchester, Jamaica; USNM].

(*fasciola* Cresson = *occipitomaculata* Packard)

femurrubrum Viereck and Cockerell sw. U.S. to c. Mexico

*Cerceris femur-rubrum** Viereck and Cockerell, 1904:135. [Male lectotype, Albuquerque, New Mexico, designated by Cresson (1928); ANSP No. 10040].

*Cerceris thione** Banks, 1947:18. [Male lectotype, Colton, California, designated by Ferguson (1983a); MCZ No. 23543]. Synonymy by Scullen (1951).

*Cerceris athene** Banks, 1947:20. [Female holotype, Claremont, California; MCZ No. 23537]. Synonymy by Bohart and Grissell (1975).

Cerceris femurrubra [sic] *rossi** Scullen, 1972:56. [Female holotype, Las Animas, Sierra Laguna, Baja California Sur, Mexico; CAS]. Synonymy by Bohart in Bohart and Menke (1976).

(*feralis* Cameron = *bothriophora* Schletterer)

(*ferruginior* Viereck and Cockerell = *californica* Cresson).

festiva Cresson Cuba

Cerceris festiva Cresson, 1865a:156. [Male holotype, Cuba; Havana ?].

*Cerceris gratiosa** Schletterer, 1887:460. [Male holotype, Cuba; Vienna]. Synonymy by Scullen in Alayo (1968).

(*fidelis* Viereck and Cockerell = *bicornuta* Guerin)

finitima Cresson s. Canada to n. Mexico

*Cerceris finitima** Cresson, 1865b:122. [Female holotype, Illinois; ANSP No. 1948].

*Cerceris finitima citrina** Scullen, 1965a:380. [Female holotype, Riverside, California; CAS]. Synonymy by Bohart and Grissell (1975).

(*firma* Cresson = *verticalis* F. Smith)

flavida Cameron s. Mexico

*Cerceris flavida** Cameron, 1890:116. [Female lectotype, Cordova, Mexico, designated by Ferguson (1984); BMNH].

*Cerceris atlacomulca** Scullen, 1972:68. [Female holotype, Atlacomulca, Mexico, Mexico; USNM]. **New Synonymy.**

Scullen (1972) left *C. flavida* as an unrecognized species, but the lectotype is conspecific with *C. atlacomulca.*

flavocostalis Cresson Cuba

Cerceris flavocostalis Cresson, 1865a:153. [Female, male syntypes, Cuba; Havana ?].

flavofasciata H. Smith e. U.S.

*Cerceris flavofasciata** H. Smith, 1908:364. [Female holotype, Lincoln, Nebraska; NEB].

*Cerceris floridensis** Banks, 1915:403. [Male holotype, Gulfport, Florida; MCZ No. 13765]. **New Synonymy**.

*Cerceris natallenus** Brimley, 1927:238. [Female holotype, La Grange, North Carolina; NCDA]. Synonymy by Scullen (1951).

Scullen (1965a) recognized *C. floridensis* as a red marked subspecies. The color variation from north to south is clinal and homeochromic with *C. rufopicta* F. Smith. The black and yellow northern form passes through a black, yellow and red phase to a black and red form in southern Florida.

(*flavomaculata* Cameron = *otomia* Saussure)

flavotrochanterica Rohwer c. Mexico

*Cerceris flavotrochanterica** Rohwer, 1912:471. [Male holotype, Federal District, Mexico; USNM].

*Cerceris duisi** Scullen, 1972:47. [Female holotype, 10 mi. sw. Mendoza, Veracruz, Mexico; USNM]. **New Synonymy**.

Synonymy is by sex association.

(*floridensis* Banks = *flavofasciata* H. Smith)

fortin Scullen s. Mexico

*Cerceris fortin** Scullen, 1972:47. [Female holotype, Fortin de las Flores, Veracruz, Mexico; CAS].

I have not identified the male of this species.

frontata Say sw. U.S., n. Mexico

*Cerceris frontata** Say, 1823:80. [Female neotype, 19 mi. e. Lordsburg, New Mexico, designated by Scullen (1965a); USNM].

*Cerceris occidentalis** Saussure, 1867:100. [Female lectotype, Texas, designated by Scullen (1961); Geneva]. Synonymy by Scullen (1961).

*Cerceris raui** Rohwer, 1920:230. [Female holotype, St. Louis, Missouri; USNM]. Synonymy by Bohart and Grissell (1975).

(*fugatrix* Mickel = *sexta* Say)

(*fulvipediculata* Schletterer = *deserta* Say)

(*fulvipes* Cresson = *deserta* Say)

fumipennis Say se. Canada, e. U.S.

*Cerceris fumipennis** Say, 1837:381. [Male neotype, 3 mi. w. Kaskaskia River, Boulder, Illinois, designated by Scullen (1965a); USNM].

*Cerceris cincta** Dahlbom, 1844:204. [Male holotype (headless), North America; Lund]. Synonymy by Cresson (1865b).

Cerceris unicincta Taschenberg, 1875:397. [Female holotype, Tennessee; Halle]. Synonymy by Dalla Torre (1897).

gandarai Rohwer c. Mexico

*Cerceris gandarai** Rohwer, 1912:470. [Male holotype, Federal District, Mexico; USNM].

*Cerceris micheneri** Scullen, 1972:86. [Female holotype, Matachic, Chihuahua, Mexico; AMNH]. Synonymy by Ferguson (1983b).

(*gandari* Scullen = *rohweri* Ferguson)

(*ganderi* Scullen = *rohweri* Ferguson)

(*garciana* Viereck and Cockerell = *californica* Cresson)

(*geniculata* Cameron = *bothriophora* Schletterer)

(*gnara* Cresson = *verticalis* F. Smith)

gnarina Banks (Revised Status) sc. Canada to sc. U.S.

*Cerceris gnarina** Banks, 1913a:237. [Female lectotype, Vinita, Oklahoma, designated by Ferguson (1983a); AMNH].

*Cerceris posticata** Banks, 1916:64. [Male holotype, Jemez Mountains, New Mexico; MCZ No. 13771]. **New Synonymy**.

Synonymy is by sex association. *C. gnarina* is a valid species and not a subspecies of *C. clypeata* as proposed by Scullen (1965a).

grandis Banks sw. U.S., nw. Mexico

*Cerceris grandis** Banks, 1913b:423. [Female holotype, Fort Yuma, Arizona; AMNH].

(*graphica* F. Smith = *intricata* F. Smith)

(*gratiosa* Schletterer = *festiva* Cresson)

grisselli Ferguson California

*Cerceris grisselli** Ferguson, 1983b:236. [Female holotype, Tanbark Flat, Los Angeles County, California; UCD].

See Ferguson (1983b) for a discussion of the synonymy of this species.

halone Banks se. Canada, e. U.S.

*Cerceris halone** Banks, 1912:24. [Female holotype, Falls Church, Virginia; MCZ No. 13777].

*Cerceris stigmosalis** Banks, 1916:64. [Male holotype, Fargo, North Dakota; MCZ No. 13778]. **New Synonymy**.

*Cerceris architis** Mickel, 1916:409. [Female holotype, South Bend, Nebraska; NEB]. Synonymy by Scullen (1960).

*Cerceris salome** Banks, 1923:21. [Female lectotype, Jones Creek, Lee County, Virginia, designated by Ferguson (1983a); MCZ No. 14705]. Synonymy by Scullen (1951).

*Cerceris shermani** Brimley, 1928:200. [Female holotype, Raleigh, North Carolina; NCDA]. Synonymy by Scullen (1951).

The holotype male of *C. stigmosalis* Banks was misidentified by Scullen (1965a, 1972) as he applied the name to the whitish form of *Cerceris sexta* Say.

hatuey Alayo Cuba

Cerceris hatuey Alayo, 1968:14. [Female, male syntypes, Cuba; Havana ?].

(*hebes* Cameron = *intricata* F. Smith)

(*hesperina* Banks = *convergens* Viereck and Cockerell)

hidalgo Scullen (New Status) c. Mexico

*Cerceris calochorti hidalgo** Scullen, 1972:75. [Female holotype, 14 mi. ne. Durango, Mexico; USNM].

Although described as a subspecies, the holotype female of *hidalgo* represents a distinct species. At least three species were included by Scullen in his determinations under the name *C. calochorti hidalgo.*

huachuca Banks (Revised Status) sw. U.S. to El Salvador

Cerceris (*Apiratrix*) [sic] *huachuca** Banks, 1947:29. [Male holotype (thorax and gaster only), Patagonia, Arizona; MCZ No. 27636].

C. huachuca was incorrectly synonymized under *C. acanthophila* Cockerell by Scullen (1942) and subsequent authors. It is a distinct species closely allied to *C. finitima* Cresson. Many of Scullen's determinations under the name *C. finitima vierecki* were this species.

(*huastecae* Saussure = *compacta* Cresson)

hurdi Scullen sw. U.S. to Nicaragua

*Cerceris hurdi** Scullen, 1972:48. [Female holotype, Ahuacatlan, Nayarit, Mexico; CAS].

(*idahoensis* Scullen = *aequalis* Provancher)

(*illota* Banks = *californica* Cresson)

(*imitator* Cresson = *clypeata* Dahlbom)

(*imitatoria* Schletterer = *clypeata* Dahlbom)

imperialis Saussure c. Mexico to Ecuador

*Cerceris imperialis** Saussure, 1867:98. [Female lectotype, Mexico, designated by Scullen (1961); Geneva].

*Cerceris exsecta** F. Smith, 1873:410. [Female lectotype, Mexico, designated by Ferguson (1984); BMNH]. Synonymy by Scullen (1961).

*Cerceris pilosa*** Cameron, 1890:128. [Male holotype, Guatemala; BMNH]. Synonymy by Scullen (1961).

insolita Cresson e. and sw. U.S., e. Mexico

*Cerceris insolita** Cresson, 1865b:129. [Male holotype, Illinois; ANSP No. 1954].

*Cerceris intractibilis** Mickel, 1916:411. [Female holotype, Child's Point, Nebraska; NEB]. Synonymy by Scullen (1962).

*Cerceris insolita albida** Scullen, 1965a:447. [Female holotype, Las Cruces, New Mexico; USNM]. **New Synonymy**.

*Cerceris insolita atrafemori** Scullen, 1965a:448. [Female holotype, Phoenix, Arizona; USNM]. **New Synonymy**.

Scullen (1965a) based his subspecies *albida* and *atrafemori* on rather minor color differences. The pale markings in this species increase clinally from east to west as in several other species.

(*interjecta* Banks = *californica* Cresson)

(*intractibilis* Mickel = *insolita* Cresson)

intricata intricata F. Smith Venezuela to Argentina

*Cerceris intricata** F. Smith, 1856:459. [Male lectotype, Santarem, Brasil, designated by Ferguson (1984); BMNH].

*Cerceris simplex** F. Smith, 1856:462. [Female lectotype, Santarem, Brasil, designated by Ferguson (1984); BMNH]. Synonymy by Fritz (1971).

*Cerceris vulpina** F. Smith, 1856:463. [Male lectotype, Brasil, designated by Ferguson (1984); BMNH]. Synonymy by Fritz (1971).

Cerceris larvata Taschenberg, 1875:391. [Male holotype, Mendoza, Argentina; Halle]. Synonymy by Fritz (1971).

*Cerceris affumata** Schletterer, 1887:455. [Female holotype, Rio de Janeiro, Brasil; Vienna]. Synonymy by Fritz (1971). Synonym of *C. simplex* by Scullen (1965b).

Cerceris melanogaster Holmberg, 1903:481. [Female holotype, Territorium Pampa Centralis, Argentina; MNBA]. Synonymy by Fritz (1971). Synonym of *C. larvata* by Fritz (1962).

Cerceris elephantinops Holmberg, 1903:485. [Male holotype, Territorium Pampa Centralis, Argentina; location of type unknown]. Synonymy by Fritz (1971). Synonym of *C. larvata* by Scullen (1965b).

Cerceris elephantinops var. *dissita* Holmberg, 1903:485. [Male holotype, Formosa, Argentina; location of type unknown]. Synonymy by Fritz (1971). Synonym of *C. larvata* by Fritz (1962).

Cerceris catamarcensis Schrottky, 1909:246. [Female holotype?, Catamarca, Argentina; location of type unknown]. Synonymy by Fritz (1971).

Cerceris cisandina Brethes, 1913:122. [Female holotype, Mendoza, Argentina; location of type unknown]. Synonymy by Fritz (1971).

intricata graphica F. Smith (Revised Status) sw. U.S. to Peru

*Cerceris graphica** F. Smith, 1873:410. [Female holotype, Mexico; BMNH].

*Cerceris hebes** Cameron, 1890:124. [Male holotype, (thorax and gaster only), Chilpancingo, Guerrero, Mexico; BMNH]. Synonymy by Bohart and Grissell (1975).

*Cerceris macrosticta** Viereck and Cockerell, 1904:133. [Male holotype New Mexico; ANSP No. 10381]. Synonymy by Bohart and Grissell (1975).

*Cerceris ampla** Banks, 1912:16. [Female lectotype, designated by Ferguson (1984); MCZ No. 13769]. Synonym of *C. macrosticta* by Scullen (1942).

This wide ranging species occurs from the southwestern U.S. to Argentina. Color varies from a highly maculated pale form in the U.S. and Mexico to an almost completely melanic form in southern South America. Scullen (1965b) divided it into four subspecies under the specific name *C. simplex*. His subspecies were (1) *simplex simplex* (=*affumata*) for the most melanic form from Brasil; (2) *simplex larvata* (=*elephantinops*) from Brasil and Argentina; (3) *simplex graphica* from Mexico to Peru; and (4) *simplex macrosticta* (=*ampla*) from northern Mexico and the southwestern U.S.

Fritz (1971) separated *intricata* from *macrosticta* as distinct species on the basis of characters in the males, but the characters used are inconsistent when large number of specimens are examined. The apicolateral corners of the male pygidium are usually bluntly rounded in the north and subspinose in Argentina. This variation is clinal with specimens from Venezuela, Colombia and Peru showing an intermediate condition.

I recognize two subspecies. The nominate subspecies occurs from Venezuela to Argentina and is characterized by having the pale bands on the terga reduced to narrow bands or absent. The subspecies *graphica* occurs from the southwestern U.S. to Colombia and Peru with the pale tergal bands wide, sometimes completely covering the terga.

irene Banks sc. U.S.

*Cerceris irene** Banks, 1912:26. [Female holotype, Fedor, Lee County, Texas; MCZ No. 13781].

(*iresinides* Rohwer = *kennicottii* Cresson)

(*irwini* Scullen = *mexicana* Saussure)

isolde Banks (Revised Status) sw. U.S., nw. Mexico

*Cerceris isolde** Banks, 1947:24. [Male holotype, Palmerlee, Arizona; MCZ No. 23540].

*Cerceris sandiegensis** Scullen, 1965a:432. [Female holotype, 2 mi. e. Anza, Riverside County, California; CAS]. **New Synonymy.**

Scullen (1960, 1965a) misidentified *C. isolde* and incorrectly synonymized it under *C. californica* Cresson.

(*josei* Scullen = *mexicana* Saussure)

jucunda Cresson (Revised Status) e. U.S.

*Cerceris jucunda** Cresson, 1872:231. [Male holotype, Texas; USNM].

*Cerceris zelica** Banks, 1912:23. [Female lectotype, Fedor, Texas, designated by Ferguson (1983a); MCZ No. 13773]. **New Synonymy.**

Scullen (1951) incorrectly synonymized *C. jucunda* under *C. compar* Cresson. Synonymy is by sex association.

kennicottii kennicottii Cresson se. Canada to s. Mexico

*Cerceris kennicottii** Cresson, 1865b:128. [Male holotype, Louisiana; ANSP No. 1952].

*Cerceris montivaga** Cameron, 1890:119. [Female holotype, Chilpancingo, Guerrero, Mexico: BMNH]. **Revised Synonymy.** Synonym of *C. kennicottii zapoteca* Saussure by Scullen (1972).

*Cerceris eriogoni** Viereck and Cockerell, 1904:139. [Male holotype, Dripping Spring, Organ Mountains, New Mexico; ANSP No. 10377]. Synonymy by Scullen (1965a).

*Cerceris kennicottii beali** Scullen, 1965a:386. [Female holotype, Scottsdale, Arizona; USNM]. Synonymy by Bohart and Grissell (1975).

kennicottii chinandegaensis Cameron (Revised Status) Guatemala to Panama

*Cerceris chinandegaensis** Cameron, 1904:66. [Male lectotype, Chinandega, Nicaragua, designated by Ferguson (1984); BMNH].

*Cerceris iresinides** Rohwer, 1914:522. [Male holotype, Gualan, Guatemala; USNM]. **Revised Synonymy**. Synonym of *C. kennicottii bakeri* by Scullen (1972).

This species varies from yellowish pale maculations in the northern and eastern U.S. to whitish pale markings in most of Mexico and parts of the southwestern U.S. Scullen (1965a) described *beali* as a subspecies for these whitish forms and later (1972) incorrectly used *zapoteca* Saussure as the subspecies name with *beali* as a junior synonym. *C. zapoteca* Saussure is a distinct species and not a subspecies of *kennicottii.*

From Guatemala to Costa Rica it has an almost completely yellow propodeum and tergum I, and apparently mimics *Polybia occidentalis bohemani* Holmgren in this area as do some other species of *Cerceris.* Scullen (1972) applied the name *bakeri* to this color form, but *bakeri* is a distinct species occurring in the same color form in the same area. Scullen (1972) applied the name *smithiana* as a subspecies to an intermediate color form, but *smithiana* is the female and a junior synonym of *zapoteca* Saussure. I here recognize the form with the mostly or entirely yellow propodeum as a subspecies, but it must take the name *kennicottii chinandegaensis* Cameron. See also discussions under the names *bakeri* and *zapoteca.*

krombeini Scullen sw. U.S.; nw. Mexico

*Cerceris krombeini** Scullen, 1965a:388. [Female holotype, Continental, Arizona; USNM].

krugi Dewitz Puerto Rico

*Cerceris krugi** Dewitz, 1881:200. [Female lectotype, Puerto Rico, designated by Ferguson (1984); Berlin].

*Cerceris margaratella** Rohwer, 1915:248. [Male holotype, Puerto Rico; USNM]. **New Synonymy.**

Synonymy is by sex association. Scullen recognized this synonymy in determinations.

laevigata F. Smith Dominican Republic

*Cerceris laevigata** F. Smith, 1856:465. [Female lectotype, Santo Domingo, designated by Ferguson (1984); BMNH].

Cerceris levigata Dalla Torre, 1897:466. Emendation.

(*larvata* Taschenberg = *intricata* F. Smith)

(*levigata* Dalla Torre = *laevigata* F. Smith)

lutzi Scullen Panama

*Cerceris lutzi** Scullen, 1972:85. [Female holotype, El Volcan Chiriqui, Panama; AMNH].

(*macrosticta* Viereck and Cockerell = *intricata* F. Smith)

macswaini Scullen sw. U.S.

*Cerceris macswaini** Scullen, 1965a:485. [Female holotype, Imperial County, California; USNM].

mandibularis Patton e. U.S.

*Cerceris mandibularis** Patton, 1880:403. [Female neotype, Glenside, Pennsylvania, designated by Scullen (1965a); USNM].

(*margaretella* Rohwer = *krugi* Dewitz)

(*marginata* Cameron = *marginula* Dalla Torre)

marginula Dalla Torre s. Mexico to Panama

*Cerceris marginata*** Cameron, 1890:117, nec F. Smith 1856. [Female holotype, Volcan de Irazu, Costa Rica; BMNH].

Cerceris marginula Dalla Torre, 1897:467. New name for *Cerceris marginata* Cameron.

(*maximiliani* Saussure = *dilatata* Spinola)

(*melanogaster* Holmberg = *intricata* F. Smith)

melanthe Banks sw. U.S., n. Mexico

*Cerceris melanthe** Banks, 1947:21. [Female holotype, Apache Canyon, Santa Catalina Mountains, Arizona; MCZ No. 23539].

mexicana mexicana Saussure s. Mexico to El Salvador

Cerceris mexicana Saussure, 1867:101. [Female, male syntypes, "Agro Mexicano calido"; types not located].

*Cerceris veracruz veracruz** Scullen, 1972:53. [Female holotype, 1 mi. e. Cordoba, Veracruz, Mexico; CAS]. **New Synonymy**.

*Cerceris veracruz josei** Scullen, 1972:53. [Female holotype, Quezaltepeque, El Salvador; UCD]. **New Synonymy**.

mexicana irwini Scullen (Revised Status) Nicaragua, Costa Rica

*Cerceris irwini** Scullen, 1972:49. [Female holotype, 7 mi. s.e. Liberia, Costa Rica; USNM].

C. mexicana is identifiable from Saussure's description and figures. *C. irwini* is conspecific with *mexicana,* but represents another mimic of *Polybia occidentalis bohemani* Holmgren, and I recognize it here as a subspecies. The subspecies *josei* is somewhat intermediate between the nominate subspecies and *irwini,* but I regard it as a minor color variant.

(*micheneri* Scullen = *gandarai* Rohwer)

militaris Dahlbom Costa Rica to Brasil

Cerceris militaris Dahlbom, 1844:224. [Female holotype, erroneously reported from "Cap Bonae Spei"; Lund].

Cerceris rufo-nigra Taschenberg, 1875:399. [Female lectotype, here designated, Rio de Janeiro, Brasil; Halle]. Synonymy by Empey (1980).

*Cerceris rufonigra turrialba** Scullen, 1972:51. [Female holotype, Turrialba, Costa Rica; USNM]. **New Synonymy**.

The subspecies *turrialba* proposed by Scullen (1972) has the same pattern of maculations as the nominate form; the individual pale marks are simply larger. Empey (1980) studied the types of both *militaris* and *rufonigra* and established their identity. Empey (personal communication) states that the type specimen bears a lectotype label affixed by Scullen, but neither he nor I have found any published reference to the designation of a lectotype. The type specimen is probably a holotype since Taschenberg (1875) stated the number of specimens at hand when he had more than one. In order to avoid any future confusion, the above specimen, labelled as described by Empey (1980) and bearing the lectotype label affixed by Scullen, is here designated lectotype despite the fact that such designation may be redundant.

(*miltosa* Scullen = *rufopicta* F. Smith)

mimica Cresson sw. U.S. to c. Mexico

*Cerceris mimica** Cresson, 1872:228. [Female lectotype, Texas, designated by Cresson (1916); ANSP No. 1943].

*Cerceris esau** Schletterer, 1887:458. [Female lectotype, Mexico, designated by Scullen (1961); Vienna]. Synonymy by Scullen (1961).

Cerceris minima Schletterer, 1887:497. *Lapsus.*

*Cerceris englehardti** Banks, 1947:12. [Male holotype, St. John, Arizona; MCZ No. 27638]. Synonymy by Scullen (1951).

(*minima* Schletterer = *mimica* Cresson)

(*minax* Mickel = *cockerelli* Viereck)

(*mitla* Scullen = *compacta* Cresson)

montealban Scullen c. Mexico

*Cerceris montealban** Scullen, 1972:51. [Female holotype, Oaxaca, Oaxaca, Mexico; CAS].

montezuma Cameron c. Mexico

*Cerceris montezuma** Cameron, 1890:108. [Female lectotype, Mexico, designated by Ferguson (1984); BMNH].

(*montivaga* Cameron = *kennicottii* Cresson)

(*morata* Cresson = *tepaneca* Saussure)

morelos Scullen (New Status) s. Mexico

*Cerceris finitima morelos** Scullen, 1972:25. [Female holotype, 14 mi. s. Cuernavaca, Mexico; USNM].

Although described as a subspecies, I regard this taxon as a distinct species closely allied to *C. finitima*. It was synonymized under *C. finitima* Cresson by Bohart in Bohart and Menke (1976).

(*munda* Mickel = *nigrescens* F. Smith)

(*nasica* Viereck and Cockerell = *tepaneca* Saussure)

(*natallena* Brimley = *flavofasciata* H. Smith)

neahminax Scullen sw. U.S.

*Cerceris neahminax** Scullen, 1965a:390. [Female holotype, Santa Fe, New Mexico; CAS].

nebrascensis H. Smith nc. U.S.

*Cerceris nebrascensis** H. Smith, 1908:368. [Female holotype, Glen, Sioux County, Nebraska; NEB].

nigra Ashmead St. Vincent, British Guiana, Panama

*Cerceris nigra** Ashmead, 1900:227. [Female lectotype, St. Vincent, British West Indies, designated by Ferguson (1984); USNM].

*Cerceris eustylicida** Williams, 1928:169. [Female holotype, Blairmont, Berbice County, British Guiana; BPBM]. **New Synonymy.**

The types of the above two species and a female from Panama [UCD] present three slightly different shapes of the longitudinal ridge on the apical portion of the clypeal midsection. They are inseparable in all other respects, and I conclude that they are all conspecific with minor interpopulation variations.

nigrescens F. Smith Alaska, Canada, n. and w. U.S.

*Cerceris nigrescens*** F. Smith, 1856:466. [Female holotype, Nova Scotia; BMNH].

*Cerceris munda** Mickel, 1918:337. [Female holotype, Sacramento, California; NEB]. Synonymy by Bohart and Grissell (1975).

*Cerceris abbreviata** Banks, 1919:84. [Male lectotype, Nelson's, Yakima River, Washington, designated by Ferguson (1983a); MCZ No. 13794]. Synonymy by Scullen (1951).

(*nigritula* Banks = *arelate* Banks)

(*nigroris* Banks = *crucis* Viereck and Cockerell)

(*nitida* Banks = *nitidoides* Ferguson)

nitidoides Ferguson (**New Name**) se. Canada, e. U.S.

*Cerceris nitida** Banks, 1913b:424, nec Wesmael 1852. [Female lectotype, Valley of Black Mountains, North Carolina, designated by Ferguson (1983a); AMNH].

Scullen (1976) incorrectly synonymized this taxon under *C. melanthe* Banks as the two are distinct species.

(*novomexicana* Viereck and Cockerell = *occipitomaculata* Packard)

oaxaca Scullen s. Mexico

*Cerceris oaxaca** Scullen, 1972:90. [Female holotype, 12 mi. se. Oaxaca, Mexico; USNM].

The allotype male and paratype males are not conspecific, but represent dark specimens of *C. truncata* Cameron.

obregon Scullen nw. Mexico

*Cerceris obregon** Scullen, 1972:34. [Female holotype, 38 mi. nw. Obregon, Sonora, Mexico; USNM].

obsoleta Cameron s. Mexico to Colombia

*Cerceris obsoleta** Cameron, 1890:118. [Female lectotype, Teapa, Tabasco, Mexico, designated by Ferguson (1984); BMNH].

(*occidentalis* Saussure = *frontata* Say)

occipitomaculata Packard se. Canada, e. U.S.

*Cerceris occipitomaculata** Packard, 1866:62. [Male neotype, Hunt County, Texas, designated by Scullen (1965a); USNM].

*Cerceris fasciola** Cresson, 1872:230. [Male holotype, Comal County, Texas; ANSP No. 1950]. Synonymy by Scullen (1965a).

*Cerceris novomexicana** Viereck and Cockerell, 1904:137. [Female holotype, Johnson Park, New Mexico; ANSP No. 10383]. Synonymy by Scullen (1965a).

(*olymponis* Strand = *dilatata* Spinola)

(*orestes* Banks = *bothriophora* Schletterer)

(*orphne* Banks = *sexta* Say)

otomia Saussure (Revised Status) s. Mexico to Colombia

*Cerceris otomia** Saussure, 1867:99. [Female lectotype, Mexico, designated by Ferguson (1984); Vienna].

*Cerceris flavo-maculata** Cameron, 1890:115. [Female lectotype, Rio Susio, Costa Rica, designated by Ferguson (1984); BMNH]. **New Synonymy.**

Cerceris otomita Dalla Torre, 1897:469. *Lapsus.*

The apical teeth of the clypeal margin of *C. flavomaculata* are somewhat larger than in *C. otomia,* but I have seen specimens intermediate between the two and have concluded that they are conspecific.

(*otomita* Dalla Torre = *otomia* Saussure)

panama Scullen (New Status) Honduras to Panama

*Cerceris insolita panama** Scullen, 1972:67. [Female holotype, 7 mi. se. Liberia, Costa Rica; USNM].

The female of this species is much like *C. bothriophora* and the males are close to *C. chiriquensis.* It is certainly not *C. insolita,* and I provisionally elevate the taxon to specific status until this species group can be more carefully studied.

(*parkeri* Scullen = *bakeri* Cameron)

(*percna* Scullen = *completa* Banks)

(*pilosa* Cameron = *imperialis* Saussure)

(*platyrhina* Viereck and Cockerell = *tepaneca* Saussure)

(*pleuralis* H. Smith = *rufopicta* F. Smith)

(*poculum* Scullen = *carrizonensis* Banks)

(*populorum* Viereck and Cockerell = *californica* Cresson)

(*posticata* Banks = *gnarina* Banks)

prominens Banks (Revised Status) e. U.S.

*Cerceris prominens** Banks, 1912:19. [Female lectotype, Falls Church, Virginia, designated by Ferguson (1983a); MCZ No. 13790].

Scullen (1965a) treated this taxon as a subspecies of *C. clypeata,* but I regard it as a distinct species based on the structure of the male clypeus.

psamathe Banks (Revised Status) e. U.S.

*Cerceris psamathe** Banks, 1912:21. [Female holotype, Fedor, Lee County, Texas; MCZ No. 13780].

Scullen (1951) incorrectly synonymized this species under *C. aequalis,* but they are distinct species.

(*pudorosa* Mickel = *convergens* Viereck and Cockerell)

(*pullata* F. Smith = *cribrosa* Spinola)

queretaro Scullen sw. U.S. to c. Mexico

*Cerceris queretaro** Scullen, 1972:91. [Female holotype, 41 mi. n. Queretaro, Mexico; USNM].

(*raui* Rohwer = *frontata* Say)

rhois Rohwer sw. U.S.

*Cerceris rhois** Rohwer, 1908:325. [Male holotype, Rio Ruidoso, White Mountains, New Mexico; USNM].

This species is very close to *C. halone* Banks, and it may prove to be a senior synonym. *C. rhois* has broader pale bands on the posterior terga than *C. halone,* and the tergal punctures tend to coalesce. In *C. halone* the punctures are separated by flat ridges.

(*rinconis* Viereck and Cockerell = *convergens* Viereck and Cockerell)

(*robertsonii* Fox = *rufopicta* F. Smith)

rohweri Ferguson se. Texas to s. Mexico

*Cerceris rohweri** Ferguson, 1983b:238. [Female holotype, 17 mi. ne. San Luis Potosi, San Luis Potosi, Mexico; USNM].

Cerceris ganderi Scullen, 1968:156. *Lapsus.*

Cerceris gandari Scullen, 1972:82. *Lapsus.*

As discussed by Ferguson (1983b) this species was misidentified as *C. gandarai* Rohwer by Scullen (1968, 1972).

(*rossi* Scullen = *fumurrubrum* Viereck and Cockerell)

(*rostrata* F. Smith = *simulans* Saussure)

rozeni Scullen New Jersey, Florida

*Cerceris rozeni** Scullen, 1971:130. [Female holotype, Archbold Biological Station, Highlands County, Florida; AMNH].

(*rubrata* Bohart and Menke = *compar* Cresson)

(*rufa* Scullen = *compar* Cresson)

rufinoda Cresson c. U.S. to c. Mexico

*Cerceris rufinoda** Cresson, 1865b:121. [Male holotype, Colorado; ANSP No. 1955].

*Cerceris argia** Mickel, 1916:412. [Female holotype, Lincoln, Nebraska; NEB]. **New Synonymy**.

This species was discussed under *C. crucis.*

(*rufonigra* Taschenberg = *militaris* Dahlbom)

rufopicta F. Smith se. Canada, e. U.S.

*Cerceris rufo-picta** F. Smith, 1856:467. [Male lectotype, St. John's Bluff, E. Florida, designated by Ferguson (1984); BMNH].

*Cerceris robertsonii** Fox, 1893a:55. [Female lectotype, Smithville, South Dakota, designated by Cresson (1928); ANSP No. 4755]. **New Synonymy.**

*Cerceris austrina** Fox, 1893b:556. [Female lectotype, Southern Florida, designated by Cresson (1928); ANSP No. 4756]. **Revised Synonymy.** Synonym of *C. robertsonii* by Scullen (1965a).

*Cerceris pleuralis** H. Smith, 1908:366. [Female holotype, Rock County, Nebraska; NEB]. **Revised Synonymy.** Synonym of *C. robertsonii* by Scullen (1965a).

*Cerceris robertsonii emmiltosus** Scullen, 1964:144. [Female holotype, Miami, Florida; USNM]. **New Synonymy.**

*Cerceris robertsonii bifidus** Scullen, 1965a:428. [Female holotype, Kill Devil Hills, North Carolina; USNM]. **New Synonymy.**

*Cerceris robertsonii miltosus** Scullen, 1965a:429. [Female holotype, Arcadia, Florida; USNM]. **New Synonymy.**

This species is variable both in color and in the shape of the membrane appended to the clypeal process of the female. Color varies clinally from north to south from a black and yellow form in the north to a black, yellow and red form in the southeastern United States to a black and red form in southern Florida. The names *robertsonii, pleuralis,* and *bifida* apply to the black and yellow form, and the remaining names apply to forms with variable amounts of red. The clypeal membrane of the female varies from the "*robertsonii*" shape to the "*bifida*" shape within the same population with all intermediate conditions present. (See Scullen 1965a, figs. 136a and 137a.)

(*salome* Banks = *halone* Banks)

(*sandiegensis* Scullen = *isolde* Banks)

(*sayi* Banks = *sexta* Say)

scapularis Schletterer (Revised Status) s. Mexico

*Cerceris scapularis** Schletterer, 1887:457. [Female lectotype, Orizaba, Mexico, designated by Scullen (1972); Vienna].

Scullen (1972) incorrectly synonymized this species under *C. simulans* Saussure. See discussion under *C. simulans.*

(*semiatra* Banks = *dilatata* Spinola)

(*seminigra* Banks = *azteca* Saussure)

semipetiolata Saussure s. Mexico to Panama

Cerceris semipetiolata Saussure, 1867:88. [Male holotype, Orizaba, Mexico; type not located].

*Cerceris williamsi** Scullen, 1972:54. [Female holotype, Fortin de las Flores, Veracruz, Mexico; CAS]. **New Synonymy.**

Synonymy is by sex association. Although Saussure described *semipetiolata* from a headless male, identification is possible from his description. The combination of long tergum I, coarsely ridged propodeal enclosure, and color pattern of the thorax and gaster is distinctive.

sexta Say sc. Canada to c. Mexico

*Cerceris sexta** Say, 1837:382. [Male neotype, Colorado, designated by Scullen (1965a); ANSP No. 5041].

*Cerceris biungulata** Cresson, 1865b:118. [Female holotype, Colorado; ANSP No. 1956]. Synonymy by Scullen (1960).

*Cerceris alceste** Mickel, 1918:333. [Female holotype, Mitchell, Nebraska; NEB]. **New Synonymy**.

*Cerceris fugatrix** Mickel, 1918:335. [Male holotype, Mitchell, Nebraska; NEB]. **Revised Synonymy**. Synonym of *C. stigmosalis* Banks by Scullen (1965a).

*Cerceris sayi** Banks, 1923:21. [Female lectotype, Steele, North Dakota, designated by Ferguson (1983a); MCZ No. 14706]. **Revised Synonymy**. Synonym of *C. stigmosalis* Banks by Scullen (1965a).

*Cerceris stevensi** Banks, 1923:22. [Female holotype, Steele, North Dakota; MCZ No. 14707]. **Revised Synonymy**. Synonym of *C. stigmosalis* Banks by Scullen (1965a).

*Cerceris orphne** Banks, 1947:15. [Male holotype, Jemez Springs, New Mexico; MCZ No. 23536]. Synonymy by Scullen (1961).

There is much variation in the size and shape of the female clypeal process in this species. Pale markings vary from whitish in the northern plains and Canada to a deep yellow in the southern plains and again whitish in south central Mexico. Scullen (1965a, 1972) placed the whitish forms under the name "*stigmosalis*," but the type of *stigmosalis* Banks is a male of *C. halone* Banks. The names *C. sayi* and *C. stevensi* apply to the northern whitish form.

sextoides Banks sw. Canada to nw. Mexico

*Cerceris sextoides** Banks, 1947:10. [Female holotype, Lone Tree, Yakima River, Washington; MCZ No. 23547].

*Cerceris eurymele** Banks, 1947:11. [Female holotype, Davis, California; MCZ No. 23546]. Synonymy by Scullen (1965a).

(*shermani* Brimley = *halone* Banks)

(*simplex* F. Smith = *intricata* F. Smith)

simulans Saussure s. Mexico

Cerceris simulans Saussure, 1867:87. [Male holotype, Mexico; type not located].

*Cerceris rostrata*** F. Smith, 1873b:409. [Female holotype, Mexico; BMNH]. **New Synonymy**.

*Cerceris chrysogastra** Schletterer, 1887:458. [Male lectotype, Orizaba, Mexico, designated by Scullen (1972); Vienna]. Synonymy by Scullen (1972).

C. simulans is identifiable from Saussure's original description and figures. Scullen (1972) identified the male, but he misassociated the female, as he treated *C. rostrata* as a separate species and incorrectly placed *C. scapularis* in synonymy as the female of *simulans. C. rostrata* shares the long tergum I, the basal platform on sternum II, and the fossette on tergum I with *C. simulans,* whereas these characters are lacking in *C. scapularis.*

(*singularis* Brethes = *binodis* Spinola)

(*smithiana* Cameron = *zapoteca* Saussure)

(*snowi* Banks = *convergens* Viereck and Cockerell)

(*solidaginis* Rohwer = *compacta* Cresson)

(*spinolae* Dahlbom = *binodis* Spinola)

squamulifera Mickel c. U.S.

*Cerceris squamulifera** Mickel, 1916:411. [Female holotype, Imperial, Nebraska; NEB].

This species is very close to *C. rufopicta.* However, the males which I have associated with it lack the sternal fimbriae present in *rufopicta.*

(*stevensi* Banks = *sexta* Say)

(*stigmosalis* Banks = *halone* Banks)

strigosa Cameron c. Mexico

*Cerceris strigosa** Cameron, 1890:110. [Female lectotype, Durango, Mexico, designated by Ferguson (1984); BMNH].

(*subpetiolata* Saussure = *cribrosa* Spinola)

tepaneca Saussure sw. U.S. to s. Mexico

*Cerceris tepaneca** Saussure, 1867:90. [Male lectotype, Orizaba, Mexico, designated by Scullen (1972); Vienna].

*Cerceris morata** Cresson, 1872:230. [Female lectotype, Texas, designated by Cresson (1916); ANSP No. 1944]. **New Synonymy**.

*Cerceris thermophila** Schletterer, 1887:463. [Female lectotype, Mexico, designated by Scullen (1972); Vienna]. **New Synonymy**. (Listed as both a synonym of *C. clypeata tepaneca* and as a good species by Bohart and Menke, 1976.)

*Cerceris nasica** Viereck and Cockerell, 1904:132. [Female holotype, New Mexico; ANSP No. 10382]. **Revised Synonymy**. Synonym of *C. morata* Cresson by Scullen (1942).

*Cerceris platyrhina** Viereck and Cockerell, 1904:133. [Female holotype, Fillmore Canyon, Organ Mountains, New Mexico; ANSP No. 10384]. **Revised Synonymy**. Synonym of *C. morata* Cresson by Scullen (1942), synonym of *C. vicina* Cresson by Scullen (1965a).

Scullen (1942) correctly placed *C. platyrhina* in synonymy under *C. morata,* but he later (1965a) incorrectly placed it in synonymy under *C.*

vicina Cresson. *C. tepaneca* is very close to *C. clypeata,* and Scullen (1972) treated it as a subspecies of the latter. However, he regarded *C. morata* to be a distinct species, and he separated the two by the distinctive red and yellow coloration of *C. morata* in the northern part of its range. All intergrades occur in a north to south cline from the red and yellow forms of the southwestern United States to the black forms with reduced yellow markings of southern Mexico. I separate *C. tepaneca* from *C. clypeata* on the basis of body sculpture.

texana Scullen Texas

*Cerceris texana** Scullen, 1965a:511. [Female holotype, Del Rio, Texas; KANS].

(*texensis* Saussure = *californica* Cresson)

(*thermophila* Schletterer = *tepaneca* Saussure)

(*thione* Banks = *femurrubrum* Viereck and Cockerell)

tolteca Saussure s. U.S. to Panama

*Cerceris tolteca** Saussure, 1867:94. [Female lectotype, Cuantla, Mexico, designated by Scullen (1972); Geneva].

*Cerceris cosmiocephala*** Cameron, 1904:67. [Male holotype, San Marcos, Nicaragua; BMNH]. Synonymy by Scullen (1961).

townsendi Viereck and Cockerell New Mexico

*Cerceris townsendi** Viereck and Cockerell, 1904:140. [Male holotype, Las Cruces, New Mexico; ANSP No. 10389].

Ferguson (1984) discussed the identity of the holotype.

triangulata Cresson Cuba

Cerceris triangulata Cresson, 1865a:154. [Female holotype, Cuba; Havana?].

*Cerceris bilunata** Cresson, 1865a:155. [Male lectotype, Cuba, designated by Cresson (1916); ANSP No. 1957]. Synonymy by Alayo (1968).

Cerceris bilinieata Schletterer, 1887:487. *Lapsus.*

trichiosoma Cameron c. Mexico

*Cerceris trichiosoma** Cameron, 1890:127. [Male holotype, Durango, Mexico; BMNH].

trinitaria Alayo Cuba

Cerceris trinitaria Alayo, 1968:10. [Female, male syntypes, Cuba; Havana?].

I have not seen this species.

truncata Cameron sw. U.S. to Costa Rica

*Cerceris truncata** Cameron, 1890:121. [Female lectotype, Temax, North Yucatan, Mexico, designated by Ferguson (1984); BMNH].

(*turrialba* Scullen = *militaris* Dahlbom)

(*unicincta* Taschenberg = *fumipennis* Say)

vanduzeei Banks sw. Canada to nw. Mexico

*Cerceris vanduzeei** Banks, 1917:114. [Female lectotype, San Diego County, California, designated by Ferguson (1983a); MCZ No. 10030].

*Cerceris complanata** Mickel, 1918:340. [Female holotype, Auburn, California; NEB]. Synonymy by Scullen (1960).

*Cerceris vanduzeei eburnea** Scullen, 1965a:399. [Female holotype, North Powder, Union County, Oregon; USNM]. Synonymy by Bohart and Grissell (1975).

(*varians* Mickel = *calochorti* Rohwer)

(*venator* Cresson = *bicornuta* Guerin)

(*venatrix* Schulz = *bicornuta* Guerin)

(*veracruz* Scullen = *mexicana* Saussure)

verticalis F. Smith se. U.S., ne. Mexico

*Cerceris verticalis*** F. Smith, 1856:466. [Female holotype, Georgia; BMNH].

*Cerceris gnara** Cresson, 1872:229. [Male lectotype, Texas, designated by Cresson (1916); ANSP No. 1938]. Synonymy by Scullen (1961).

*Cerceris firma** Cresson, 1872:229. [Female lectotype, Texas, designated by Cresson (1916); ANSP No. 1945]. Synonymy by Scullen (1961).

vicina Cresson nc. U.S.

*Cerceris vicina** Cresson, 1865b:120. [Female lectotype, Colorado, designated by Cresson (1916); ANSPNo. 1939].

*Cerceris dakotensis** Banks, 1915:402. [Female lectotype, Fargo, North Dakota, designated by Ferguson (1983a); MCZ No. 13770]. **New Synonymy**.

Scullen (1965a) treated *dakotensis* as a subspecies of *clypeata,* but the type of *dakotensis* is clearly conspecific with *vicina* Cresson. The shape of the clypeal process is quite distinctive. In his determinations under the name *C. clypeata dakotensis* Scullen included specimens of *clypeata* and *prominens* as well as *vicina.* The range of *vicina* is allopatric with that of *C. tepaneca,* and I am able to separate males of *vicina* from males of *tepaneca* only on the basis of locality even though the females are quite distinct.

vicinoides Viereck and Cockerell (Revised Status) sc. U.S.

*Cerceris vicinoides** Viereck and Cockerell, 1904:140. [Female holotype, Pecos, New Mexico; ANSP No. 10387].

Scullen (1951) incorrectly synonymized this species under *C. aequalis* Provancher, but it is a distinct species.

(*viduata* F. Smith = *binodis* Spinola)

vierecki Banks (Revised Status) sw. U.S. to c. Mexico

Cerceris (*Apiratrix*) [sic] *vierecki** Banks, 1947:30. [Female holotype, Tempe, Arizona; MCZ No. 23544].

Cerceris (*Apiratrix*) [sic] *arizonella** Banks, 1947:32. [Male holotype, Tempe, Arizona; MCZ No. 23538]. **New Synonymy**.

Synonymy is by sex association. Scullen (1965a) left *C. arizonella* as an unrecognized species, and treated *vierecki* as a whitish subspecies of *C. finitima. C. huachuca* is a closely related whitish species, and *C. finitima* occurs in a whitish phase also. A high percentage of Scullen's determinations under the name *vierecki* have been found to be *huachuca.* Bohart and Grissell (1975) synonymized *vierecki* under *finitima,* but I regard the two as distinct species.

(*vigilii* Brethes = *dilatata* Spinola)

(*vulpina* F. Smith = *intricata* F. Smith)

watlingensis Elliott and Salbert San Salvador, Bahamas

*Cerceris watlingensis** Elliott and Salbert, 1979:359. [Female holotype, San Salvador Island, Bahamas; USNM].

(*williamsi* Scullen = *semipetiolata* Saussure)

wyomingensis Scullen c. U.S.

*Cerceris wyomingensis** Scullen, 1965a:519. [Female holotype, 28 mi. e. Laramie, Wyoming; USNM].

zacatecas Scullen c. Mexico

*Cerceris zacatecas** Scullen, 1972:98. [Female holotype, 9 mi. n. Ojo Caliente, Zacatecas, Mexico; UCD].

zapoteca Saussure (Revised Status) s. Mexico to Costa Rica

*Cerceris zapoteca** Saussure, 1867:89. [Male lectotype, Cordova, Mexico, designated by Ferguson (1984); Vienna].

*Cerceris smithiana** Cameron, 1890:119. [Female lectotype, Atoyac, Veracruz, Mexico, designated by Ferguson (1984); BMNH]. **New Synonymy.**

Scullen (1972) treated *zapoteca* and *smithiana* each as a subspecies of *C. kennicottii* Cresson based on color characters, but they represent opposite sexes of a distinct species. Most of Scullen's determinations under these names are *C. kennicottii.*

(*zelica* Banks = *jucunda* Cresson)

(*zobeide* Brimley = *clypeata* Dahlbom)

(*zonata* Cresson = *cubensis* Cresson)

(*zosma* Brimley = *clypeata* Dahlbom)

zumpango Scullen s. Mexico

*Cerceris zumpango** Scullen, 1972:38. [Female holotype, Zumpango, Guerrero, Mexico; UCD].

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RECOGNITION OF HOST NEST ODOUR BY THE BUMBLEBEE SOCIAL PARASITE *PSITHYRUS ASHTONI* (HYMENOPTERA: APIDAE)

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Abstract.—The ability of the social parasite *Psithyrus ashtoni* to identify and discriminate between nest odours of different bumblebee species was investigated. Female *P. ashtoni* were presented with various combinations of host nest, non-host nest and nest material alone. Parasites showed preference for the odour of the host nests rather than nest material or nests of non-host bumblebees. The importance of host nest odour identification to searching parasites is discussed.

Bees belonging to the genus *Psithyrus* are obligate brood parasites of bumblebees (Hymenoptera: Apidae). Female *Psithyrus* emerge from hibernation some time after host bumblebee queens and search for established nests, most of which are underground in abandoned rodent burrows (Alford, 1975). How are host nests located? Early investigators of *Psithyrus* biology (e.g., Sladen, 1912; Plath, 1934) believed that the scent of host nests were detected by searching parasites. More recently, Cederberg (1979) suggested that *Psithyrus rupestris* Fab. follows odour trails produced by host *Bombus lapidarious* Linn. workers. These trails are made by workers as they wander in and out of subterranean burrows leading to the nest (Cederberg, 1977). Worker extract daubed on filter paper is followed by *P. rupestris* females.

P. ashtoni Cr. is parasitic in nests of *Bombus affinis* Cr. and *B. terricola* Kby. (Plath, 1922). It searches for nests within one–two weeks of host queen emergence (Fisher, unpubl.), at a time prior to emergence of the first worker brood, and therefore cannot use odour trails of workers to recognize nests. Since bumblebee queens incubating incipient brood clumps leave the nest at irregular intervals to forage (Alford, 1975), their nests may be difficult to locate if odour trails of queens are being used. In addition, *P. ashtoni* is found only in nests of *B. terricola* and *B. affinis,* unlike many other *Psithyrus* species which are not host specific. Can *P. ashtoni* identify host nests by odour without relying on worker trails, and can it discriminate host from non-host bumblebee species? Investigation of the ability of *P. ashtoni* fe-

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males to identify and discriminate between odours of different bumblebee species is the subject of this paper.

METHODS AND MATERIALS

Bumblebees were reared in the laboratory using the techniques of Plowright and Jay (1966) and Pomeroy and Plowright (1980) during May 1982. Female *P. ashtoni* were caught as they searched for nests and maintained in small wire cages with access to pollen and sugar-water solution.

Each bumblebee nest starting unit consists of a 17.5 × 12.5 × 10 cm outer box with glass lid where queens collect sugar water and void faeces. The outer box is connected by a 1cm diameter hole to an inner box (ID 77 × 77 × 50 mm) with closed glass lid. The inner box contains upholsterer's cotton and a moist pollen lump in which captive queens lay eggs. Each inner box is detachable and easily moved about once the entrance hole is plugged.

I chose representative nests of *B. terricola, B. affinis,* and a non-host species (*B. bimaculatus* Cr.) for this experiment; all were at the same stage of development (first brood workers in cocoon stage, second brood eggs laid). This is the approximate stage of nest development when *P. ashtoni* is nest searching. I plugged and removed boxes containing nests and queens and placed them in a darkroom cubicle in another room. The glass lid from each box was removed and replaced with wire mesh screen stapled in place.

A plexiglass cage which exactly fit the outer dimensions of two nest boxes placed side by side was constructed. This cage had a removable plexiglass lid and detachable wire mesh floor. The cage was supported off the nest boxes by 4 mm strips of plexiglass so that no part of the cage floor came in contact with the wire mesh tops of the nest boxes.

Boxes containing nests of the three bumblebee species or upholsterer's cotton alone were placed side by side in various combinations. A female *Psithyrus* was brought into the darkroom and placed in the plexiglass cage. It was allowed one minute to wander around the cage. A single 40 W red light illuminated the apparatus from a central location. The midline of the cage floor had been marked; when the female *Psithyrus* was in the middle of the cage it was lowered onto the nest boxes. The proportion of time each female *Psithyrus* spent on either side of the midline was then monitored for a five-minute period. Following the five-minute experimental period the mesh floor of the plexiglass cage was removed and replaced with another clean screen floor. Nest boxes were replaced with other combinations and the procedure repeated.

The following nest box pairings were presented to ten different *Psithyrus* females: cotton only–cotton only, cotton only–*B. terricola* nest, cotton only–*B. affinis* nest, *B. affinis* nest–*B. terricola* nest, host nest–*B. bimaculatus* nest. The order in which these pairings were presented was determined randomly, except for the host nest–*B. bimaculatus* nest pairing, which was always

Table 1. Percent time spent by *Psithyrus ashtoni* females in either half of plexiglass cage covering nest pairs (N = 10).

	Cotton only	Cotton only	*terricola* nest	Cotton only	*affinis* nest	Cotton only	*affinis* nest	*terricola* nest	Host nest	*bimaculatus* nest
% time spent in cage-half	47.20	52.80	78.28	21.72	78.93	21.07	49.78	50.22	73.57	26.43
χ^2	0.470		47.997		50.228		0.003		37.332	
P	NS[1]		<0.001		<0.001		NS[1]		<0.001	

[1] Not significant at 0.05 level.

presented last. Left–right box pairings were also randomized. Each female *Psithyrus* was tested five times, one test for each pairing. The host nest chosen for the host nest–*B. bimaculatus* nest pairing was that nest over which the female *Psithyrus* spent the least time during the *B. affinis–B. terricola* test.

RESULTS

The preference of *P. ashtoni* females for nest odours of host and non-host bumblebees is shown in Table 1. Female *Psithyrus* were able to distinguish host nest odour from the odour of the nest material alone, and could also discriminate between the odour of host nests and non-host nests. Collectively, *Psithyrus* females showed no preference in the cotton–cotton and *B. affinis–B. terricola* pairings. When over a host nest the movements of female *Psithyrus* slowed, and they often spent considerable time chewing at the screen mesh floor, apparently attempting to get to the nest below. They never were observed chewing at the wire mesh floor when over nests containing only cotton, or when over *B. bimaculatus* nests.

It was not possible to determine individual preference for either *B. affinis* or *B. terricola* nests in one five-minute experiment period. Collectively the ten females used in this experiment showed no preference. Two *Psithyrus* females which spent greater than 70 percent of their time over *B. terricola* nests during the *B. terricola–B. affinis* pairings were given two additional five-minute periods under the same conditions. In one case the percent time spent over the *B. terricola* nest dropped to 48 percent; in the other, the preference for *B. terricola* nest odour remained high (78%).

DISCUSSION

The results support the hypothesis that *P. ashtoni* females can recognize host nest odour without actual contact with the nest or with worker-laid trails. The active detection distance of host nest odour is unknown. Plath (1934) found that when he dug up nests of *B. bimaculatus* he observed *P.*

citrinus females flying nearby making a 'bee-line' for the nests and alighting on them. Presumably, female *Psithyrus* can recognize nest odour while flying. *P. ashtoni* females characteristically fly a slow searching pattern close to the ground, often alighting and searching in detail under leaves and twigs. Since both *B. affinis* and *B. terricola* nest underground (Fisher, unpubl.), often with extensive tunnels leading to the nest, the female *Psithyrus* may at first be guided by sight to appropriate looking nest entrances, and then localize nests using odours.

That *P. ashtoni* can distinguish host nests from those of *B. bimaculatus* is consistent with their never being found in nests other than those of hosts. *P. ashtoni* females do not fight with host queens, but when placed in non-host nests are attacked by queens (Fisher, unpubl.). Mistakes in host identification in the field could be costly. It would be of interest to test generalist *Psithyrus* species in the same apparatus, using a variety of bumblebee nests as odour sources. I hypothesize that host odour discrimination is weakly developed in *Psithyrus* generalists.

The data presented here suggest that *P. ashtoni* females either do not discriminate between their two hosts, or that discrimination is weakly developed. More detailed analysis of individual responses is needed to satisfactorily answer this question. In areas where both hosts occur, *B. affinis* queens often usurp incipient nests of *B. terricola* (Plath, 1934; Fisher, unpubl.). A female *Psithyrus* invading a nest of *B. terricola* very early could find itself in a nest subsequently usurped by a *B. affinis* queen. It is unlikely that *B. terricola* host specificity could occur under these conditions. *P. ashtoni* from areas where *B. affinis* does not occur can be placed in laboratory nests of this species where they successfully rear offspring (Fisher, unpubl.). *B. terricola* and *B. affinis* are closely related phylogenetically and may have colony odours which are difficult to distinguish. *B. affinis* queens which usurp *B. terricola* nests are able, at least in small nests, to dominate *B. terricola* workers (Fisher, in prep.), indicating that there is some similarity in pheromonal communication between these species. The degree of relative nest parasitism which occurs in field colonies may simply depend on which host nests are first encountered by searching parasites.

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NOTES AND COMMENTS

MIMICRY, PREDATION AND POTENTIAL POLLINATION BY THE MANTISPID, *CLIMACIELLA BRUNNEA* VAR. *INSTABILIS* (SAY) (MANTISPIDAE: NEUROPTERA)

Mantispids are little-known members of the order Neuroptera. As the name Mantispidae implies, the adults bear considerable resemblance, at least superficially, to the more familiar Mantidae, or praying mantids. Indeed, this similarity may represent an interesting case of convergence in the insect world (Poivre, 1976). The life cycles and parasitic habits of the larvae of many species of mantispids have been previously described by a number of investigators (Batra, 1972; Hungerford, 1936; Kaston, 1938; Killebrew, 1982; Milliron, 1940; Parfin, 1958; Redborg, 1982; Rehn, 1939; Smith, 1934; Viets, 1941). However, little is known about adult mantispids. Recently, Batra (1982) studied courtship and mating in adults of the mantispid, *Climaciella brunnea,* and Opler (1981) studied polymorphism in this species. Here I report some previously unrecorded observations on mimicry, predation, and possible pollination by adults of *C. brunnea* var. *instabilis.*

Climaciella brunnea ranges from the central and western United States to Central and South America. The five morphs of this species are Batesian mimics of different species of paper wasps (*Polistes* spp.) that occur throughout its range (Opler, 1981). Adults of *C. brunnea* var. *instabilis* mimic adults of the wasp, *Polistes instabilis.* The similarity in color and pattern between model and mimic has already been described in detail by Opler (1981).

Observations were made in Meeker Co., Minnesota, from 15–30 July 1982. Although mantispids are uncommon in Minnesota, I discovered an aggregation of about 20 individuals on flowering plants of milkweed, *Asclepias syriaca* L. (Asclepiadaceae).

The adult mantispids showed two types of mimetic behavior in response to a disturbance. The first was usually exhibited when I approached a plant they were resting on. A disturbed individual would curl its abdomen beneath it and retain this position for several minutes. In this posture, with its wasp-like coloration, it strongly resembled a wasp in the stinging position. The second type of observed behavior was a startling mimetic display performed by two different individuals (Fig. 1). When threatened by the close proximity of photographic equipment, the first mantispid spread all four of its wings and held them erect in a vertical position above its body. The main part of the abdomen was expanded laterally, so that its conspicuous yellow, wasp-like stripes were even more prominent than usual. The mantispid then repeatedly catapulted its abdomen high into the air over its head and thorax

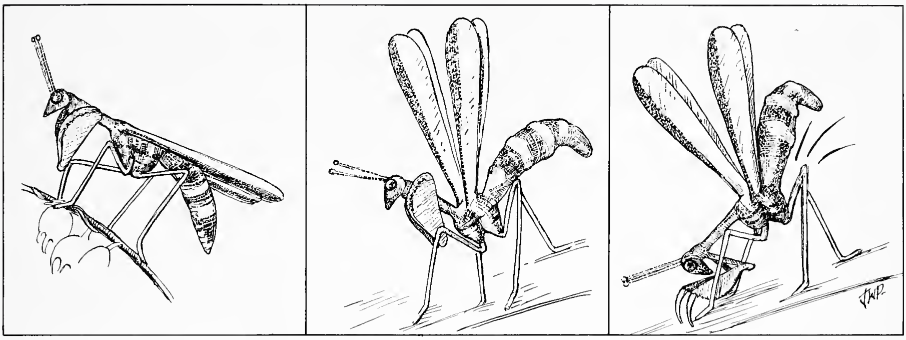

Fig. 1. Adults of the mantispid, *Climaciella brunnea* var. *instabilis* in (left) normal prey-capture position (center) mimicry display, first position, where wings are held vertically over thorax, abdomen inflated (right) mimicry display, second position, where abdomen is flipped over thorax and head.

and brought it back down again. This was done in rapid sequence, causing the insect to rock back and forth. Throughout this display, the tip of the abdomen was held downwards at nearly a right angle to the rest of the abdomen, simulating a stinging wasp. This performance lasted about 7 seconds. The display is probably designed to startle or frighten a potential predator and to show off the mantispid's vivid wasp-like warning colors, rather than to exactly simulate a wasp's behavior. The behavior of a second individual (when threatened by my finger) was similar to that of the first in all respects. To my knowledge, this is the first time such a display has been described for any mantispid species.

When hunting prey, adults of *C. brunnea* generally hung motionless on the underside of milkweed leaves or flowers. They are sit-and-wait ambush-predators that depend on the flowers to attract their prey. Their food consists of small insects, primarily flies. Prey capture occurred infrequently during the course of this study. Only three mantispids were observed with prey (small flies), although the study site was visited daily.

Each mantispid normally occupied a separate plant, but on a few occasions, several individuals were found together on the same milkweed stalk. These temporary groupings might have been breeding aggregations, attracted by the production of a pheromone by males, which is used during courtship (Batra, 1972; Eltringham, 1932).

The wasp models (*P. instabilis*) also occurred in the study area and behaved quite differently from the mantispids when searching for food. Unlike the sessile mantispids, the wasps moved quickly from plant to plant in search of prey. Their movements were jerky and aggressive. Several wasps, also hunting on plants of *A. syriaca,* captured large syrphid flies, which they quickly dismembered and ate on the spot. I observed both the wasps and

Table 1. Pollen loads of honeybees (*Apis mellifera* and mantispids (*Climaciella brunnea* var. *instabilis*) captured on milkweed plants (*Asclepias syriaca*).

	No. of pollinaria of *A. syriaca* insect was carrying	No. of corpusculae of *A. syriaca* insect was carrying
Honeybee no. 1	5	0
2	4	0
3	7	0
4	5	0
5	10	0
6	8	1
7	7	1
8	6	0
9	2	0
10	4	0
11	11	2
Total	69	4
Mantispid no. 1	1	0
2	6	0
3	0	0
4	1	0
5	2	0
6	0	0
7	0	1
8	3	1
9	2	0
10	0	1
11	0	0
Total	15	3

the mantispids drinking nectar from flowers of *A. syriaca.* As Opler (1981) suggests, the similarity of habits and habitats of wasp and mantispid may have led to the evolution of mimetic polymorphism in *C. brunnea.*

Honeybees (*Apis mellifera*) were the most frequent visitors to the milkweed flowers in the study area. For purposes of comparison, and to see if mantispids might also function as pollinators of *A. syriaca,* I captured an equal number of mantispids and honeybees and examined them for pollen.

Asclepiad flowers, like orchids, have compact pollen masses called pollinia that adhere to and are carried from flower to flower by insects. The complete set of pollinia with its associated parts (the corpusculum, or viscidium in orchids, and stipe) is known as the pollinarium. In the case of *Asclepias* flowers, the corpusculae (which are grooved, clasp-like structures) remain behind, attached to the insect's legs or body after the pollinia are given up to the flower.

Eight of the 11 mantispids examined carried *A. syriaca* pollinaria or corpusculae, while these were present on all 11 bees (Table 1). On both the bees and the mantispids these were attached to the legs or the mouthparts. Although the honeybees sampled carried many more pollinaria than the mantispids, the number of pollinia the two groups had given up was nearly equal. Thus, the mantispids, though uncommon, may function as incidental or occasional pollinators by their habit of capturing prey on milkweed flowers.—*Thomas C. Boyden, Department of Botany (KB-15), University of Washington, Seattle, Washington 98195.*

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BOOK REVIEWS

The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutive Approach.—Gonzalo Halffter and W. D. Edmonds. 1982. Publication 10, Instituto de Ecologia, Mexico, D.F., 176 pp. $40.00 in the United States and Canada, $45.00 elsewhere. Available in North America from Bioquip Products, P.O. Box 61, Santa Monica, CA 90406.

Evolutive? When I first saw the title of this book, I feared that it might simply be a clone of *The Natural History of Dung Beetles of the Subfamily Scarabaeinae (Coleoptera, Scarabaeidae)* by Halffter and Matthews (1966). While the lines of descent between these two works are clearly indicated, I was pleasantly surprised to see that the new book is not a rehash of old material at the expense of the reader's time and patience, but a delightful refinement and reanalysis of both old and new data on the nesting behavior of scarabaeines. The book is, appropriately enough, dedicated to Jean Henri Fabre, the French entomologist who first described in any detail the nesting behavior of dung beetles and who can be rightly considered the founder of dung beetle ethology. The contents of this current work add substantially to the cornerstone molded by Fabre in *Souvenirs Entomologique.* Halffter and Edmonds are both eminently qualified to address the nesting behavior of dung beetles because of their long and productive research with these animals.

The chapters are entitled (1) The Scarabaeinae, (2) The Ecological Evolution of Scarabaeinae, (3) Patterns of Nesting Behavior in Scarabaeinae: An Overview, (4) Evolution of Nesting Behavior and Sexual Cooperation, (5) Nest Construction and Architecture in Burrowing Scarabaeinae, (6) Other Sexual Relationships in Scarabaeinae, and (7) The Ovary and Nesting Behavior. The appendices are (1) Outline/Classification of the Subfamily Scarabaeinae, (2) Nidification Behavior of Old World Oniticellini by Yves Cambefort, (3) Nesting Strategies of Three Species of Coprophagous Scarabaeinae in the Sahel Region of Niger by Daniel and Christiane Rougon, and (4) Commentaries on Recent Literature. An extensive bibliography concludes the volume.

Chapter one is a general introduction to the subfamily Scarabaeinae and provides a good, concise picture of dung beetles. Also included is a very informative table comparing characteristics of scarabaeines, geotrupines and aphodiines. The major adaptive features of scarabaeines are listed as (1) food relocation behavior, (2) accentuation of body structure to enhance fossorial capabilities, (3) subterranean nesting behavior, (4) de-emphasis of courtship behavior, (5) increased male/female cooperation, (6) reduction in fecundity, (7) adaptation by larvae and pupae for development within an enclosed space, (8) mouthparts modified for soft food, and (9) adult digestive tract modified to rapidly process large amounts of food. Halffter and Edmonds state that there is little doubt that the Scarabaeinae is a monophyletic group. I know of no substantive discussion concerning the derivation and/or presumed phylogeny of this group of scarabs, and such a *prima facie* statement seems out of place without further scientific evidence or documentation. With the vast array of morphological and behavioral data available to them, Halffter and Edmonds seem to be in an ideal position to now address such a phylogenetic analysis at the generic level, and we may hope that they will engage in such a project in the future.

The principal (and only) shortcoming in the first chapter is near the end of the third paragraph where the authors confuse the concepts of primitive and derived conditions in their discussion. Firstly, they indicate that ". . . coprophagy is the *primitive* (plesiomorphic) condition . . . and that it *derived from the general saprophagous habit* of the family; all other feeding behaviors (necrophagy, mycetophagy, *saprophagy,* etc.) we consider derived (apomorphic)" (italics mine). Their contention that coprophagy is *primitive* after having been *derived from* another state as well as calling saprophagy both primitive and derived in the same sentence are *non sequiturs.* Secondly, they use the terms plesio*morphic* and apo*morphic* (indicating body structure) when they mean to use the terms plesio*typic* or apo*typic* (referring to characters other than structure, such as behavior). It seems the authors attempted to use some catch words currently popular in the phylogenetics and evolution literature but tripped over their application. While initially confusing and somewhat bothersome, their foray into *terra incognita* should not detract from the overall value of the chapter.

Chapter two delves into the ecological evolution of dung beetles. The major adaptive features of the subfamily listed in chapter one are discussed in more detail using the framework of r- and K-selection theory to explain much of the exploitation of the soil/excrement system. The authors are quick to note that r- and K-selection represent extremes of a continuum, and that the evolution of any given species may result in a mixture of r- and K-selected traits; therefore, these concepts are relative. They conclude that the Scarabaeinae, relative to other scarabs and most other beetles, are essentially K-strategists. A convincing discussion follows of scarabaeine traits that exemplify the tactics assumed to be promoted by K-selection. These life history traits characteristic of Scarabaeinae are (1) survivorship influenced primarily by density dependent factors mostly operating directly on the adults, (2) ecological specialists, (3) delayed reproduction, slow development and repeated reproductive periods, (4) low fecundity and production of few, large sized offspring, (5) some degree of brood care, (6) low rates of juvenile mortality relative to adult mortality, and (7) superior competitors relative to other groups. This group of traits is a correlated set of adaptations which collectively define scarabaeines as K-strategists and as insects for which ecological and reproductive efficiency is maximized. Prior to their discussion of evolutionary trends within the Scarabaeinae, the authors offer an *aplogia* for their lack of a statistically rigorous analysis of populations upon which to base largely quantitative theory. Their approach is that of natural historians and not population ecologists. No such apology is necessary for this method of establishing a working hypothesis. As the authors themselves point out, their experience has produced information that shows strong tendencies of consistency which demand explanation. Moreover (and much to their credit) Halffter and Edmonds distill all the descriptive data written on dung beetles and their own extensive observations into a persuasive, unified theory describing the ecological evolution of these animals, and they do this well. This chapter is the the most interesting and significant part of the book to me. It would be of supreme interest to see how the results of a study on the taxonomic evolution of these beetles would correlate with the scenario of behavioral evolution so expertly proposed by Halffter and Edmonds.

Chapter three explores the different ways dung beetles nest. A classification of nesting behaviors is included and is an extension and elaboration of that of Halffter and Matthews (1966) and Halffter (1977). A classification of nest morphologies, or patterns, is also provided. There is a great deal of descriptive information in this chapter which, although synoptic in nature, is valuable to understanding scarabaeine nidification behavior. It is here that we find much of the supportive evidence for the conclusions about ecological evolution proposed in the preceding chapter.

The fourth chapter explores the evolution of nesting behavior and sexual cooperation and, like chapter three, provides data supporting the conclusions reached in chapter two. Halffter and Edmonds conclude that nesting behaviors originated as derivatives of feeding behavior. Detailed discussion is given to the evolution of nesting behavior in burrowing scarabaeines and ball rolling scarabaeines respectively.

The next three chapters are largely descriptive. A detailed review of each nest type, the taxa constructing it, and the behavior associated with these taxa constitutes chapter five. The sixth chapter deals with sexual relationships with a summary of encounter and recognition, copulatory, and combat behaviors as well as bisexual cooperation independent of nesting. The last chapter relates the ovary of dung beetles to nesting behavior with the observation that there is a reduction in the number of maturing egg follicles as nesting behavior becomes more highly developed, i.e., there is greater parental care for fewer offspring.

The first appendix is an outline classification of the subfamily at the generic level. The classification differs in various respects to that given in Halffter and Matthews (1966). Immediately noticeable in this respect is the increased use of subgenera, a move that will be variably accepted depending, in large measure, upon which side of the Atlantic a scarab systematist works. *Neocanthidium* continues as a valid genus even though it was synonymized by Howden and Young (1981); a difference of opinion, no doubt.

The papers by Cambefort and Rougon and Rougon constitute the next two appendices and result from a symposium held on evolution and nesting behavior in beetles. Cambefort details nicely the nesting behavior of Old World Oniticellini and formulates an evolutionary scenario for nest building in these insects. His first conclusion equates low fecundity with a primitive state which seems to be just the opposite conclusion reached by Halffter and Edmonds. Cambefort notes that additional species of Oniticellini must be studied before a firm idea of their behavioral and phylogenetic relationships can emerge.

The following short paper by the Rougons is a well executed descriptive work describing the nesting strategies of three African species that live in a very hot, dry climate.

The book is nicely produced on good quality paper. However, I found many of the photographs to be unclear because too coarse a photographic screen was used (see especially Fig. 65) and because of lack of suitable contrast. The line drawings are good, but many should have been reduced in size to eliminate their coarse look and provide snap to the illustrations. The size of the book (about 25 × 25 cm) is awkward because it will not conveniently rest on most book shelves without protruding excessively from the shelf. Editing is generally good although there are some glaring exceptions in the two invited papers and on p. 58 where there are six misspellings. Considering its moderate size, I thought the book was somewhat overpriced at $40.00, but this seems to be a contagious malaise within the entire publishing industry.

In summary, then, I can strongly recommend this book. It will have its greatest appeal to scarab workers, coleopterists in general, ecologists, and those conducting research on the evolution of taxa, behavior, or ecological relationships. I know that some paleontologists as well as some applied entomologists have also been stimulated by this book. It will have broad appeal and application to anyone whose life is touched by these remarkable creatures.—*Brett C. Ratcliffe, Systematics Research Collections, W436 Nebraska Hall, University of Nebraska, Lincoln, Nebraska 68588-0514.*

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Ecologie des Insectes Forestiers.—Roger Dajoz. 1980. Gauthier-Villars, Paris, 478 pp. 280 f.f.

This is a fine attempt to present the essential ecological information on the insects associated with forests; particularly, the forests of France and Europe. The first part of the book (4 chapters) describes the forests of France and the general associations of insects. In addition, the last two chapters (17 and 18) on the role of insects in the decomposition of wood and the fauna of the soil constitute an outline of how insects interact with trees. The remaining chapters concentrate on the biology of the defoliators, scales, gall makers, seed utilizers, and wood utilizers. In these chapters there is no attempt to correlate their activities with soil quality, gross stand effects or stability influences. It would have been useful to relate ecological effects of defoliators to changes in soil quality, for example.

Because of the limitation of space, much information about the ecology of forest insects has been omitted. Despite this, the book provides a summary of the life and activities of some of the more economically important insects in European forests. The French literature is particularly well covered with less emphasis on the German and British contributions.

The emphasis on "pest" species is a natural tendency but there are many other species in the forest that contribute to the ecology and survival of trees and associated plants. These species and their interactions should have been discussed in an ecology textbook. Nevertheless, there is much useful information supplemented by numerous graphs, tables and figures which should prove to be valuable to both the advanced student and professional entomologist. Precise analyses of the population dynamics of several species are particularly important because attention is often focused on the physiological adaptations affecting abundance and dispersal. It is this aspect of the book that makes it most useful.—*Gordon R. Stairs, Department of Entomology, Ohio State University, Columbus, Ohio 43210.*

The Biology of Social Insects.—M. D. Breed, C. D. Michener, and H. E. Evans (eds.). 1982. Westview Press, Boulder, Colorado, 419 pp. $25.00.

During August 9–13, 1982, the International Union for the Study of Social Insects (IUSSI) held its Ninth Congress in Boulder, Colorado. Upon arrival, each participant received a copy of the book, *The Biology of Social Insects,* which contains papers from 10 symposia as well as abstracts representing most of what was to be seen and heard during the meeting. Given the usual hustle and bustle of organizing an international meeting, the production of a finished book, before the start of the meeting, is laudatory, and it reflects the current status of knowledge and ideas about many aspects of the study of social insects. The topics covered were chosen by specialists on social insects from all over the world who were asked to suggest symposium topics. The Organizing Committee of the Congress then chose ten from the approximately 100 suggested subjects. The result was ten very different but complementary symposia.

The best way to present this book of such varied chapters and authors is to list each symposium title and to mention what I found to be notable about each. Before proceeding I should mention that within each symposium were invited papers and submitted papers, the latter represented by abstracts. Abstracts of presented papers are useful when one is attending a meeting, however, the usefulness of abstracts within the book is scant. One immediately knows what kinds of studies are being done, but details of the majority of the abstracted studies are necessarily lacking. A total of 72 of the total 414 text pages is devoted to the abstracts alone.

Symposium I: Foraging Behavior and Pollination. Four papers and an introduction by G. D. Waller. Waller states that the direction of future research on foraging behavior and pollination may be profoundly affected by what transpired at this symposium. Models are presented which challenge the theory of optimal foraging and R. Jander discusses a new theory called 'modal tuning theory.' The papers vary from empirical to theoretical.

Symposium II: Competition and Population Dynamics in Social Insects. Three papers and an introduction by J. H. Sudd. Especially interesting is a paper by N. Koeniger on the interactions among the four species of the genus *Apis.* The importation of *A. mellifera* has occurred worldwide with little consideration of the unstable condition that occurs when competing species are brought together. Koeniger examined competition for nesting sites, competition for food, interference during mating, interspecific robbing, predators and exchange of parasites. The results of this study highlight the importance of applied, as a complement of basic, studies. The oftentimes neglected but far-reaching effect of introducing social insects to foreign habitats is also stressed.

Symposium III: The Roles of Social Insects in Ecosystems. Six papers and an introduction by W. L. Nutting. This symposium considers the effect of termites, ants and wasps on ecosystems through modification of habitat, contribution to energy flow and cycling of nutrients, and interactions with other organisms. The numerical dominance of social insects in tropical forests is well known, yet the ecological role of these organisms is only vaguely understood. Abe's paper on the ecological role of termites in a tropical rain forest helps to fill this gap in our understanding. Data on density and biomass of termites as well as food consumption by fungus-growing termites are presented in valuable summary tables. Collins' study of the interaction and impact of cattle and termites in Kenya stresses again the important interaction between applied and basic research. Another notable paper is Greene's report on comparative early growth and foraging of two naturally established vespine wasp colonies. *Vespula germanica* and *V. vidua* colonies were observed in hopes of determining why *V. germanica* tends to be the more successful yellowjacket. In spite of the equal early growth rates of the colonies, a striking disparity appeared due to longer adult life span and ability to maintain greater numbers of brood because of more efficient foraging by *V. germanica* (1,167 cells for *germanica* vs. 531 for *vidua*). In addition, there was an almost complete lack of overlap in food items with *germanica* being omnivorous while *vidua* is more specialized on arthropod prey. The results of this study allow insight as to why *germanica* is one of the world's most pestiferous social wasps. Indeed, more comparative studies such as this may lead to an understanding of the evolution of generalists versus specialists within the social insects.

Symposium IV: Economically Important Social Insects. Eight papers and an introduction by S. B. Vinson. By far this symposium is the best written and most interesting. In a time when insect behavior is a popular field of study, the potential for applied research exists. Indeed, in a field flooded with new PhDs, the need for career alternatives increases. The papers presented in this symposium highlight the opportunity for studies on economically important social insects. Topics include yellowjackets (according to Akre, responsible for millions of dollars of damages in the U.S.), leaf-cutting ants, the use of JH-analogue for control of *Monomorium pharaonis* (the control takes advantage of the recruitment behavior of the ants), fire ants, *Polistes* and caterpillar suppression, and Africanized bees.

Symposium V: Presocial Behavior. Five papers and an introduction by G. C. Eickwort. As stated in Eickwort's introduction, analyses of presocial behavior are providing significant insights into the conditions under which reproductive division of labor and eusocial behavior might evolve. One of the more interesting findings in recent years, in support of kin-selection hypotheses, is Aoki's finding of soldiers in parthenogenic aphid colonies. These soldiers are morphologically distinct and reproductively sterile. Aoki's paper on aphids discusses new findings as well as leads the reader to his numerous other references on aphid soldiers. Evans and Hook report on communal nesting in *Cerceris* digger wasps, which appears to have evolved in response to natural predators. The comparison between solitary and communal *Cerceris* species represents the type of study needed to determine the factors involved in the evolution of social behavior. Another interesting paper is on subsocial behavior in Coleoptera. In contrast to E. O. Wilson's (1975) ideas of the evolution of sexuality as an antisocial phenomenon, Halffter presents the hypothesis that in Coleoptera there is an evolution towards subsocial forms of behavior through development of patterns based on sexuality. Also included in the symposium are a paper on membracid sociality and one on an experimental induction of multifemale associations in solitary *Ceratina* bees. As a whole, this symposium presents four distinct studies that all emphasize the varied routes from solitary to social behavior.

Symposium VI: The Evolution and Ontogeny of Eusociality. Six papers and an introduction by M. J. West-Eberhard. The theme of this symposium is intracolony reproductive competition, with parasitic ovipositions by unmated females and polygynous queens. The data reported increase the amount of evidence of intracolony competition, thus promoting even further the decline of the once popular image of a social insect colony as an harmonious supraorganism. The studies stress the need for detailed studies of individual and colony histories necessary to evaluate evolutionary interpretations. A notable paper was by Hunt on trophallaxis in Hymenoptera; he proposes that trophallaxis may be central to the evolution of sociality within the Hymenoptera. Once proposed as the cornerstone of vespid sociality by Roubaud (1916), the idea of trophallaxis as critical to the evolution of eusociality recently lost favor. Hunt's ideas may rekindle an interesting controversy.

Also dealing with the evolution of eusociality is a plenary address by R. H. Crozier (pp. 4–9). Although brief, this overview of the recent controversies in this important question in evolutionary biology is valuable and quickly takes the reader to the more important recent papers on this topic.

Symposium VII: Caste and Ergonomics. Four papers and an introduction by J. M. Herbers. Dominance behavior in primitively eusocial species (*Lasioglossum* and *Polistes*) is correlated with reproductive status. In an interesting study, Breed determined that in the highly eusocial honey bee, where overt dominance interactions are rare, a relationship exists between aggressive behavior towards queens and factors that affect the endocrine status of the worker honey bee. Another interesting study was by J. M. Herbers on queen number and colony ergonomics in *Leptothorax longispinosus.* In an attempt to determine the significance of multiple queens in a nest, Herbers constructed an hypothesis which states that increased genotypic variation in polygynous colonies could result in a broader distribution of worker phenotypes leading to higher efficiency and higher fitness. No correlation was found, however, and thus the hypothesis was rejected. Even though the maintenance of polygynous colonies in nature remains a mystery, Herbers' study is stimulating and hopefully will lead to more hypothesis-testing.

Symposium VIII: Predation, Social Parasitism and Defense. Six papers and an introduction by R. W. Matthews. Matthews states that this is a series of definitive papers focusing on slavery in ants, ant predation and wasp and bee colony defensive strategies. Most striking were the two papers on army ants and their effect on social insects. Chadab-Crepet and Rettenmeyer present a well-written report on the comparative behavior of social wasps when attacked by army ants. Intriguing points were that some wasps can discriminate between ant species; *Protopolykia exigua,* for example, becomes alarmed by the odor of army ants enabling this species to evacuate before the ants have plugged the tiny nest entrance. Surprisingly, social wasps have no effective direct defense against army ants; the only escape is evacuation. The suggestion that development of polygyny in the Polistinae may be a result of army ant predation again highlights the importance of natural enemies in the evolution of eusociality.

Symposium IX: Communication. Six papers and an introduction by R. Boch. Included were papers on chemical communication in ants and new exocrine glands, honey bee mandibular glands, swarming in honey bees, behavior genetics and recruitment in ants. Two papers, one applied and one theoretical, stood out as exceptional. The first, 'The adaptive value of probabalistic behavior during food recruitment in ants . . .' by Pasteels, Verhaeghe and Deheubourg, via experimental and theoretical evidence, showed that some level of inaccuracy in communication (recruitment) can be advantageous for the society by increasing the probability of discoveries. The second, 'Behavior genetics of honey bee alarm communication' by A. M. Collins, was a study of genetic selection as a way to combat the defensiveness of the Africanized bee.

Symposium X: Neurobiology and Behavior of Social Insects. Twelve papers and an introduction by R. Menzel. Insects, especially the honey bee, have long been considered prime subjects for the study of neurobiology. Within this symposium are technical papers on morphology, a good review of recent studies of memory, a presentation of the celestial map used by honey bees in orientation and a study on control of heart rate. Interestingly, the heart rate in honey bees is not under direct nervous control but rather the beat frequency is sensitive to the sodium concentration in the hemolymph.

How does this book compare with the newly published four volume set, *Social Insects,* edited by H. R. Hermann? In other words, was another book on social insects needed at this time? Hermann's book contains lengthy reviews of many groups of social insects, caste differentiation and evolution of eusociality. The last two topics were covered in the IUSSI publication as well and perhaps add little to the available literature. In contrast, the chapters on the economic importance of social insects, foraging, communication, competition, neurobiology, and predators are distinct, and the mixture of applied, empirical and theoretical studies makes the IUSSI book unique. My impression was that much of the detail would be lost on today's specialists, but an overview of studies being conducted on social insects is worthwhile. The necessarily short papers, although lacking in detail, will lead the interested reader directly into relevant literature. The book is a valuable reference for this reason alone.

Most of the contributions to the book were prepared as camera-ready by the authors and published as received; typographical errors and inaccurate and sometimes confusing translations are not uncommon distractions. But on the whole, the papers are of high quality.—*Janice S. Edgerly, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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Insects of an Amazon Forest.—Norman D. Penny and Jorge R. Arias. 1982. Columbia University Press, New York, 269 pp. $30.00.

The authors present the results of a full year of sampling in Brazil. Using five sampling techniques, aerial (1 and 15 m) light traps, soil emergence traps, Berlese-Tullgren extractions of leaf litter, Malaise traps, and baited pitfall traps, a large number of insects were obtained. Specimens were sorted by order, and, for a few orders, by family. Dry weight estimates were obtained for those groups collected during the last week of sampling. Undoubtedly the scope of sampling would preclude the identification of the majority of specimens unless a large team of taxonomists was involved. Still, the results of such a study could be highly informative.

The book jacket, and the publisher's advertisements, proclaim it to be a "classic study unlike any other for an area of Amazon forest . . . of major interest to tropical ecologists and entomologists as well as biologists concerned with evolution, classification, or the tropics." Given such a glowing introduction, readers will undoubtedly be disappointed. Indeed, it is unclear as to the exact nature of the readership for which the book was written, but it was not for those previously cited. Excellent drawings of representatives of many families are given, but their treatment is scarce—averaging about one paragraph per family. Even here, the treatment is very general, giving the estimated world-wide number of species for that family, as well as generalizations of their biology. The book is highly reminiscent of Swan and Papp's *The Common Insects of North America,* although its treatment is much less clear. If the attempt of the authors was to produce a similar book, they almost made it, but it is highly doubtful if swarms of amateur entomologists will be able to use their book, unlike *The Common Insects of North America.*

However, the large print, and the ample number of illustrations, as well as the lack of any substantive data, make the book easy reading, and, if one has any interest in entomology, the entire book can be read in from one to two hours. This book may make a good gift for a beginning amateur entomologist, but will not serve any useful function in the library of a professional.—*Harold Fowler, University of Florida, Gainesville, Florida 32611.*

The Semiaquatic Bugs (Hemiptera, Gerromorpha): Phylogeny, Adaptations, Biogeography, and Classification.—N. Møller Andersen. 1982. Entomonograph Vol. 3. Scandinavian Science Press Ltd., Klampenborg, Denmark, 455 pp. $35.00.

Andersen's book represents something of a landmark in the study of the Hemiptera, for seldom does such a comprehensive treatment of a group appear. The last obvious example was "Monograph of Cimicidae" (Usinger, 1966), which dealt with the bedbugs in more detail but with a somewhat different emphasis. Andersen has singlehandedly attempted a generic level morphological review and phylogenetic analysis as well as presenting a discussion of adaptations, historical biogeography, and classification. In the form of appendices he presents for the Gerromorpha lists of names and keys for all higher taxa and genera.

The semiaquatic bugs in Andersen's sense include the families Gerridae, Hebridae, Hermatobatidae, Hydrometridae, Macroveliidae, Mesoveliidae, Paraphrynoveliidae, and Veliidae. This usage may be unfamiliar to some workers, especially in North America, where groups such as the Saldidae, Gelastocoridae, and Ochteridae are often referred to as semiaquatic Hemiptera. Andersen presents an interesting review of the history of the classification of the Gerromorpha, documenting its monophyly with what appears to me to be strong morphological evidence. One must conclude from the results of his analysis that the more inclusive use of the term semiaquatic should be abandoned by hemipterists.

Andersen demonstrates his skill as an artist and a technician, presenting several hundred well executed line drawings based on original light microscopic work as well as many scanning electron micrographs—some published here for the first time with the remainder gathered from a string of revisionary works which Andersen began on the Gerromorpha nearly two decades ago.

This volume appears at a time when systematics and biogeography are being revolutionized by methodological innovation. Nils Andersen has made a serious attempt to incorporate both the techniques of cladistics and vicariance biogeography into his analysis. I consider his initial explication of principles basically redundant with what already exists in the literature. Nonetheless, these principles as outlined by Andersen clearly indicate the somewhat divergent emphasis in phylogenetics in Andersen's work—and probably that of most continental Europeans—with the approach adopted by many North Americans. Notable is Andersen's emphasis on reconstruction of the ground plan.

The minor differences in cladistic methods as espoused by Andersen and practiced by others are far less important than his desire to be explicit about his methods. His book presents a theory of relationships for the Gerromorpha that contradicts the findings of Cobben (1978) and Popov (1971). Nonetheless, it appears to me that Andersen offers a consistent interpretation of the available evidence and has presented an example of the type of comprehensive documentation for which all of us should strive. Whatever the merits of his conclusions, his hypotheses can be easily understood and readily tested by all future workers.

The analysis presented by Andersen will be most enthusiastically read by systematists. Nonetheless, the synthetic nature of Andersen's work will make this comparatively inexpensive volume a valuable reference for all biologists interested in the Gerromorpha.—*Randall T. Schuh, Department of Entomology, American Museum of Natural History, New York, New York 10024.*

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REVIEWERS FOR 1983

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