

PSY 6188

HARVARD UNIVERSITY



Library of the
Museum of
Comparative Zoology





Frax
W. L.
E. G.
B. K.
P.

PSYCHE

A Journal of Entomology

Volume 86

1979

Editorial Board

FRANK M. CARPENTER, *Editor*

P. J. DARLINGTON, JR.

W. L. BROWN, JR.

H. W. LEVI

E. O. WILSON

ALFRED F. NEWTON, JR.

B. K. HÖLDOBLER

R. E. SILBERGLIED

RONALD J. MCGINLEY

Published Quarterly by the Cambridge Entomological Club

Editorial Office: Biological Laboratories

16 Divinity Avenue

Cambridge, Massachusetts, U.S.A.

The numbers of PSYCHE issued during the past year were mailed on the following dates:

Vol. 85, no. 4, December, 1978: September 18, 1979

Vol. 86, no. 1, March, 1979: December 28, 1979

Vol. 86, no. 2-3, June-September, 1979: June 25, 1980

21

PSY 2615

MUSEUM OF COMPARATIVE ZOOLOGY
LIBRARY

JAN 2 1980

HARVARD
UNIVERSITY

PSYCHE

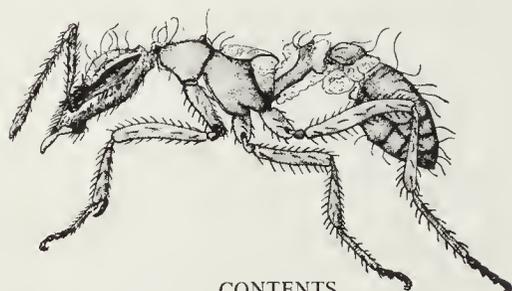
A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 86

March, 1979

No. 1



CONTENTS

The Phenology of <i>Pieris napi microstriata</i> (Lepidoptera: Pieridae) During and After the 1975-77 California Drought, and Its Evolutionary Significance. <i>Arthur M. Shapiro</i>	1
A New Quasisocial <i>Anelosimus</i> Spider (Araneae, Theridiidae) from Paraguay. <i>Harold G. Fowler and Herbert W. Levi</i>	11
Territorial Behavior in Males of <i>Philanthus psyche</i> (Hymenoptera, Sphecidae). <i>Kevin M. O'Neill</i>	19
Rediscovery of <i>Scolecbythus madecassus</i> , with a Description of the Male and of the Female Sting Apparatus (Hymenoptera: Scolecbythidae). <i>Howard E. Evans, Charles Kugler, William L. Brown, Jr.</i>	45
Life History and Ecology of <i>Baetisca bajkovi</i> Neave, in Beech Fork of Twelvepole Creek, Wayne County, West Virginia (Ephemeroptera: Baetiscidae). <i>Dwight L. Chaffee and Donald C. Tarter</i>	53
Dispersal by Male Doryline Ants in West Africa. <i>Dennis Leston</i>	63
Habitat Structure and Colonial Behavior in <i>Metepeira spinipes</i> (Araneae: Araneidae), an Orb Weaving Spider from Mexico. <i>George W. Uetz and J. Wesley Burgess</i>	79
Rhythm Variables as Taxonomic Characters in Ants. <i>Elwood S. McCluskey and Siu-Ming A. Soong</i>	91

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1978-1979

<i>President</i>	JOHN A. SHETTERLY
<i>Vice-President</i>	BARBARA THORNE
<i>Secretary</i>	NORMAN WOODLEY
<i>Treasurer</i>	FRANK M. CARPENTER
<i>Executive Committee</i>	JO B. WINTER MARGARET THAYER

EDITORIAL BOARD OF PSYCHE

- F. M. CARPENTER (Editor), *Fisher Professor of Natural History, Emeritus, Harvard University*
ALFRED F. NEWTON, JR., *Curatorial Associate in Entomology, Harvard University*
W. L. BROWN, JR., *Professor of Entomology, Cornell University and Associate in Entomology, Museum of Comparative Zoology*
P. J. DARLINGTON, JR., *Professor of Zoology, Emeritus, Harvard University*
B. K. HÖLLDOBLER, *Professor of Biology, Harvard University*
H. W. LEVI, *Alexander Agassiz Professor of Zoology, Harvard University*
R. E. SILBERGLIED, *Associate Professor of Biology, Harvard University*
E. O. WILSON, *Baird Professor of Science, Harvard University*

PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: \$9.50, domestic and foreign. Single copies, \$3.50.

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

Orders for missing numbers, notices of change of address, etc., should be sent to the Editorial Office of Psyche, 16 Divinity Avenue, Cambridge, Mass. 02138. For previous volumes, see notice on inside back cover.

IMPORTANT NOTICE TO CONTRIBUTORS

Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

Authors are expected to bear part of the printing costs, at the rate of \$24.50 per printed page. The actual cost of preparing cuts for all illustrations must be borne by contributors: the cost for full page plates from line drawings is ordinarily \$18.00 each, and for full page half-tones, \$30.00 each; smaller sizes in proportion.

The December, 1978, Psyche (Vol. 85, No. 4) was mailed September 18, 1979

PSYCHE

Vol. 86

March, 1979

No. 1

THE PHENOLOGY OF *PIERIS NAPI MICROSTRIATA*
(LEPIDOPTERA: PIERIDAE) DURING AND AFTER
THE 1975-77 CALIFORNIA DROUGHT, AND ITS
EVOLUTIONARY SIGNIFICANCE*

BY ARTHUR M. SHAPIRO
Department of Zoology,
University of California,
Davis, California 95616, U.S.A.

INTRODUCTION

Interest in the theoretical basis of insect phenology has increased very markedly in recent years (Bradshaw, 1974; Cohen, 1970; Giesel, 1976; Levins, 1969). The evolution of phenological "strategies" via natural selection is of interest to ecologists and applied entomologists alike. Insect phenology involves responses to both "normal" and "abnormal" weather. The developmental plasticity displayed by a population may determine its survival in seasons of unusual meteorological stress and in turn may reflect a history of selection by recurrent exposure to that stress.

The 1975-77 California drought was a short-term climatic anomaly with no equal in the meteorological records of that state. Any event of such magnitude would be expected to affect both phenology and reproductive success of a great variety of organisms, especially annual or ephemeral species. Since 1972 the phenology of entire butterfly faunas has been monitored along a transect paralleling Interstate Highway 80 from sea level at Suisun Bay to 2750 m at Castle Peak, north-central California. This has permitted year-to-year comparisons within localities as well as within-year comparisons among localities. This long-term study involving over 150 species includes the 1975-77 drought and the tremendous rains of winter 1977/78. Certain butterfly populations showed very pro-

*Manuscript received by the editor June 30, 1979.

nounced fluctuations during this period. One of the most dramatic, and one whose behavior can be rationalized at a mechanistic (proximate) level, is *Pieris napi microstriata* Comstock.

SEASONALITY OF *P. N. MICROSTRIATA*

The *Pieris napi* (L.) complex, which probably includes several genetic species, is circumpolar in distribution and largely restricted to cool-temperate to subarctic climates. In California about four subspecies occur, only two of which are well-known biologically: *P. n. venosa* Scudder, confined to the coastal fog belt, and *P. n. microstriata* which occurs farther east in the Inner Coast Ranges and on the west slope of the Sierra Nevada. These populations, now disjunct, were probably connected in riparian forest in the Central Valley as recently as the mid-19th century (Shapiro, 1978). *P. n. venosa* is normally double- to partially triple-brooded, with two seasonal phenotypes (Shapiro, 1975, 1977) under photoperiod and temperature control. *P. n. microstriata* is normally univoltine, with only a spring phenotype (Shapiro, 1975, 1976a, 1977). It is capable of producing a summer phenotype and may have a partial second brood in some localities in some years. This most often occurs in Coast Range localities subject to occasional maritime influence, as around the Napa Valley.

Populations of *P. n. microstriata* occur at two of the regular sampling stations along I-80: Gates Canyon, an east-facing canyon on the east slope of the Vaca Hills (Inner Coast Range) near Vacaville, Solano Co. (50–600 m), and Lang Crossing of the South Yuba River in the mixed-conifer belt of the Sierran west slope, Nevada Co. (1350–1500 m). These are matched with nearby U.S. Weather Bureau stations of record at Vacaville and Blue Canyon Airport, respectively. Some aspects of the host-plant relations of the butterflies are described in Shapiro, 1974 and 1976b. Both populations fluctuated during the most anomalous year (1977), but in opposite directions. Both were quantified by direct census of both adults and immatures.

GATES CANYON

The history of this population since 1972 is given in Table 1. The 1972 estimate is unreliable because only one sampling day is involved, but all of the others are based on weekly to biweekly visits through the flight season.

The California drought began with the failure of the 1975 autumn rains. The 1975 flight of *P. n. microstriata* was rather poor, and both adult and immature numbers were down. Spring 1976 started warm (January +1.1°C compared to Vacaville means), turned cooler in April, then very warm (+1.9°) in May. The flight of *P. n. microstriata* was the largest ever observed at Gates and lasted for three months, although only one generation was involved. The sex-ratio was normal (about 1.7:1) and over 200 eggs and 50 larvae were seen. The host plants, *Barbarea verna* (Mill.) Asch. and *Dentaria californica* Nutt. (both Cruciferae) were early, of somewhat better than average luxuriance, and senesced early with the onset of hot weather in May–June. There was nothing meteorologically unusual about the months when 1975 eggs and larvae were developing, which would have promoted unusual survival. The very large adult population in 1976 could be due to diminished mortality due to predators, parasites, and disease or to direct meteorological effects on the dormant pupae.

Winter 1976/77 was the second grossly deficient rainfall season. January–March 1977 were statistically unremarkable for temperature. The adult population of *P. n. microstriata* was almost non-existent, despite the great burst of reproduction the previous year. Four males were seen—one each on four days—and at least one

Table 1. Populations of *Pieris napi microstriata* at study sites.

Year	Inclusive dates of flight season	N (rounded up to nearest 5 from census)
(a) Gates Canyon, Solano County, California		
1972	iii.28 (only visit)	—
1973	iii.23–iv.18	30
1974	iii.13–v.19	50
1975	iv.9–v.2	25
1976	ii.21–v.2	75+
1977	iii.10–iv.28	5
1978	iii.14–v.7	30
	and (2nd brood) v.20–v.28	5
(b) Lang Crossing, Nevada County, California		
1974	v.5–vi.2	20
1975	v.18–vi.9	30
1976	not studied	
1977	iv.17–v.13	50
1978	v.3–vi.9	20

female must have flown because a single egg was found 11 April. It must have failed to develop since there was no damage at all to the plant on the 28th. The biomass of *Barbarea* was reduced by roughly an order of magnitude relative to 1976, and the number of plants decreased very markedly. This facilitated search for early stages, and host plant coverage was especially good in 1977. It is thus uncertain that any successful reproduction by *P. n. microstriata* took place in Gates Canyon this year.

Winter 1977/78 brought record heavy rainfalls (Table 2). Rather than being extinct, as would be expected for an obligate annual, *P. n. microstriata* was back at pre-drought numbers. Most of the emergence was early: females were already present on 14 March and eggs were found on the less-preferred host *Dentaria* (*Barbarea* was late). By 9 April there were eggs, small larvae, and large larvae on most of the *Barbarea* plants and some on *Dentaria*. One male each was seen on 21 April and 7 May (none on 29 April). By 7 May only a handful of large larvae remained. On 20 and 28 May single males of the rare second generation (*castoria* phenotype)—the first ever recorded in the Vaca Hills—were found.

Simultaneously, the Pierid *Anthocaris sara* Lucas, which is also facultatively bivoltine, produced an abundant second generation which flew from 20 May–21 June, as in southern California coastal localities (Emmel and Emmel, 1973). The Hesperiid *Erynnis proper-tius* (Scudder & Burgess) and the Lycaenid *Incisalia iroides* (Boisduval) also produced second broods which flew to 21 June and 2 July respectively.

LANG CROSSING

Here there are no 1976 data, and the irregular topography makes coverage of potential hosts less accurate. However, the 1977 events make a striking counterpoint to those in Gates Canyon (Table 1).

The 1976/77 winter produced very little snow at mid-elevations. Although it was a mild winter, cumulative chilling experienced by diapausing pupae near ground level was undoubtedly enhanced by lack of snow cover. Lang Crossing was completely snow-free on 17 April and 20 species were flying, including male *P. n. microstriata*. By 22 April females were flying and laying on *Barbarea* and on *Nasturtium officinale* R. Br. April temperature was below normal but the weather was fair until the very end of the month, after most

Table 2. Precipitation at nearest weather stations to study sites.

Water year (July 1–June 30)	Vacaville	Blue Canyon Airport	
	rainfall, cm	total precip., cm	snowfall, cm
1971–72	26.19	133.48	676.15
1972–73	88.67	180.28	743.46
1973–74	66.35	244.43	769.62
1974–75	55.73	175.06	743.20
1975–76	23.47	88.27	302.26
1976–77	23.32	68.53	225.55
1977–78	95.78	223.19	751.84

of the egg-laying had been completed. Cold rains then began and turned to snow: on 5 May, 15 cm of snow fell; by 8 May this had increased to 33 cm. There were daily rain showers thereafter until 18 May. On 13 May, with north-facing slopes snow-covered, as many plants as were exposed were censused. 43 eggs and 2 small larvae were found on *Barbarea*. On 21 May the same plants, along with others and several *Arabis glabra* (L.) Bernh., were again censused but not one egg or larva was found. Larval feeding damage was limited to the pinholes inflicted by first-instar larvae. Insofar as could be determined, the entire 1977 reproductive output was lost. Other than a soft-winged female found 13 May, no more adults were seen.

Harcourt (1966) found that rain was a major mortality factor for eggs and larvae of *Pieris rapae* (L.) on cabbage in Canada.

Winter 1977/78 saw a return of heavy snowfall, but there was also so much warm rain that snow packs were not good, and Lang was snow-free 12 April: 10 species, not including *P. n. microstriata*, were flying. 32 cm of snow fell 15 April, with cold rain 24–25 and 28 April. On 3 May one male was seen. Snow fell again 23–24 May. On 29 May and 2 June *P. n. microstriata* were common, with eggs on the latter date on (in descending order of preference), *Arabis*, *Nasturtium*, and *Barbarea*. The last adult seen was 9 June; on 15 June 3 mature larvae were still found on *Arabis*.

DISCUSSION

There is little in the literature on catastrophic extinctions of natural butterfly populations (Ehrlich *et al.*, 1972). Both populations of *P. n. microstriata* under study flirted with extinction in 1977, for

different reasons. As an early spring insect, *P. n. microstriata* trades off lateness of emergence (to reduce the probability of catastrophic weather-induced mortality) against earliness (to match the phenology of the vernal Crucifers). The former factor would seem more compelling at Lang, the latter at Gates. How do *P. n. microstriata* "decide" when to emerge?

Under controlled laboratory conditions populations show an astonishing intrapopulation variance in the "chilling requirement" to break pupal diapause. There seem to be interpopulational differences as well, but for the purposes of Table 3 pupae from four

Table 3. "Chilling requirement" to break diapause in *P. n. microstriata*. Dormant pupae were held at 3° C and tested at intervals at 20° to ascertain whether diapause had been broken. Pooled data for several broods (see notes), 1972 through 1978.

Number of weeks ³ held at 3° prior to activation	Genetic diapausers ¹		Facultative diapausers ²	
	Number of pupae activating	Percent of all pupae	Number of pupae activating	Percent of all pupae
5-9	12	2.9	0	0
10-14	14	1.0	9	9.2
15-19	9	2.2	30	30.6
20-24	11	2.7	24	24.5
25-29	49	12.1	13	13.3
30-34	78	19.3	8	8.2
35-39	111	27.4	5	5.1
40-44	37	9.1	1	1.0
45-49	41	10.1	1	1.0
50-54	15	3.7	0	0
55-59	3	0.7	0	0
60-64	7	1.7	0	0
65-69	3	0.7	1	1.0
70-74	8	2.0	0	0
75-79	4	1.0	0	0
greater than 79	13	3.2	6	6.1

notes:

¹defined as individuals which diapaused under continuous light at 20° C+. From 14 females ex 3 foothill populations and 1 mid-elevation Sierran population.

²defined as individuals which diapaused under inducing photoperiods at 20° C+. Since these broods included some genetic diapausers which would have diapaused anyway, these are included in the tally. From 4 females ex 2 foothill populations.

³time elapsed does not include pre-testing time and testing time to assess dormancy at 20°.

populations are pooled. There is a difference between genetic "obligate" diapausers, which are refractory to photoperiod, and facultative diapausers which have been reared on inducing regimes, as well as a large spread of developmental times in each group. How this variability is expressed afield is unclear. Except for some pupae which do not develop at all in the first year, all individuals probably come out of diapause in January and subsequent development is temperature-dependent. The accumulated chilling in continuous cold storage is much greater than the wild pupae experience in fluctuating temperatures, so the "chilling requirement" is really a more complex chilling-time interaction. Except for pupae which carry over to a second or subsequent year, the effect of intrapopulation variance may be largely masked in cold, wet springs and maximally expressed in warm, dry ones.

The carryover pupae provide the only reasonable explanation for the large 1978 population at Gates after the 1977 disaster. The numbers, however, suggest that a large number of carryover pupae may have been involved. This in turn suggests that something about the 1976/77 season cued a carryover response in a larger-than-usual fraction of the population. The temperature pattern is conveniently similar to 1977/78; the striking difference is rainfall.

Carryover pupae occur in other Pierids, including *Anthocaris sara* and *A. cethura* (Felder & Felder), *A. lanceolata* Lucas, *Euchloe hyantis* (Edw.), *E. ausonides* Lucas, and *Pieris sisymbrii* Bdv. in western North America. They also occur in *Papilio rudkini* Comstock (Papilionidae), a desert swallowtail noted for its aseasonality, correlation of flights with heavy rains, and diapause pupae which may carry over for 6 years or more (Emmel and Emmel, 1973 and *pers. comm.*). There is strong circumstantial evidence for this species that a physiological response to water initiates post-diapause development—the insect behaves like a desert annual plant with a water-soluble seed-germination inhibitor. Of the Pierid species listed above, some occur in xeric and some in more mesic habitats, but not enough data are available to say whether the frequency of carryover pupae is correlated with rainfall uncertainty in the habitat.

In any case, *P. n. microstriata* is a surprising insect to have the carryover response, given that it is almost certainly of Arcto-Tertiary mesic origin (Shapiro, 1975, 1977). Years of 25 cm or less of rain have occurred 14 times at Sacramento since 1849 and 14 times

at Davis, Yolo County, since 1871. For both only the 1975/76 and 76/77 water years stand as consecutive severe droughts. At both stations 1930/31 and 32/33 were dry, separated by an average year, and at Davis 1917/18 and 1919/20 were dry, separated by a wet year. Is the long-run rainfall variance in central California adequate to select for a carryover response, or is it a preadaptive property of Pierids generally? Data on populations from other climates are needed.

It is dangerous to argue that because an aspect of the biology of an animal is adaptive in a particular situation, it evolved as a response to that situation in evolutionary time. In the case of *P. n. microstriata* at Gates it is not clear that a tenfold reduction in host biomass would have adversely affected fitness, had the insect attempted to reproduce. (Compare Murdoch, 1966 for a Carabid beetle case.) We simply do not know if intra- or interspecific competition for food would have occurred. Because *P. n. microstriata* is usually out of phase with *Dentaria* at Gates, it uses that plant mainly at the beginning of the flight and in early years, and most of its eggs are placed on the phenologically better-matched *Barbarea*, even though *Dentaria* is more abundant. Its eggs are strongly contagiously distributed, and it does not assess egg load on individual hosts, so that single plants sited such that females find them easily may receive overloads of eggs. It can thus be argued that with fewer and smaller plants intraspecific competition would have been aggravated—but we do not know if oviposition behavior might have been modified. *P. n. microstriata* is also positively associated with *A. sara* on individual hosts. This butterfly seems to assess its own egg load but not that of *P. n. microstriata*. The *Pieris* is a leaf-, the *Anthocaris* a silique-feeder. In 1977 there was no conspicuous reduction in numbers of *A. sara* adults or eggs at Gates, even though it is able to carry over (indeed, most captive pupae do); its 1978 performance was outstanding. A major reduction in host biomass, then, failed to adversely affect it, perhaps because it distributes eggs more evenly.

We do not know where the 1978 butterflies at Lang came from. Some may have been carryovers, but here the destruction of the 1977 egg crop may have been more apparent than real. Many hosts at Lang are inaccessible for censusing, and precisely these—on steep, wooded slopes—may have afforded more benign microclimates to eggs and larvae than those at and near canyon bottoms. In

most years 75–80% of potential hosts are censused at Gates, but only 50% at Lang.

There are two major modeling approaches to insect phenology. One, the physiological-time or degree-day approach, began with Shelford's (1927) study of the codling moth, *Laspeyresia pomonella* (L.) (Tortricidae). This is still the best-quantitated species (Riedl, Croft and Howitt 1976; Riedl and Croft, 1978). Here the emphasis is on the development of predictive algorithms from empirical data. The other approach proceeds from Darwinian principles and is exemplified by the treatment of Levins (1969) or Cohen (1970) who derive strategies from survival and reproduction parameters. The two approaches are complementary: responses to real meteorological events are the proximate consequences of selection for a genetic blueprint of development. The fusion of the two approaches into a comprehensive theory of insect phenology will require data on how seasonality contributes to resource utilization, competition, and survival.

ACKNOWLEDGEMENTS

Field assistance in 1977 was provided by Susan J. Katz. This research was funded in part by grant D-804 from the Committee on Research, U.C. Davis.

LITERATURE CITED

- BRADSHAW, W.E. 1974. Phenology and seasonal modeling in insects. in H. Lieth, ed., *Phenology and Seasonality Modeling*. Springer, New York. pp. 127–138.
- COHEN, D. 1970. A theoretical model for the optimal timing of diapause. *Amer. Nat.* 104: 389–400.
- EHRlich, P. *et al.* 1972. Weather and the "regulation" of subalpine populations. *Ecology* 53: 243–247.
- EMMEL, T. C. AND J.F. EMMEL. 1973. *The Butterflies of Southern California*. Los Angeles County Museum of Natural History.
- FIGGINS, W. E. 1971. Climate of Sacramento, California. *NOAA Tech. Mem. NWS-WR65*. 63 pp.
- GIESEL, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7: 57–79.
- HARCOURT, D. G. 1966. Major factors in survival of the immature stages of *Pieris rapae* L. *Can. Ent.* 98: 653–662.
- LEVINS, R. 1969. Dormancy as an adaptive strategy. *Symp. Soc. Exptl. Biol.* 23: 1–10.

- MURDOCH, W. W. 1966. Aspects of the population dynamics of some marsh Carabidae. *J. Anim. Ecol.* 35: 127-156.
- RIEDL, H. AND B. A. CROFT. 1978. The effects of photoperiod and effective temperatures on the seasonal phenology of the codling moth (Lepidoptera: Tortricidae). *Can. Ent.* 110: 455-470.
- RIEDL, H., B. A. CROFT, AND A. J. HOWITT. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological time models. *Can. Ent.* 108: 449-460.
- SHAPIRO, A. M. 1974. Host-plant utilization by *Pieris napi* populations in California. *Psyche* 81: 361-366.
- . 1975. Developmental and phenotypic responses to photoperiod in uni- and bivoltine *Pieris napi* in California. *Trans. R. Ent. Soc. London* 127: 65-71.
- . 1976a. Photoperiodic responses of phenologically aberrant populations of Pierid butterflies. *Great Basin Nat.* 35: 310-316.
- . 1976b. The role of watercress, *Nasturtium officinale*, as a host of native and introduced Pierid butterflies in California. *J. Res. lepid.* 14: 158-168.
- . 1977. Phenotypic induction in *Pieris napi* L.: role of temperature and photoperiod in a coastal Californian population. *Ecol. Ent.* 2: 217-224.
- . 1978. Photoperiod and temperature in phenotype determination of Pacific Slope Pierini: biosystematic implications. *J. Res. Lepid.* 16: 193-200.
- SHELFORD, V. E. 1927. An experimental investigation of the relations of the codling moth to weather and climate. *Ill. Nat. Hist. Survey Bull.* 16, number 5.
- U.S. DEPARTMENT OF COMMERCE, ENVIRONMENTAL DATA SERVICE 1971-77. Annual climatological summary, Vacaville, CA.
- . 1977. Annual summary with comparative data. Blue Canyon, CA.

A NEW QUASISOCIAL *ANELOSIMUS* SPIDER
(ARANEAE, THERIDIIDAE)
FROM PARAGUAY

BY HAROLD G. FOWLER¹ AND HERBERT W. LEVI²

INTRODUCTION

The genus *Anelosimus* was last revised by Levi (1956, 1963). Since these revisions, considerable attention has been given to the study of the social behavior of spiders (Kullmann, 1968, 1972; Shear, 1970), and especially to the social behavior of species of *Anelosimus* (Brach, 1977). One species, *Anelosimus eximius*, constructs communal webs that encompass many cubic meters (Simon, 1891), and is considered by Wilson (1971) to have reached the level of quasisociality. We now describe and provide observations on a new quasisocial *Anelosimus* from southern South America.

Anelosimus lorenzo Levi, new species
Figures 1-4

Holotype. Male holotype and numerous female paratypes, all in poor condition, having once been dry, San Lorenzo, Paraguay, collection 25 July, 1976, (H. Fowler) in the Museum of Comparative Zoology.

Diagnosis. The male of this species differs from *Anelosimus rupununi* Levi by the shape of the conductor in the palpus. No differences are known in females.

Description. Female. Carapace brown with wide darker median longitudinal band. Sternum, legs brown. Dorsum of abdomen white, with a line of black patches. Sides dark. Venter black with white spots toward sides. White behind and above spinnerets. Anterior median eyes subequal in size, larger than posteriors which are 0.7 diameters of anteriors. Anterior median eyes 1.8 diameters apart, a third of their diameter from laterals. Posterior median eyes 2 diameters apart, 1.5

¹Department of Entomology and Economic Entomology, Rutgers University, New Brunswick, N.J.

²Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138. The junior author is responsible only for naming and describing the new species.

Manuscript received by the editor February 13, 1979.

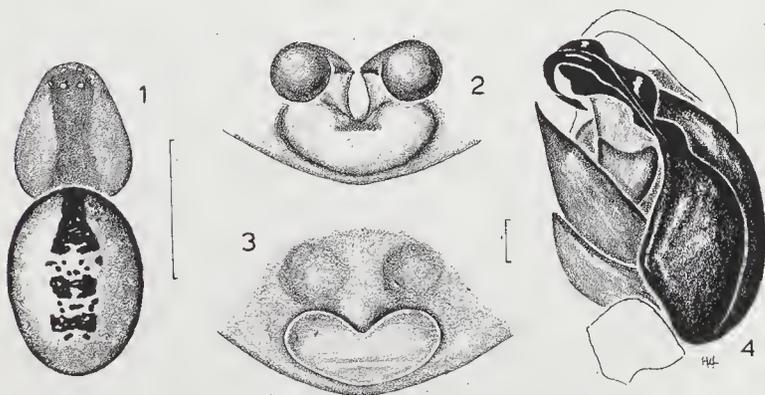
diameters from laterals. The height of the clypeus equals 3 diameters of the anterior median eyes. The abdomen is suboval, longer than wide, and high. Total length, 2.3 mm. Carapace 1.1 mm long, 0.9 mm wide. First femur, 1.2 mm long; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 0.9 mm long; third, 0.7 mm; fourth, 1.1 mm.

Male. Coloration like female except that the abdominal patches are fused, forming a longitudinal band with wavy outlines. Eyes subequal in size. Anterior median eyes 1.2 diameters apart, 0.3 from laterals. Posterior median eyes 1.5 diameters apart, 1 diameter from laterals. Height of the clypeus is 2.5 diameters of the anterior median eyes. Total length 2.3 mm. Carapace 1.3 mm long, 1.0 mm wide. First femur, 2.2 mm long; patella and tibia, 2.5 mm; metatarsus, 2.0 mm; tarsus, 0.8 mm. Second patella and tibia, 1.7 mm long; third, 1.0 mm; fourth, 1.7 mm.

Distribution. It is probable that the southernmost records of *Anelosimus rupununi* belonged to this species. All were females and may have been misidentified.

BEHAVIOR

Observations were conducted from November, 1975, through January, 1976, (Period I), and from March through June, 1976, (Period II), in a citrus orchard located within the municipal limits of



Figs. 1-4. *Anelosimus lorenzo* new species. 1. Female, dorsal view without appendages. 2-3, Epigynum. 2. Dorsal view, cleared. 3. Ventral view. 4. Left male Palpus. Scale line: Fig. 1, 1.0 mm, Figs. 2-4, 0.1 mm.

San Lorenzo, Paraguay, approximately 15 km east of Asuncion. Initial searches confirmed the presence of 5 colonies during Period I, with 12 additional smaller colonies found during Period II. A large colony of approximately 550 adults and juveniles, and 50 egg sacs, was collected and established in a 1 m³ screen cage on a potted *Coleus* plant within an entomological greenhouse. The following observations were made on both field and laboratory colonies.

Spinning behavior and webs. The 5 colonies observed during Period I ranged in estimated volumes of web enclosures from 0.3 m³ to 1.4 m³. The 12 smaller colonies observed during Period II were much smaller, with the largest having an estimated volume of 0.2 m³. The web periphery of all colonies was covered with loosely spun silk, while the interior consisted of densely spun silk platforms. Webs housing the colonies did not differ from the webs of *A. eximius* figured by Millot (1949) and Brach (1975), or from the webs of *A. rupununi* illustrated by Levi (1972). Additional webs of unspecified colonial species of *Anelosimus* are illustrated in Stejskal (1976).

The remains of many large insects, notably cerambycid, carabid and scarabaeid beetles, were observed throughout the web structure. Portions of the web of the larger colonies had apparently fallen into disuse, as these were cluttered with dead vegetation and insect parts, as described by Millot (1949). Dead or dying leaves in the interior of the communal web were curled and sheathed with silk to form retreats. Stejskal (1976), in a still unconfirmed report, contended that unspecified species of *Anelosimus* pierce the epidermis of the undersides of mango, citrus and coffee leaves and actively imbibe the cytoplasm, and further hypothesized that these species would not survive on other species of trees. More observations on the feeding behavior of these spiders are obviously needed to check the validity of these claims. The colony figured by Brach (1975) was not located in these plants. He observed no dead leaves, perhaps because spiders were not piercing and drinking from the leaves.

Citrus trees housing all 5 colonies during Period I were heavily attacked by mealybugs, *Pseudococcus* sp., which were tended by ants, *Crematogaster quadriformis vezenyii* Forel. The distribution of both mealybugs and ants reached the colonial web on the branches where the colonies were located. Many mealybugs, and a few ants, were found entangled at the branch-web interface. No abnormal fruit or leaf developments were noted within the communal web, with the exception of the dead and curled leaves serving as retreats. Stejskal

(1976) concluded that colonial species of *Anelosimus* were more harmful than beneficial in Venezuelan orchards, where they are actively treated with pesticides.

Most web spinning and repair occurred at night. Webbing was spun as several spiders reinforced draglines from which they dispersed to spin subsequent peripheral silk or dense platform silk. This behavior was qualitatively the same as that found in *A. eximius* (Brach, 1975). Unlike *A. eximius* (Brach, 1975), *A. lorenzo* did not always found colonies at the extremities of leaves or branches. 3 of the 5 large colonies, and 7 of the 12 smaller colonies were located at positions intermediate between the twig or branch junction and its tip. This behavior is much like other species of *Anelosimus* (Stejskal, 1976).

Small colonies were always found in trees adjacent to large colonies, hinting that colony foundation is carried out by small groups of spiders, or sociotomy (Jackson and Joseph, 1973). All the small colonies observed appeared before the onset of cooler winter weather. The large size of colonies, both in populations and webbing, and conversations with local farmers, suggest that colonies are perennial. Stejskal (1976) observed repeated colony relocation over a 3 yr period, and attributed this activity to the dry microenvironment produced when the spiders' activities killed leaves.

Social interactions. In a rigorous analysis of social behavior in the Theridiidae, Kullmann (1968, 1972) ranked *A. eximius* (= *Theridion eximius*) at the pinnacle of social evolution within this family. Wilson (1971) considered *A. eximius* to be quasisocial, due to the presence of members of the same generation in communally constructed and maintained webs, the existence of communal cooperation in prey capture, and the indiscriminate feeding of the juveniles. Brach (1977) emphasized the importance of cooperation between adults, or parasociality (Shear, 1970), in the evolution of social behavior in *Anelosimus*. That *A. lorenzo* parallels *A. eximius* at every level of behavior observed (Table 1), suggests that quasisociality is probably quite widespread within *Anelosimus*. *A. rupununi*, with extensive communal webs and populations in excess of 1,000, is also probably quasisocial, and as more observations are made on other species, this list will undoubtedly have to be increased. It is tempting to speculate that some reports on the social behavior of *A. eximius* may have inadvertently been of other species, especially due to the high degree of morphological similarity found within species groups.

TABLE 1

COMPARATIVE BEHAVIORAL AND ECOLOGICAL PARAMETERS OF THREE SPECIES OF *ANELOSIMUS*. DATA FOR *A. STUDIOUS* AND *A. EXIMIUS* TAKEN FROM BRACH (1975, 1977). DATA FOR *A. LORENZO* FROM THIS STUDY. BEHAVIORS ARE DESCRIBED IN BRACH (1975, 1977).

PARAMETER	<i>Anelosimus studiosus</i>	<i>Anelosimus eximius</i>	<i>Anelosimus lorenzo</i>
Geographic range	Temperate-subtropical North America	Tropical South America	Subtropical southern South America
Colony populations	~50	>200	>200
Cooperative prey capture	present	present	present
Communal feeding	present in juveniles, not in adults	always present	always present
Reproductive females/colony	1	>1	>1
Cannibalism	present	present	present
Brood feeding	discriminate	indiscriminate	indiscriminate
Dispersal	solitary gravid females	sociotomy?	sociotomy?
Colony life span	annual	perennial	perennial
No. females/ No. males	~1.0	~20-79	~50
Species recognition	strong	weak	weak
Social level	subsocial	quasisocial	quasisocial

Field colonies of *A. lorenzo* accepted spiders from other colonies without any overt sign of aggression. Other unidentified species of Theridiidae, when placed in webs, were ignored until they were apparently accidentally encountered by resident spiders, at which time they were attacked. Other behavioral observations (Table 1) were made much the same way as by Brach (1977), and will not be further elaborated. Nevertheless, Brach (1977) failed to comment on sex ratios: Although field data are few, it is apparent that the sex ratios of quasisocial *Anelosimus* are strongly skewed in favor of females. Brach (1975) speculated that the preponderance of females was the product of differential cannibalism on males, resulting in the female biased quarternary sex ratio. However, data are not available on primary and secondary sex ratios for these spiders to ascertain if cannibalism is a valid hypothesis. Whatever the cause, female dominated populations undoubtedly affect the population genetics of these species (Fisher, 1930), and one would expect that females are the mobile sex (Cannings and Cruz Orive, 1975), which would tend to indicate that inbreeding may be quite high.

The influence of sex ratio on the population genetics of these spiders becomes more evident when the mode of sex determination is considered. Although spiders are diploid, sex determination in the Araneae is characteristically through a complex system of multiple chromosomes, with males being heterogametic (White, 1973). Under normal conditions, brothers and sisters within a colony would share the same number of genes in common with one another through common descent. However, if the female homogametic chromosomes have significantly more active gene sites, then sisters would share more genes with one another through common descent, than do brothers. Thus, at the sex-linked loci, kin-selection (Hamilton, 1972) could contribute to the evolution of social behavior in the species of *Anelosimus* in a manner somewhat analogous to the assumed action in the Hymenoptera. Undoubtedly, if such a situation does indeed occur, morphological and behavioral modifications would to have evolved before sociality could be achieved, such as the loss of species-specific tactile recognition (Brach, 1977). If indeed quasisocial *Anelosimus* are highly inbred, the possibility that kin selection is important would be much more probable (Hamilton, 1972).

Sex ratios dominated strongly in favor of females may also inadvertently produce a reproductive division of labor, especially in light of the indiscriminate feeding of juveniles by adults. If there are

not a sufficient number of males present in the colony to inseminate all reproductively receptive females, only inseminated females would produce viable young as thelytoky is unknown in spiders (White, 1973). Species of *Anelosimus* that are now considered to be quasisocial may thus be found to be functionally eusocial (*sensu* Wilson, 1971). However, there is still no evidence of an actual anatomical or physiological distinction among non-reproducing spiders that would qualify them as a true caste in the usual sense employed in the study of social insects.

ACKNOWLEDGEMENTS

We extend our thanks to the valuable comments that have been given on previous drafts by E. O. Wilson, F. M. Carpenter, R. B. Roberts, E. Rajotte, and R. Buskirk.

LITERATURE CITED

- BRACH, V.
1975. The biology of the social spider *Anelosimus eximius* (Araneae: Theridiidae). Bull. So. Cal. Acad. Sci., 74: 37-41.
1977. *Anelosimus studiosus* (Araneae, Theridiidae) and the evolution of quasisociality in Theridiid spiders. Evolution, 31: 154-161.
- CANNINGS, C. & L. M. CRUZ ORIVE.
1975. On the adjustment of the sex ratio and the gregarious behavior of animal populations. J. theor. Biol., 55: 115-136.
- FISHER, R. A.
1930. The genetical theory of natural selection. Clarendon, Oxford. 272 pp.
- HAMILTON, W. D.
1972. Altruism and related phenomena, mainly in social insects. Ann. Rev. Ecol. Syst., 3: 193-232.
- KULLMANN, E.
1968. Soziale Phaenomene bei Spinnen. Ins. soc., 15: 289-298.
1972. Evolution of social behavior in spiders (Araneae: Eresidae and Theridiidae). Amer. Zool., 12: 419-426.
- LEVI, H. W.
1956. The spider genera *Neottiura* and *Anelosimus* in America. Trans. Amer. Micros. Soc., 75: 407-421.
1963. The American spiders of the genus *Anelosimus* (Araneae, Theridiidae). Trans. Amer. Micros. Soc., 82: 30-48.
1972. Taxonomic-nomenclatural notes on misplaced Theridiid spiders (Araneae, Theridiidae), with observations on *Anelosimus*. Trans. Amer. Micros. Soc. 91: 533-538.
- MILLOT, J.
1949. Araignees sociales. In P. Grasse (ed.) *Traité de Zoologie*, 6: 979 pp. Masson, Paris.

STEJSKAL, M.

1976. Aranas sociales destructoras de las plantas de cafe, citricos y mangos en Venezuela. *Turrialba*, **26**: 343-350.

WHITE, M. J. D.

1973. *Animal cytology and evolution*. 3rd Edition. 961 pp. University Press, Cambridge.

WILSON, E. O.

1971. *The insect societies*. 548 pp. Belknap Press-Harvard, Cambridge.

TERRITORIAL BEHAVIOR IN MALES OF
PHILANTHUS PSYCHE (HYMENOPTERA, SPHECIDAE)*

BY KEVIN M. O'NEILL

Department of Zoology and Entomology
Colorado State University
Fort Collins, Colorado 80523

INTRODUCTION

The comparative ethology of the family Sphecidae has been the subject of intensive study over the last thirty years, although the behavior of these wasps was observed and recorded by Fabre as early as the mid-1800's. The majority of work has been done on females, probably because of the conspicuousness of their activities and their complex, species-specific behavior patterns. In the past few years, an increasing amount of work has concentrated on the behavior of male sphecsids, revealing complex and sometimes puzzling behavior patterns. Lin's paper (1963) on male territoriality in *Sphecius speciosus* was one of the first attempts at a rigorous study of male behavior. The conspicuousness of female activity is often matched by the inconspicuousness of the males, particularly when they do not frequent the nesting area subsequent to emergence. Even when males are easily observed, in the nesting area or elsewhere, matings are rarely observed. Male sphecsids, except in a few species, do not participate in the nesting activities of the females.

Alcock et al. (1978) classify the mating strategies of male aculeate Hymenoptera as taking the form of either searching for females (e.g., the "sun dance" of Nyssonine sand wasps, Evans 1966) or waiting for (e.g., territoriality) females at particular localities where they are most likely to be found. The distribution of receptive females in time and space has been a major influence on the evolution of male mating strategies. A recent review of territorial behavior in male sphecsids (Alcock 1975a) shows that in all known cases this behavior is associated with securing females for copulation. I define territoriality here as "a fixed area from which intruders are excluded by some combination of advertisement, threat or

*Manuscript received by the editor March 27, 1979.

attack" (Brown 1975). Since territoriality is the exception rather than the rule in male sphecids, some ecological factors must impinge, favoring the evolution of the behavior in some species and not in others. According to Alcock, territoriality seems to evolve when males can locate areas where females are clumped or occur predictably. In addition, these areas must be defendable in terms of the time and energy budgets of the males. Lacking these conditions the large time and energy expense associated with defending a territory may not maximize reproductive success.

Recently particular attention has been paid to male and female behavior in the sphecid genus *Philanthus*. In most North American species in which male behavior has been observed males exhibit territoriality. They also exhibit a specific behavior referred to as abdomen dragging which has been suggested to function in scent marking the territories with a mandibular gland secretion (Gwynne 1978) which may attract females (Alcock 1975a).

Philanthus psyche Dunning is a relatively small member of its genus, females and males averaging 9 and 8 mm in length, respectively. It is found in western and central North America (Great Plains and Great Basin) occupying sand dunes with low sparse vegetation, particularly grasses. Nesting areas are usually on the periphery of blowouts or similar dunal features.

METHODS

Observations on *Philanthus psyche* were made about two miles east of Roggen, Weld Co., Colorado during July and August 1976 and 1977 and occasionally throughout the summer of 1978. The general study area may be classified as sand sagebrush (Harrington 1964). The specific study site was the area immediately surrounding a vegetation-free blowout, one side of which was bordered by a sandy ridge. The nesting area of *P. psyche* was in the border of the blowout and was level to slightly sloping. It was dominated by blowout grass [*Redfieldia flexuosa* (Thurb.) Vasey] and lanceleaf scurfpea (*Psoralea lanceolata* Pursh). Further away the dominant plants were sunflower (*Helianthus* spp.) along with various grasses.

At the main observation area measuring 12 by 8 meters, detailed observations were made of male and female behavior and of locations of marked males, occupied territories and female nests. Individual males were marked with one or two spots of enamel paint

on the thorax. Periodic observations were made of other areas where there were territorial males to compare male behavior and territory and nest distribution, and to check for movement of marked males between the areas.

Wind speed measurements were made with a Datametrics Airflow multimeter Model 800 VTP anemometer. Males and females for dissection were preserved in alcoholic Bouin's solution which maintains the turgidity of the glandular tissue (Humason 1967).

RESULTS

Daily Activity Patterns

At Roggen, males and females emerge in late June, the males preceding the females by a few days to a week. Both become active daily at about 1000 and remain so until between 1400 and 1600 hours. Females spend the night in the nest while males sleep in short (6 cm) sleeping burrows which they dig. After emergence from these burrows each morning, males perch on the low vegetation in the nesting area, grooming and occasionally changing perches but not interacting with other insects, even digging females. Males begin setting up territories, on warm clear days, between 1030 and 1100.

For seven different clear days during the summer of 1977, twelve territories in the main observation area were censused every 15 minutes during the observation period. Only 22% of the territories observed at 1100 were occupied. However, from 1130 until 1300 approximately 50% were occupied on the average. The number thereafter declined, few males being present by 1600. On warm clear days at the peak of seasonal activity, nearly 100% of the territories were occupied during the afternoon hours; on overcast days, few males were territorial.

Location and Characteristics of Territories

Both nests and territories occurred in areas of generally short, sparse vegetation rather than in nearby areas of relatively high and dense vegetation or open sand (Figure 1). The mean distance from a nest to the center of the nearest territory was only 35 cm ($N = 29$; S.D. 17.4; see Figure 2). Where both *P. psyche* and *P. albopilosus* occur in the same habitat, the former nests in the peripheral areas around the blowout which contain plants, while the latter nests in the bare, fine-grained sand in the central portion of the dune. This is the situation at Roggen (Evans: 1975). The open sand poses restric-

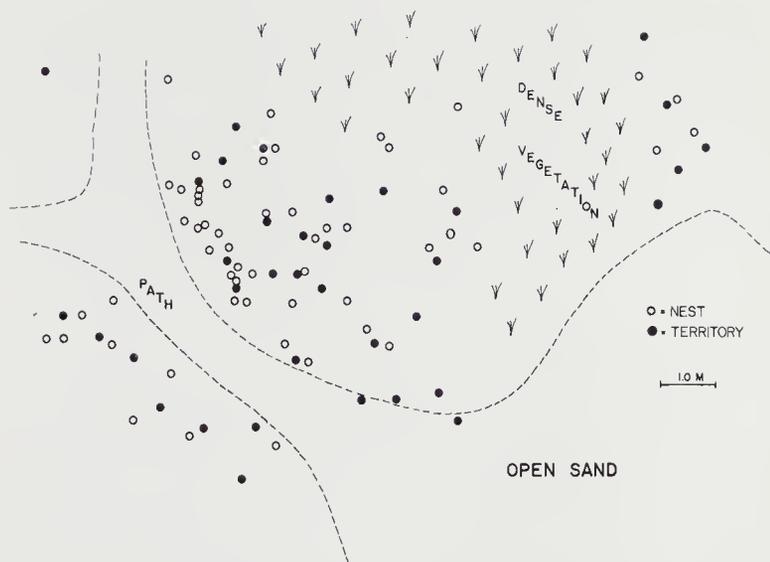


Figure 1. Map of main observation area showing vegetation, nests and territories.

tions to nesting. For species such as *P. albopilosus* which nest in the open sand, it may be adaptive to dig much deeper nests because shifting sands can disrupt the cells in the nest. Mean cell depth for *P. psyche* and *P. albopilosus* at Roggen are 21.5 and 52.0 cm, respectively (Evans 1975 and unpublished data). The ability of females of *P. psyche* to nest in the peripheral area with stabilizing vegetation allows them to dig shallower nests and possibly more per season and to avoid the high surface temperatures of the open sand during the middle of the day.

On the other hand, areas of more dense vegetation may restrict nesting due to the fact that plant roots interfere with digging. Therefore, although plants stabilize the dune, females require at least a small amount of space between plants for digging. Nests occurred in small bare spots in the vegetation at least a short distance from the base of the plants. Female *P. psyche* consistently nest in this type of situation, not only in the Roggen area (where the species is extremely abundant), but also in other areas of Colorado and New Mexico where I have observed this species.

It was evident that males set up territories in small plots devoid of vegetation (or nearly so) within the nesting area (Figure 2). By

recording the location of plants on which males "scent marked" around the territory and perching points on the sand and marking off the area which they encompassed, a rough measure of territory size can be made. These areas visibly coincide with the bare areas of sand occupied by males in the field. (If we chose, instead, to take the boundary of the territory as the maximum distance from its center at which a male will sight and approach a passing insect, the above measurement would be only a slight underestimate of functional territory size.) The mean size for twelve territories was 0.17 m^2

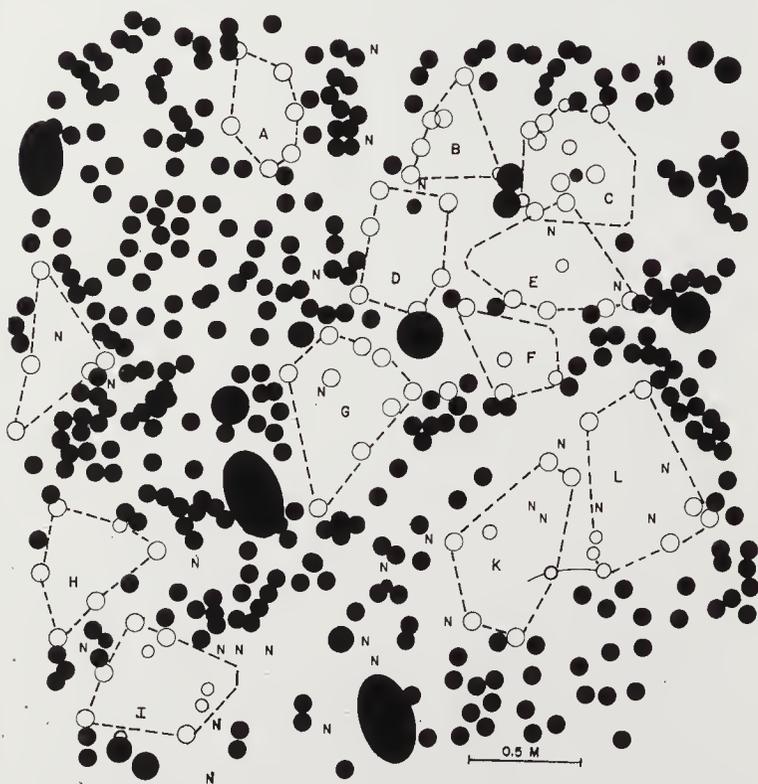


Figure 2. Map of 3 m^2 area in which most observations were made in 1977. Dotted lines indicate the area encompassed by all marked plants and/or perches of male(s). For several territories it was necessary to record, on two separate days, plants marked by different males. Solid circles and ovals indicate plants that were marked by males. N indicates a nest entrance.

(range 0.10 to 0.25 m²). It was not apparent that territory size changed through the season as has been shown for the territorial bee *Hoplitis anthocopoides* (Eickwort 1977).

Patterns of Territory Occupation

Both casual observation and censusing showed that certain territories were occupied more frequently than others. Three of the twelve territories censused (A, K and D in Figure 2) were occupied at least 85% of the time in which at least one of the territories in the plot contained a territorial male. Territory D was occupied during 95% of the period. These territories and several others were usually occupied during peak activity periods. Others contained males only sporadically, often for a few consecutive days followed by a lull of a week or more. Furthermore on overcast days and during the latter part of the season, when few males were territorial, males were nearly always observed on the most "popular" territories. In contrast to these, five territories censused (B, E, F, G and H) were each occupied less than 30% of the time.

For eleven of these territories, there was information on both size and frequency of occupation. Comparison of these two parameters shows no appreciable relationship between size and quality of the territory, the latter determined by the frequency of occupation ($r = 0.316$; regression not significant). Therefore, the size of the territory (through the given range) or at least of the vegetation-free perch area does not seem to be a factor in choosing a territory, although there is probably a minimum acceptable space that males will utilize.

For certain males that were watched continuously or were marked with paint, it was possible to record approximately how long they occupied a certain territory on a given day. The mean duration of occupation of a territory was 80 minutes ($N = 25$; S.D. = 45 minutes).

During the summer of 1976, the distribution of territories occupied by individual males was recorded within observational limits. Probably due to the difficulty of marking these small wasps without killing them or hindering their movement, only 13 males were seen subsequent to the day on which they were marked, with only six being observed two or more times. The maximum time period over which a marked male was seen was fourteen days and the maximum

number of territories a marked male was seen to occupy was nine. Fifty-two territories were recorded for males returning after the day on which they were marked. Of these, forty-six (88%) were in the area of grass in which they were originally marked (area in Figure 1). Only six (12%) were recorded outside this area with only one being more than 5 m away. These six were found during periodic checks of nearby areas (within 50 m) where there were known to be territories and it is possible that others were missed because of the area to be covered.

Intraspecific and Interspecific Interactions

Much of the male's time while on the perch is occupied by interaction with intruding insects, particularly conspecifics. An intruder is defined as an insect that flies into or through a territory (or immediately adjacent to it). A male's response towards an intruder may fall into one of two functional categories: aggression towards a conspecific male or investigation of a potential mate. Barash (1977) designates aggression as an interaction between individuals with the result that one must relinquish access to some resource important to its fitness. It is difficult in this species to distinguish between these two functional responses. However, observations support the fact that at least one type of male-male interaction (the swirling flight) represents aggression, suggesting that *P. psyche* exhibits true territorial behavior. The swirling flight consists of two (or rarely three) males repeatedly circling one another in loops with a radius of 5 to 15 cm, at a speed making them difficult to follow. These flights usually last from less than 1 to approximately 10 seconds. The term was used by Alcock (1975a) to refer to a similar behavior in males of *P. multimaculatus*. Swirling flights take place between males holding adjacent territories or between territorial and non-territorial males, the latter probably trying to usurp the former's area. Since they take place repeatedly between the same two males over a short period of time, it is unlikely that this behavior could be continued mutual investigation of a potential mate. Swirling flights do not resemble any observed male-female interaction, and are usually terminated by the intruder leaving the immediate area. However, on three occasions at least, it was observed that the continual harassment by the intruder resulted in its usurping possession of the resident's territory. I assume that

this may have been a relatively common occurrence, since territories often changed hands (noticed during periodic scans of the territories). Non-contact aggressive behavior is known for the males of several other species of insects: conocephaline grasshoppers (Morris 1971), praying mantids (Edmunds 1967), cockroaches (Breed 1972), the sphecid *Eucerceris flavocinctus* (Steiner 1978) and nymphalid butterflies (Baker 1972). Baker reported that intruding males in the species *Inachis io* may usurp another male's territory without physical contact, using a behavior similar to the swirling flight.

One other type of interaction seems to be a form of aggression at first glance. A territorial male will drop from a height of approximately 10 to 30 cm onto the back of a male perched on the ground. The perched individual may be within the male's territory or an adjacent territory and does not necessarily have to move to elicit the "attack." The striking male seemingly discontinues the encounter himself immediately leaving after a grapple of one second or less. Alcock (1975a) refers to this as "strike and flee" in *P. multimaculatus*. A similar behavior was observed when a male hovered above and dropped onto the back of a female working at her nest entrance or one that had landed within his territory. As with male-male grapples, the striking male orients head-to-head with the female when landing upon her. This is the posture necessary to initiate copulation. For these interactions the period of grappling was longer (several seconds) and was terminated when the female managed to break free of the male's grasp. Occasionally two males were seen simultaneously grappling a female in this manner. Upon breaking free, the female continued working on the nest or flew away a short distance, perching on the sand for a short period of time before returning. The latter behavior is similar to parasite avoidance noted for this and other species of *Philanthus* (Evans 1970) and may function to reduce the number of energetically expensive encounters with males. The encounter may be repeated and may result in the female losing her prey. The similarity of this behavior ("strike and flee") towards both males and females suggests that the motivation behind it is the same. In other words, the male is pouncing upon a potential mate and terminates the interaction himself when some proximate cue signals that it is not a conspecific female. This has been suggested as an explanation for a similar form of male-male interaction in the western cicada-killer wasp, *Sphecius grandis* (Alcock 1975b). Therefore, the swirling

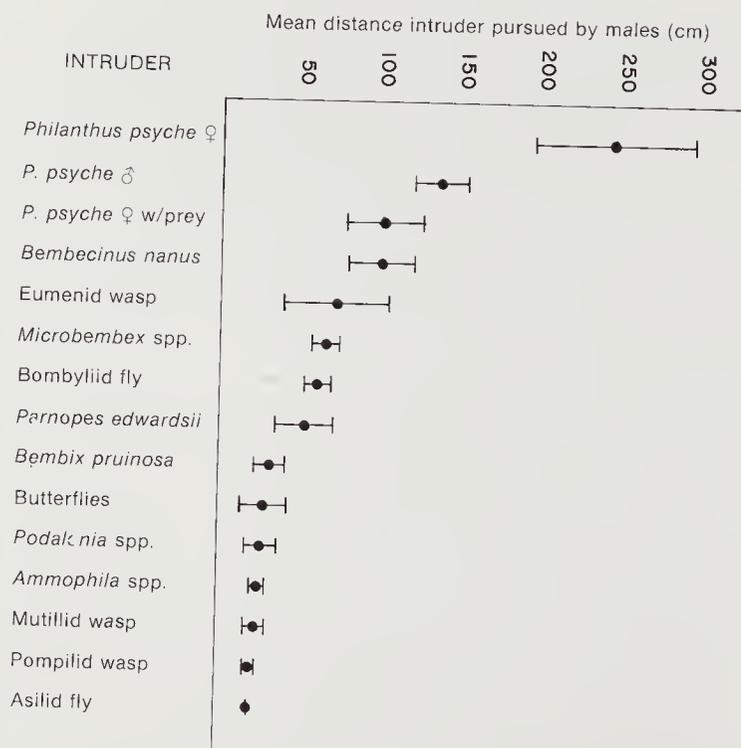


Figure 3. Intensity of response (distance pursued) of male *P. psyche* for each species of intruder. Intruder species are on the horizontal axis, arranged from left to right in order of decreasing similarity to a conspecific female (see Table 1).

flight seems to be the only distinctive aggressive male-male interaction in *P. psyche*.

A frequent response of a male to an intruder involved approach and/or pursuit of an insect passing through or near the territory. Different insects were pursued different distances by the territorial males, some simply being approached with the male not leaving his territory. Others were pursued relatively long distances. The question arose that if there is a relationship between the distance pursued and the identity of the intruder, is the intensity of the male's response (distance pursued) based upon the similarity of the intruder to male or to female conspecifics (i.e., is the response aggressive or an attempt at securing a mate, respectively)? In order

to answer this, I measured the distance pursued by a male when possible to identify the intruder. Distance pursued refers only to those encounters in which males chased an insect that flew straight through or adjacent to the territory. It does not include swirling flights in which the intruder's response would complicate measurement of the resident's response. If the response was a simple instantaneous approach, the encounter was given an a priori value of 20 cm since this approximates the radius of the territories. The male did not make contact with the intruder in mid-air as occurs in other territorial sphecids (Lin 1963, Alcock 1975a, Gwynne 1978) except in a few cases where conspecific females were grappled at the end of a flight. For two hundred forty-seven responses to intruders of thirteen different species (minimum of seven per species), I was able to record the pursuit distance. Many more encounters were observed, but could not be recorded either because the distance or the identity of the intruder could not be accurately determined. The responses to conspecifics were differentiated into female, male, and female with prey. Gwynne (1978) has carried out a similar analysis with *P. bicinctus* using distinct levels of behavior (approach, butt, grapple and grapple to ground, in increasing order) as a measure of response intensity. The intruder species can be used as "natural models" of female conspecifics and one may compare the intensity of response to the degree of similarity to the female. Figure 3 shows the mean distance pursued for each type of intruder. If we compare these distances to a list of characteristics of each type of intruder (Table 1) we see that the degree of similarity to the female is roughly positively correlated with the intensity of response of the male. There is at least a rough relationship with response intensity (distance) for all characteristics considered, so it is difficult to determine to which the male responds and which are most important.

As with *P. bicinctus* the response is greatest towards the females not carrying prey. The response to females ranged from 1.4 to 4.0 m ($N = 13$; mean = 2.45 m). Several times it terminated with the male pouncing upon the female. The response to males averaged much less ($N = 13$; mean = 1.37 m; range 1.0 to 2.0 m; t-test for difference between females and males significant, $p \leq .0001$) but the attribute responsible for this difference was not distinctly discernable. Apparently some subtle difference between male and female flight characteristics is sufficient to elicit responses of different intensities

by the territorial males. It is evident that the pursuit response as measured above was investigative rather than aggressive. The response becomes aggressive only if a pursued male reacts and a swirling flight ensues.

The response to females with prey is less than that to males ($p \leq 0.016$; t-test) and females without prey. The proximate cause for this may be that the female with prey flies slower and is bulkier in appearance because of the burden she carries. An ultimate cause may be that the females with prey are not sexually receptive, having in all likelihood mated prior to or early in the sequence of nest provisioning.

Species that differ greatly in appearance and habits from female *P. psyche*, such as male velvet ants, spider wasps, asilid flies, butterflies and *Ammophila* spp. were merely approached or chased a short distance (never more than 70 cm; $N = 110$). In contrast, *Bembecinus nanus*, a sphecid wasp similar in appearance and habits to conspecific females, drew nearly the same response as females with prey (t-test, difference not significant). Coloration seems to be an important characteristic, but not the only one to which the males cue. This is evident because the bombyliid fly and the cuckoo wasp, which differ greatly in appearance from the females, usually (twenty-eight of thirty-four cases combined) drew more than a simple approach response from the males. The response to these two was significantly different ($p \leq 0.05$) than that given to *Bembix pruinosa* (= *B. pallidipicta*) a sphecid with color patterns similar to *P. psyche* but of differing flight characteristics. Evidently, flight characteristics (speed and/or flight pattern) of the intruder are involved in motivating the male.

Predation Upon Males

One possible constraint upon the evolution of a mating system is the susceptibility to predation which a particular strategy imposes upon the males. There is a perceivable risk of predation by visually hunting robberflies (Asilidae) caused by the exposure of males during the large number of flights they take while on the territories. The risk is particularly high when these flights are directed towards robberflies intruding on the territory. Robberflies constituted almost 5% of the intruders that the males approached and/or pursued while territorial. Four attempted predations were observed, two of these successful. Predation will be discussed in more detail in another paper (Gwynne and O'Neill in press).

Table 1 (continued)

Species	Size	Coloration	Speed of flight*	Height of flight*	Flight characteristics
<i>Parnopes edwardsii</i> (Cuckoo wasp)	7-9 mm stouter	metallic green	same	same	similar to ♀♀ of <i>Philanthus psyche</i> straight
<i>Bembix pruinosa</i> (Sphecidae)	15-18 mm stouter	white & black w/ striped abdomen	much faster	higher	
Butterflies	~50 mm	dark brown or white	faster	higher	straight but wobbling
<i>Podalonia</i> spp. (Sphecidae)	~15 mm	black	slower	same or lower	walks or short flights
<i>Ammophila</i> spp. (Sphecidae)	15-20 mm slender	orange & black; not striped	slower	same or lower	walks or short flights
Mutillid wasp ♂	~10 mm	red & black	slower	same	straight
<i>Anoplius</i> spp. (Pompilidae)	~20 mm	black	slower	usually lower	walks or short flights
Asilid fly	~25 mm	gray	much faster	same or higher	straight

* = relative to *Philanthus psyche* female

Abdomen Dragging and Scent Marking

A common behavior of males on territories is abdomen dragging. All species of *Philanthus* known to be territorial exhibit this behavior. Abdomen dragging begins by the male flying from his perch on the sand to a plant in or bordering his territory (usually blowout grass or lanceleaf scurfpea). Upon landing, the male walks along the stem or leaf in an inverted V position, the mandibular area and the posterior venter of the abdomen touching the plant. The abdomen is also "waggled" back and forth while in contact with the stem. The average number of times a male dragged his abdomen in a 5 minute period was 7.75 ($N = 20$; S.D. = 3.8). Alcock (1975a) has suggested that a pheromone is being deposited by the male during abdomen dragging functioning to attract conspecific females to the territory for the purpose of mating. Although no bioassays were conducted, several lines of evidence suggest that this may be the case.

In nearly all cases (e.g., twenty-three of twenty-five for one male) abdomen dragging is preceded by what I will term a weaving flight. The male leaves his perch and flies back and forth about 10 cm above the ground, always perpendicular to wind direction and facing into it. The lateral portion of the flight is wide (up to about 30 cm) at first, but usually narrows down to the vicinity of one upwind plant (Figure 4). I have also observed a similar flight in *P. pulcher* and *P. tarsatus* (unpublished). *P. multimaculatus* also makes short flights downwind of and facing the plant on which it perches and drags its abdomen (Alcock 1975a). If a chemical is being deposited, economical use of the male's pheromone supply could involve some way in which he could receive feedback on the airborne concentration in order to regulate the rate of scent marking. The weaving flight places the male in a position to detect the pheromone since he is downwind of the source. Interestingly enough, although a weaving flight usually precedes abdomen dragging, it often ends with the immediate return of the male to his perch. At some point during the weaving flight the male (after testing the airborne pheromone concentration) may make the decision whether to scent mark or not.

Wind direction affects the behavior of males associated with abdomen dragging and the weaving flight. For five males observed only seven of two hundred and six (3.4%) abdomen draggings were on plants downwind of the perch, while one hundred eighty-two (88.3%) and seventeen (8.3%) were on plants upwind of and lateral

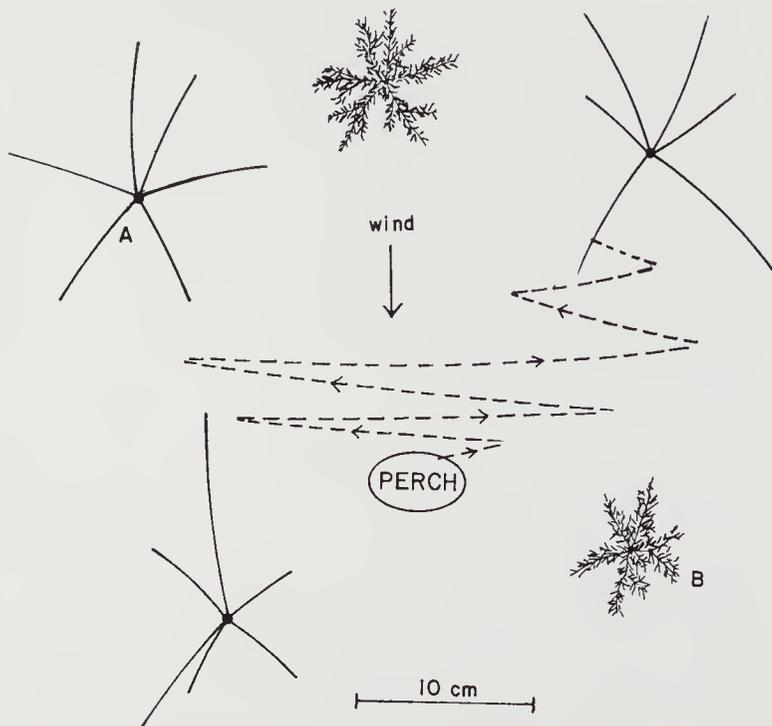


Figure 4. The weaving flight of the male. The solid arrow indicates the wind direction. The dashed line indicates the flight path of the male.

to the perch, respectively. Even when plants downwind of the perch were marked, the male often flew downwind of the plants before dragging his abdomen.

When wind direction reverses, perches moved to the opposite side of the territory and different plants were marked (Figure 5). In another area when vegetation was more sparse, males often had only one plant per territory and would always perch on the downwind side. The relative position of the perch to the plants on which the male drags his abdomen, as determined by wind direction, may be related to the same reason that the weaving flight occurs (i.e., he is in a position to detect the pheromone). Since he faces or is lateral to over 95% of the plants which he has marked the male is also in position to detect any females which have landed upon or near them.

Wind velocity also affects abdomen dragging behavior. The mean wind velocity (measured every 15 seconds) and the wind velocity when the males initiate abdomen dragging were recorded for six different males (20 minutes of observation each; two 5 minute periods for determining mean wind velocity were alternated with two for measuring velocity at the initiation of abdomen dragging). For the total 120 minutes, the mean wind velocity was 34.3 m/minute (S.D. = 32.5) while the mean wind velocity at the initiation of abdomen dragging was 60.1 m/minute ($N = 87$; S.D. = 27.5) (Figure 6). The means were significantly different (t-test, $p \leq 0.001$). Using readings taken to find mean wind velocity as the expected values the distributions were shown to be significantly

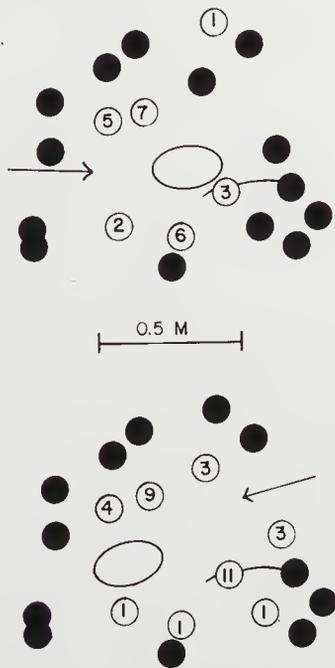


Figure 5. The effect of wind direction on position of the scent-marked plants for territory K (see Figure 2). Solid arrow indicates wind direction which on different days may come from different directions. Solid circles are plants not scent marked. Hollow circles are marked plants with the number of times it was marked in 10 (above) and 15 (below) minutes. The ellipse is where the male perched on the sand.

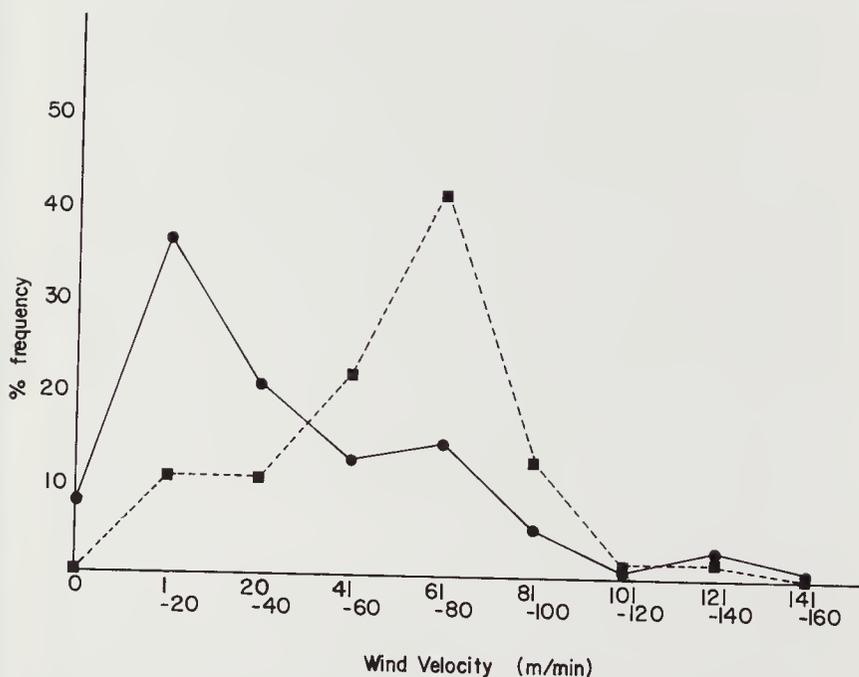


Figure 6. Frequency distribution of wind velocity readings, grouped in 20 m/min. intervals. The solid line indicates distribution of readings taken to measure mean wind velocity ($N = 287$). The dashed line indicates frequency distribution of readings taken at initiation of abdomen dragging.

different ($\chi^2 = 89.8$; 8 d.f.; $p \leq 0.001$). Thus, there may be an optimal wind velocity range above and below which the males scent mark less often. Indeed, for the above males, 76% of all abdomen draggings were done at wind velocities between 41 and 100 m/minute, while only 31.8% of the overall wind velocity readings were in this range ($N = 287$). A general conclusion might be made that males do not scent mark randomly with respect to the wind, but in some manner (possibly during the weaving flight) cue to the wind velocity and adjust their marking behavior accordingly. In fact, detection of wind velocity during weaving flight may be its function alternative or simultaneous to monitoring airborne pheromone concentration. Sower et al. (1973) have shown that for a species which releases a sex pheromone in discrete pulses, there are both upper and lower limits to wind velocity between which communication is feasible.

This may be the situation in *P. psyche* and other species in the genus which scent mark. Even in a short-range communication system, conservation of energetically costly pheromone supplies should involve consideration of wind speed.

There is a line of morphological evidence supporting the idea that abdomen dragging serves to scent mark. Two parts of the male's body (excluding the legs) are in contact with the plant while abdomen dragging occurs, the mandibular area and the distal venter of the abdomen. A small tuft of hair, termed the clypeal brush (Bohart and Grissell 1975), is located near the base of the mandibles at the point where the head touches the plant. It is possible that the pheromone could be applied to the plant via the clypeal brush, the chemical itself being produced in the mandibular glands (Gwynne 1978). Close examination of the brush (prior to preservation in Bouin's solution) reveals that the hairs adhere to one another as if saturated with a liquid. Hair tufts are known to be associated with the deposition of trail pheromones in ants (Fletcher and Brand 1968).

Dissection of the male heads reveals a large pair of mandibular glands which nearly fill the portion of the head cavity beneath the eyes. This is also true for *P. bicinctus* (Gwynne 1978) and other species of *Philanthus* which I have examined (*gibbosus*, *tarsatus*, *zebratus*, *crabroniformis* and *pacificus*). The last two also have clypeal brushes but are not known to set up territories or to exhibit abdomen dragging, so it is possible that the glands serve some other function. *P. albopilosus* is the only species that I have examined in which the males have neither clypeal brushes nor large mandibular glands. This species does not exhibit abdomen dragging or establish territories (Evans 1975). The presence of clypeal brushes in most *Philanthus*, as well as in other genera of the subfamily Philanthinae, suggests that the absence of the brush in this species is a derived character. The mandibular gland as a source of pheromones is well documented in the Hymenoptera (Wilson 1971).

The third structure associated with the deposition of a pheromone is a brush of hair on the venter of the abdomen which is more diffuse than the clypeal brush but covers a wider area. There are no known glands associated with the hair brush (Evans personal communication). This hair brush may serve to spread the pheromone more evenly on the stem, facilitating evaporation. The abdominal and clypeal hair brushes are not present in females of this species. While

perched on the territory the males spend time grooming, particular attention paid to the mandibular area and the venter of the abdomen.

Mating

Three matings were seen in the nesting area and none elsewhere. Two of these were observed already in progress, the male and female coupled on a stem in the territorial area. The third copulation was initiated when a female flew upwind (orienting to pheromone?) and landed on the edge of a territory. The resident male immediately pounced upon her. They coupled at once and flew to a plant about 1 m away where they remained still for about 4 minutes. At this point and again several minutes later, a second male landed on the back of the female resulting in the original pair changing perches once. They finally uncoupled after 8 minutes and 30 seconds. It was common to see females flying upwind through the territorial area in a low zig-zag flight.

DISCUSSION

The mating strategy that males of a particular species adopt during the course of evolution can be evaluated in terms of probabilities. The optimal strategy is one which most often places the male in the right place at the right time to intercept or attract a sexually receptive female. The nature of this strategy is influenced by the habits of the females, the degree of competition with other males, the physiological limitations of the species, predation risks and other factors (Brown 1964, Alcock et al. 1978). Exact probabilities associated with a given mating strategy may be extremely difficult to obtain, especially when matings are rarely observed and when females presumably mate only once in their lifetime. However, relative probabilities may be obtained by studying the daily and seasonal activities of males and females. A comparative approach, utilizing the ecological and ethological characteristics of closely related species may also help in understanding the factors determining the optimal mating strategy.

Males of *Philanthus psyche* are territorial in an area where potential mates are most likely to occur, that is, the nesting area. There are four other rendezvous places at which copulation is known to occur in the Sphecidae (Alcock et al. 1978). These are: the hunting area, flowers (nectar sites), landmark flyways and the

nest entrance. Why is there a greater probability for males of *P. psyche* of intercepting a receptive female in the general nesting area, rather than in one of the other four above mentioned locations?

As far as the first three rendezvous places are concerned, they should be fairly localized in order for the chance of encountering a female to be sufficiently high relative to the nesting area. At Roggen, females of *P. psyche* prey upon a diverse array of small hymenopterans (at least nineteen species in eight families; Evans unpublished data). Such a great variety of prey, assuming they themselves have diverse feeding habits as a group, would not likely be found in one place. Therefore, it is likely that the female hunting area is not concentrated. There are also no obvious concentrated patches of flowers of the type that females are likely to feed upon (e.g., *Eriogonum* spp.). Therefore, since foraging and feeding sites are relatively diffuse, clumping of females in these sites is improbable. As an effect of the above, there would be no concentrated landmark flyways between the nesting area and the foraging and/or feeding localities over which the females would be likely to pass. Males of *P. zebratus*, in the Jackson Hole, Wyoming aggregation of this species, intercept females in flyways above the nesting area (Evans and O'Neill 1978).

Mating at the nesting entrance occurs in the sphecids *Oxybelus subulatus* (Peckham 1977) and *Oxybelus sericeus* (Bohart and Marsh 1977, Hook 1978). In these species the male is territorial at or nearby the nest entrance, mating with the female each time she returns with prey. Although he concentrates his activities on a single female, it is assured that their eggs are fertilized by him. Males of *P. psyche* often attempt to mate with females working at the nest entrance but in all cases observed are unsuccessful, as the female wards off all efforts of the males or temporarily leaves the area. Without the prospect of multiple matings, it would not pay the male to wait at the nest entrance for the female as the time and energy could be better spent searching for other females.

Are males territorial in the nesting area because nesting females are present or because virgin females emerge there? In species in which the females mate only once, a male would gain an advantage by locating females as close to the beginning of their receptive period as possible. Assuming this, it may actually be the female emergence area that the male is interested in as a territory location. Males that scent mark closest to the emergence points would most likely be successful if females mate upon emergence for the first

time. Males of the cicada-killer wasp, *Sphecius speciosus* establish territories near emergence holes and mate with newly emerged females (Lin 1963). However, there is evidence that in *Philanthus* spp. (including *P. psyche*) males do not establish territories until the females begin nesting; suggesting that mating does not occur at emergence but at some point during the nesting sequence. In *P. psyche*, *P. bicinctus* (Gwynne in preparation), *P. zebratus* (Evans and O'Neill 1978 and unpublished), *P. triangulum* (Simon-Thomas and Poorter 1972), *P. multimaculatus* (Alcock 1975a), and *P. pulcher* (personal observation) copulations were observed after females began nesting.

Given that the general nesting area seems to be the location with the highest probability of encountering a female that becomes sexually receptive sometime during the nesting sequence, a male of *P. psyche* can identify this spot by simply establishing a territory where he first emerged since the previous year's nesting area is likely to be this year's. Even if successional changes result in females moving a short distance to a new nest area, the habitat type is such that males should be able to recognize it and move with them. Therefore, following Alcock's (1975a, see introduction) criteria, a territorial sphecid such as *P. psyche* is characterized by clumping of females and an apparent ability of males to locate areas where this occurs.

The third of Alcock's criteria is the defendability of the territory in terms of the male's time and energy budget. One limitation on defendability is the amount of time spent on intraspecific male-male encounters, a function of the relative population density. If a male spends too much time on aggressive interactions with conspecific males, he wastes time and energy that could be used for scent marking and contacting females. Although these encounters are common, they by no means occupy the majority of the male's time. In addition, the territories are nonresource-based (i.e., they contain no food, plants, or foraging sites and males do not control access to nesting sites). Thus, defendability is not limited by the need to include resources in the territory; which, if a minimum number were necessary, might result in territories too large to be defended and occupied exclusively. Several consistently occupied territories of this species contained only one plant.

Evidence thus far collected substantiates the suggestion of Alcock (1975a) that abdomen dragging functions to deposit a pheromone. However, at this point in the research a description of the specific

role that the chemical plays in the mating system of *Philanthus* spp. is not possible; though some educated guesses can be made. The common occurrence of interactions between non-territorial and territorial males on the latter's territory suggests that scent marking does not function to warn conspecific males that they are intruding at another's perch, as commonly occurs in mammals (Shorey 1977) and in certain species of ithomiine butterflies (Pliske 1975). In fact, something to the contrary may occur. An intruding male could capitalize on the energetic investment of another male by usurping a territory on which a pheromone has already been applied (Alcock 1975a). The advantage of the action depends upon the persistency of the chemical. It also seems unlikely that the combined pheromone of all territorial males is equivalent to a lek, serving to attract females to the general area. Females chose the location based on requirements for nesting not because of the presence of the males. In *P. triangulum* (Simon-Thomas and Poorter 1972) and in *P. zebratus* where the territories are some distance from the nests, the function of the pheromone in attracting females is obvious. In *P. psyche* and *P. bicinctus* (Gwynne 1978) where the territories are within the nesting area the function is less obvious unless short range communication is useful. Alternatively or simultaneously the pheromone may function as an aphrodisiac stimulating the female to copulate, as has been shown in a variety of insects (Butler 1970).

SUMMARY

The general predictions made by Alcock (1975a) concerning the evolution of a territorial mating strategy in male sphecids are borne out in *Philanthus psyche*. That is, females are clumped in space in a manner which the males can predict and the potential territories are defendable by the males in terms of time and energy limitations. Males of *P. psyche* apply a pheromone to plants surrounding the territory. This is believed to attract sexually receptive females. Male behavior associated with pheromone usage varies with respect to various ecological factors (e.g., wind speed, wind direction). As shown by a study of the "swirling flights" of males, this species shows true aggression, and thus, true territoriality. Pursuit behavior of the males functions in investigating intruders on the territory that may be potential mates and is not an aggressive response.

ACKNOWLEDGMENTS

I would like to thank Dr. Howard E. Evans for initiating this study and for help throughout the course of the research. This paper is dedicated to him on the occasion of his sixtieth birthday. Thomas A. Gorell, Thomas Bennett and James Ellis made important suggestions in the early stages of the study. Darryl T. Gwynne, Mary Hathaway, Allan Hook, and William Rubink reviewed the manuscript. This paper is part of a study of the comparative behavior of solitary wasps, supported by the National Science Foundation, Grant No. BNS 76-09319 to Howard E. Evans.

LITERATURE CITED

- ALCOCK, J.
1975a. Territorial behavior by males of *Philanthus multimaculatus* (Hymenoptera: Sphecidae) with a review of territoriality in male sphecids. *Anim. Behav.* 23(4): 889-895.
1975b. The behavior of western cicada-killer males *Sphecius grandis* (Sphecidae, Hymenoptera). *J. Nat. His.* 9: 561.
- ALCOCK, J. ET AL.
1978. The ecology and evolution of male reproductive behavior in the aculeate Hymenoptera. *Zoo. J. Linn. Soc.* 64: 293-326.
- BAKER, R. R.
1972. Territorial behavior of the nymphalid butterflies, *Aglais urticae* (L.) and *Inachis io* (L.). *J. Anim. Ecol.* 41: 453-469.
- BARASH, D. P.
1977. *Sociobiology and Behavior*. Elsevier: New York.
- BOHART, R. M. AND E. E. GRISSELL
1975. California wasps of the subfamily Philanthinae (Hymenoptera: Sphecidae). *Bull. of the California Insect Survey, Volume 19*. University of California Press.
- BOHART, R. M. AND P. M. MARSH
1960. Observations on the habits of *Oxybelus sericeum* Robertson (Hymenoptera: Sphecidae). *Pan-Pac. Ent.* 36: 115-118.
- BOHART, R. M. AND A. S. MENKE
1976. *Sphecid Wasps of the World*. Berkeley: University of California Press.
- BREED, M. D., C. M. HINKLE AND W. J. BELL
1975. Agonistic behavior in the german cockroach, *Blattella germanica*. *Z. Tierpsychol.* 39: 24-32.
- BROWN, J. L.
1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 6: 160-169.
1975. *The Evolution of Behavior*. New York: W. W. Norton and Co., Inc.

- BUTLER, C. G.
1970. Chemical communication in insects: behavior and ecologic aspects. Pp. 36-78 in *Advances in Chemoreception, Vol. 1, Communication by Chemical Signals*. J. W. Johnson and A. Turk eds. New York: Appleton-Century-Crofts.
- EDMUNDS, J.
1976. The defensive behavior of Ghanaian praying mantids with a discussion of territoriality. *Zoo. J. Linn. Soc.* **58**: 1-37.
- EICKWORT, G.
1977. Male behavior in the mason bee *Hoplitus anthocopoides* (Hymenoptera: Megachilidae). *Anim. Beh.* **25**(3): 542-554.
- EVANS, H. E.
1966. *The Comparative Ethology and Evolution of the Sand Wasps*. Harvard Univ. Press: Cambridge, Mass. xiv + 526 pp.
1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. *Bull. Mus. Comp. Zool.* **140**(7): 451-511.
1975. Nesting behavior of *Philanthus albopilosus* with comparisons between two widely separated populations. *Ann. Amer. Ent. Soc.* **68**(5): 888-892.
- EVANS, H. E. AND K. M. O'NEILL
1978. Alternative mating strategies in the digger wasp *Philanthus zebratus* Cresson. *Proc. Nat. Acad. Sci.* **75**(4): 1901-1903.
- FLETCHER, D. J. C. AND J. M. BRAND
1968. Source of the trail pheromone and method of trail laying in the ant *Crematogaster peringueyi*. *J. Insect Physiol.* **14**: 783-88.
- GWYNNE, D. T.
1978. Male territoriality in the bumblebee wolf, *Philanthus bicinctus* Mickel (Hymenoptera: Sphecidae): Observations on the behavior of individual ♂♂. *Z. Tierpsychol.* **47**: 89-103.
- GWYNNE, D. T. AND K. M. O'NEILL
Sex-biased predation as a result of male territoriality in *Philanthus* (Hymenoptera: Sphecidae). In press, *J. Kans. Ent. Soc.*
- HOOKE, A. W.
1978. Sex, territoriality and biology of *Oxybelus sericeus* Robertson (Hymenoptera: Sphecidae). M.S. Thesis, University of Georgia.
- HUMASON, G. L.
1967. *Animal Tissue Techniques*. 2nd ed. San Francisco: W. H. Freeman and Co.
- HARRINGTON, H. D.
1964. *Manual of Plants of Colorado*. 2nd ed. Sage Books, Chicago.
- LIN, N.
1963. Territorial behavior in the Cicada Killer Wasp, *Sphecius speciosus* (Drury) (Hymenoptera: Sphecidae). *Behaviour* **XX**(1-2): 115-133.
- MICHENER, C. D.
1974. *The Social Behavior of Bees*. Cambridge, Mass: Harvard University Press.
- MORRIS, G. K.
1971. Aggression in male conocephaline grasshoppers (Tettigoniidae). *Anim. Behav.* **19**(1): 132-137.

- PECKHAM, D. J.
1977. Reduction of miltogrammine cleptoparasitism by male *Oxybelus subulatus* (Hymenoptera: Sphecidae). *Ann. Ent. Soc. Amer.* **80**(6): 823.
- PLISKE, T. E.
1975. Courtship behavior and use of chemical communication by males of certain species of ithomiine butterflies (Nymphalidae: Lepidoptera). *Ann. Ent. Soc. Amer.* **68**(6): 935.
- SHOREY, H. H.
1977. The adaptiveness of pheromone communication. *Proc. XV Int. Congress of Entomology*.
- SIMON-THOMAS, R. T. AND E. P. R. POORTER
1972. Notes on the behavior of males of *Philanthus triangulum* (F.) (Hymenoptera: Sphecidae) *Tijdschrift Voor Entomologie, Deel 115, AFL.* 2,141-151.
- SOWER, L. L. ET AL.
1973. Sex pheromones of Lepidoptera. XLI. Factors limiting potential distance of sex pheromone communication in *Trichoplusia ni*. *Ann. Ent. Soc. Amer.* **66**(5): 1121-1122.
- STEINER, A. L.
1978. Observations on spacing, aggressive and lekking behavior of digger wasp males of *Eucerceris flavocincta* (Hymenoptera: Sphecidae; Cercerini). *J. Kans. Ent. Soc.* **51**(3): 492-498.
- WILSON, E. O.
1971. *The Insect Societies*. Cambridge, Mass.: Harvard University Press.

REDISCOVERY OF *SCOLEBYTHUS MADECASSUS*,
WITH A DESCRIPTION OF THE MALE AND OF
THE FEMALE STING APPARATUS
(HYMENOPTERA: SCOLEBYTHIDAE)

BY HOWARD E. EVANS,¹ CHARLES KUGLER,²
AND WILLIAM L. BROWN, JR.²

INTRODUCTION

Scolebythus madecassus was described by Evans (1963) from a single female taken by Wulsin at Mandritsara, Madagascar. It is the monotype of the genus *Scolebythus*, which in turn is the type genus of family Scolebythidae, a small and rare taxon related to Bethyliidae, containing two other monotypic genera in addition to *Scolebythus*: *Clystopsenella* (widespread in Brasil) and *Ycaploca* (South Africa and Australia). Females and males were known for all of these genera except *Scolebythus*, in which only the female holotype has been collected until now (Evans 1963, Nagy 1975, Day 1977).

During February 1977, one of us (WLB) found six living specimens of *Scolebythus madecassus* in a single small piece of rotten wood in disturbed rain forest along the road south from Andasibé (formerly Périnet), Madagascar, about 1 km from the railroad station and hotel. One of the females among these has been compared with the holotype (MCZ) by WLB, and is considered to be conspecific.

The collection was made at about 14.00 hr, just at the beginning of a heavy thundershower, on a heavily shaded part of the forest floor, where WLB was searching for ants. A small, very rotten stick, about 15 cm long by 3 cm thick, was picked up out of the leaf litter and twisted by hand, so that one end of the stick was split open. A small black wasp, appearing in life like a large, long-necked bethylid, was found in the large, irregular chamber thus breached;

¹Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523.

²Department of Entomology, Cornell University, Ithaca, N.Y. 14853. Present address: Department of Biology, Radford University, Radford, VA 24142.

A report of research from the Cornell University Agricultural Experiment Station. Research supported in part by National Science Foundation Grant DEB 75-22427.

Manuscript received by the editor May 18, 1979.

the wasp stayed still, clinging to the wall of the chamber, but when picked out with finger and thumb, it stung the thumb, producing a sting about like that of a honeybee in intensity of pain and duration. For a few seconds the wasp eluded capture and ran slowly over the captor's hands, without attempting to fly. It was soon put into alcohol.

Next, the other end of the stick was twisted open, though without much expectation of finding anything — unfortunately, because in the darkness and confusion of the storm's beginning, it was not seen what part of the stick's contents were dropped on the ground and lost. What was found within were five more of the wasps, all resting in one large, irregular, continuous chamber or hollow. Some ran slowly over the collector's hands before being put into a plastic bag with the remains of the stick, and it is not known whether there had been more wasps that escaped clean away without being seen. Later indoor examination of the fragments of rotten stick turned up only the five adult wasps (four females and one male) in addition to the one female put in alcohol at the collection site.

The significance of this aggregation is unknown. The wasps are fully pigmented, and do not seem to have been associated with cocoons or large prey remains. They were resting together in hollows (beetle or millipede burrows?) much larger than their own bodies. Perhaps this was a "sleeping aggregation" during daylight hours (or rainy weather). In temperate areas, certain Bethyidae form clusters under the bark of trees during the winter (e.g., *Holepyris habilis*, Evans 1977).

There is also the remote possibility that *Scolecbythus* is at some relatively advanced stage of presocial behavior. The unfortunate circumstance that much of the contents of the stick were dropped and lost prevents us from knowing whether eggs or small brood, or possible small prey, may have been present. One of the females, chosen at random, was dissected, and the ovaries proved to contain a number of elongate ova. It seems useless to speculate further about these matters without more evidence, but it is worth emphasizing that the kind of aggregation observed is unusual and should be investigated from the life-history and behavioral points of view.

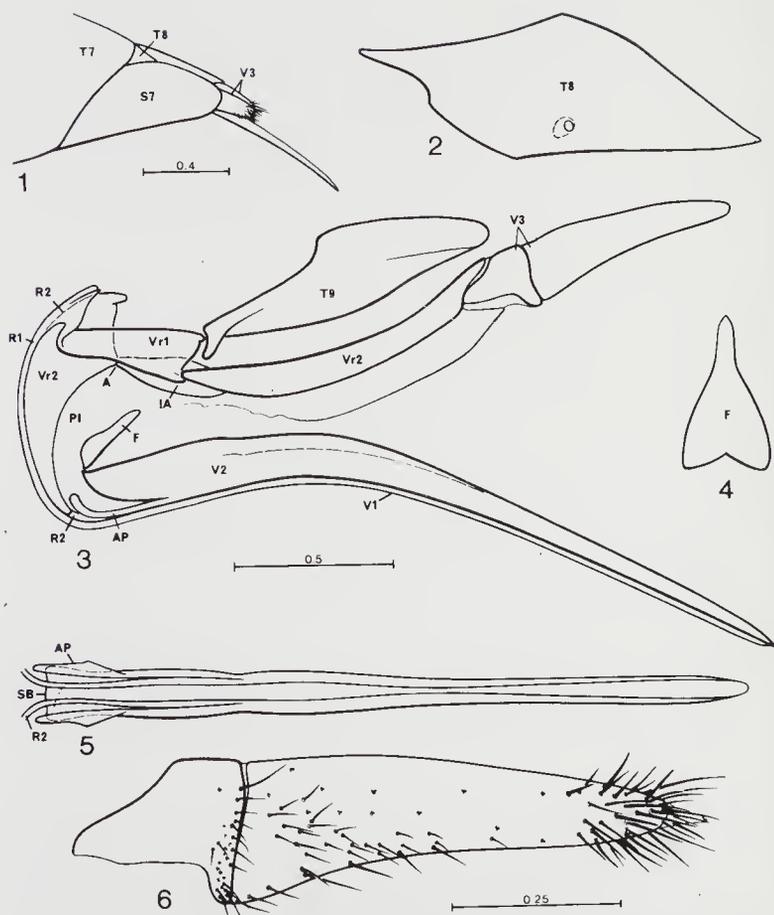
STING APPARATUS (Figs. 1-6)

The following description is based on a single specimen, prepared as described in Kugler (1978). The terminology is that of Daly

(1955) and Oeser (1961), but other commonly used synonyms are given as well. Numbers of abdominal, rather than metasomal, segments are used throughout.

Apparatus not completely internalized; sides of sternum 7 large, enclosing all but a small triangle of tergum 8 and tips of third valvulae and aculeus (Fig. 1). Eighth tergum (spiracular plate) (Fig. 2) subconical in dorsal view, not reduced mesad, with heavy antecostal ridge that terminates anterolaterally in long acute processes. Ninth tergum (quadrate plates) (Fig. 3) completely divided medially by membrane, narrow (max W/max L = 35%) moderately sclerotized, apodeme prominent only in upper half of length. No tenth tergum (anal plate). First valvifers (triangular plates, gonocoxites 8) (Fig. 3) long and slender; attached to near the apex of first ramus, but slung beneath it on a narrow stalk. First valvulae (lancets, gonapophyses 8) (Fig. 3) long, very slender, acute; each with a large proximal valve and a smaller, weaker distal valve; apex with a single small barb and 3 tiny denticles. Dorsal lamina (above groove) sclerotized only in distal third of length from valves. Second valvifers (oblong plates, gonocoxites 9) (Fig. 3) hinged between the dorsal and ventral arms. Dorsal arm long and narrow, its ventral edge grading into membrane cephalad; intervalvifer articulations with 23 and 27 trichoid sensilla. Ventral arm curved and evenly tapered to articular process of sting; second rami with 63 and 67 trichoid sensilla present on all but extreme ends. Second valvulae (sting, gonapophyses 9) (Fig. 3) moderately arched so that tip is directed obliquely ventrad. Profile tapers evenly to tip, which is about twice as wide as high and is free of ridges and barbs. Placoid or coeloconic sensilla present along caudal 45% of length, increasingly dense apicad. Sting base truncate, with rounded shoulders when seen from below (Fig. 5), not arched when viewed from the front. Articular processes long, slender and curved. Furcula (Figs. 3, 4) with short, blunt ventral arms that do not curve over sides of sting base. Third valvulae (gonostyli) (Figs. 3, 6) 2-segmented, both parts well sclerotized and with numerous trichoid and basiconic sensilla.

The morphology of the *Scolebythus madecassus* sting apparatus supports the close association of the Scolebythidae with the Bethyliidae (Evans, 1963; Brothers, 1975), rather than with Sapygidae or Anthoboscinae (Evans, 1963). The presence of a furcula and postincision (incisura postarticularis of Oeser), and lack of socii (pygostyles, cerci) separates *Scolebythus* from the terebrantes (though siricids and some proctotrupids lack socii) (Oeser, 1961,



Figs. 1-6. Sting apparatus of *Scolobythus madecassus*. 1. Lateral and slightly dorsal view of end of abdomen of female. 2. Lateral view of eighth abdominal tergum. 3. Lateral view of sting apparatus. 4. Anterior view of furcula. 5. Ventral view of second valvulae (sting). 6. Lateral view of third valvula (gonostylus). Figures 2, 3 and 5 to same scale; 4 and 6 to same scale, all in millimeters. A, articulation of dorsal and ventral arms of second valvifer; AP, articular process; F, furcula; IA, intervalvifer articulation; PI, postincision (incisura postarticularis); R1, first ramus; R2, second ramus; S7, seventh abdominal sternum; SB, sting base; T7, T8, T9, seventh, eighth and ninth abdominal terga; V1, first valvula (lancet); V2, second valvulae (sting); V3, third valvula (gonostylus); Vr1, first valvifer (triangular plate); Vr2, second valvifer (oblong plate).

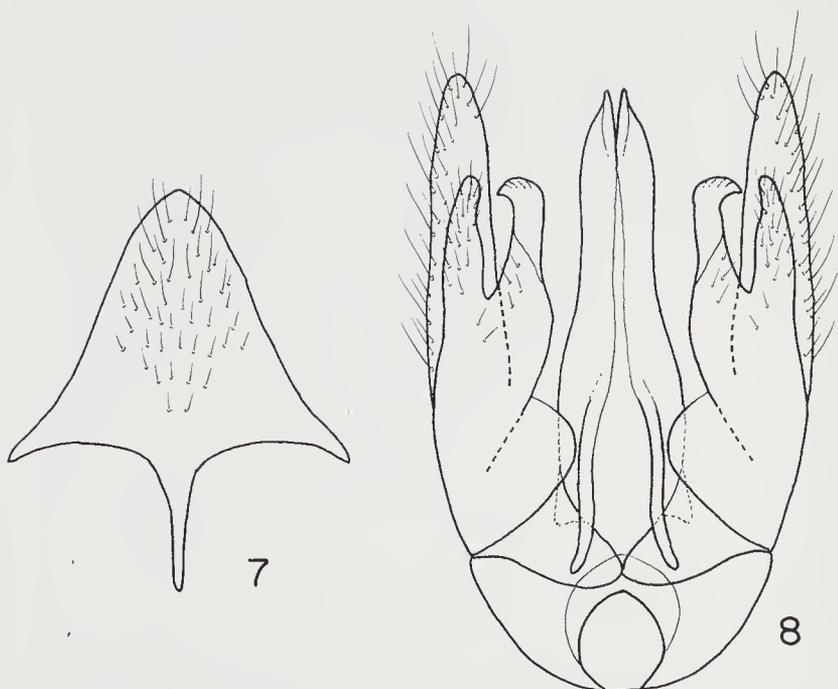
1962). Then the incomplete closure of the abdomen by the seventh segment and the articulated second valvifer separates *Scolebythus* from other aculeates, and its half-cone shaped eighth tergum places it more specifically with the Bethylidae, rather than the Cleptidae or Chrysididae (Zander, 1899; Oeser, 1961; Brothers, 1975). The affinity of the bethylids and *Scolebythus* can clearly be seen by comparing this description with that of *Cephalonomia* sp. (Oeser, 1961:74-75, 119; figs. 101-105). The degree of internalization of the apparatuses is the same, as are the shapes of the seventh sterna and eighth terga. Also similar are the ninth hemitergites, the first and second valvifers, and the first and second valvulae. *Cephalonomia* differs in having a more reduced apodeme on the ninth tergum, 1-segmented third valvulae, a distinctly V-shaped furcula, a somewhat differently shaped sting base, and long, narrow processes that extend from the dorsal arm of each second valvifer to the fulcral processes of the sting.

DESCRIPTION OF MALE (Figs. 7-8)

The single male is smaller than any known female, measuring 5.5 mm in length, the fore wings 4.1 mm (body length of the females varies from 7 to 9 mm). Color of body, appendages, and wings similar to female. Mouthparts and clypeus as in female; antennae 13-segmented, very slightly more slender than in female, but similar in length of individual segments and in total length. Temples less well developed than in female, and head not much produced above eye tops, the vertex forming a smooth arc between eye tops. Minimum distance between eyes $1.1 \times$ eye height, inner orbits closest near the middle, as in female. Thorax essentially as in female in all details, including legs and wings; scutellum with a well formed basal transverse groove (this is also true in the females; see below).

Abdomen slightly more slender than in female, with 7 distinct segments. Socii (pygostyles) absent; subgenital plate tongue-shaped (Fig. 7). Aedeagus large, with a pair of acute apical processes; parameres slightly exceeding the aedeagus, slender and somewhat hirsute; volsellae with the cuspis finger-like, digitus expanded and acute lateroapically (Fig. 8).

The subgenital plate resembles closely that of *Clystopenella longiventris*, as figured by Day (1977). The genitalia also resemble



Figs. 7-8. Male terminalia of *Scolebythus madecassus*, ventral aspect. 7. Subgenital plate. 8. Genitalia.

that species, except that the parameres are more elongate. The genitalia of *Ycaploca evansi* as figured by Nagy (1975) appear to lack one element in the volsella, but they are otherwise basically similar. The genitalia of three genera of Scolebythidae thus appear to be very similar and of the basic bethylid type. The lack of socii is also a bethylid feature; these structures appear to be present in most Scolioidea and most other Aculeata.

One further point needs to be made. In the original description of *Scolebythus* it was stated that the scutellum has a "pair of widely separated, transverse pits". In fact, all specimens in the present series have a transverse groove at the base of the scutellum. The "transverse pits" represent a misinterpretation of the structure of the type specimen of *madecassus*, where the groove appears to be closed except laterally. This feature cannot be used to separate *Scolebythus* and *Ycaploca*, as Nagy (1975) has done, but one must rely on the

presence of a prominence between the eyes and the much shorter malar space in the latter genus.

REFERENCES CITED

- BROTHERS, D. J.
1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. Univ. Kans. Sci. Bull. **50**: 483-648.
- DALY, H. V., JR.
1955. A comparative study of the sting of aculeate Hymenoptera. Unpublished M.A. thesis, University of Kansas; pp. i-iv, 1-67, + 7 pl.
- DAY, M. C.
1977. A new genus of Plumariidae from southern Africa, with notes on Scolebythidae (Hymenoptera: Chrysidoidea). Cimbebasia, Windhoek, Namibia (A) **4**: 171-177.
- EVANS, H. E.
1963. A new family of wasps. Psyche **70**: 7-16.
1977. A revision of the genus *Holepyris* in the Americas (Hymenoptera: Bethyloidea). Trans. Amer. Ent. Soc. **103**: 531-579.
- KUGLER, C.
1978. A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). Stud. Entomol. **20**: 413-548.
- NAGY, C. G.
1975. A new genus of Scolebythidae (Hymenoptera) from South Africa and Australia. J. Ent. Soc. S. Africa **38**: 75-78.
- OESER, R.
1961. Vergleichend-morphologische Untersuchungen über den Ovipositor der Hymenopteren. Mitt. Zool. Mus. Berlin **37**: 3-119.
1962. Der reduzierte Ovipositor von *Pseudogonalos hahni* (Spin.) nebst Bemerkungen über die systematische Stellung der Trigonalidae. Tagungsber. Deutsch. Akad. Landwirts.-wiss. **45**: 153-157.
- ZANDER, E.
1899. Beiträge zur Morphologie des Stachelapparates der Hymenopteren. Z. Wiss. Zool. **66**: 289-333.

LIFE HISTORY AND ECOLOGY OF
BAETISCA BAJKOVI NEAVE, IN
BEECH FORK OF TWELVEPOLE CREEK,
WAYNE COUNTY, WEST VIRGINIA
(EPHEMEROPTERA: BAETISCIDAE)¹

BY DWIGHT L. CHAFFEE² AND DONALD C. TARTER³

The primary objective of this study was to investigate the life history and ecology of the mayfly *Baetisca bajkovi* Neave in Beech Fork of Twelvepole Creek, Wayne County, West Virginia. Several investigators, including Traver (1931), McDunnough (1932), Berner (1940, 1955), Edmunds (1960), Schneider and Berner (1963), Lehmkuhl (1972), Pescador and Peters (1971, 1974), Morris (1976), and Tarter and Kirchner (1978), have reported taxonomical and ecological information on the genus *Baetisca* in North America.

TAXONOMY AND DISTRIBUTION

The family Baetiscidae is endemic in North America and contains only the genus *Baetisca*. The genus was established by Walsh (1862). Neave (1934) and Daggy (1945) described the nymph and imago, respectively, of *B. bajkovi*. The Nearctic distribution of *B. bajkovi* includes Alberta, Manitoba, and Saskatchewan in Canada (Neave, 1934 and Lehmkuhl, 1972), and Illinois, Indiana, Minnesota (Burks, 1953), Wisconsin (Hilsenhoff, 1970), and West Virginia in the United States. Chaffee (1978) recorded it from 17 counties in West Virginia.

The *B. bajkovi* nymphs were found mostly in a stream substrate that was predominantly small stones and sand, and with leaf litter and other plant material present. They were found only in the riffles, and were most frequently collected from water 10 to 26 cm in depth.

¹Part of a thesis submitted by the first author to the Graduate School, Marshall University, in partial fulfillment of the requirements for the degree of Master of Science, December 1978.

²Box 72, Spring Branch Rd., Ironton, Ohio 45638

³Dept. of Biological Sciences, Marshall Univ., Huntington, W.Va. 25701.

*Manuscript received by the editor May 5, 1979.

MATERIALS AND METHODS

Beech Fork in Wayne County, West Virginia, is the study area. It is 45.9 km long and drains moderate to steep slopes of mesophytic hardwood forest. It originates at an elevation of approximately 343 m and flows northwesterly to enter Twelvepole Creek at an elevation of 165 m near Lavalette, West Virginia. The average gradient is 3.9 m/km. The study site is located at 38° 18' 57" N latitude and 82° 25' 22" W longitude, and is 3.7 km above the mouth of Beech Fork. It is a slow to medium speed riffle 55 m long that averages 5.2 m in width and 25.4 cm in depth. The substrate consists of large rocks and stones, and a mixture of gravel, sand, and silt. The more dominant species of the riparian forest are Boxelder *Acer negundo* L., Silver Maple *A. saccharinum* L., Black Walnut *Juglans nigra* L., Sycamore *Platanus occidentalis* L., and Slippery Elm *Ulmus rubra* Muhl.

Monthly sampling for *Baetisca bajkovi* nymphs began in June 1976 and continued through May 1977. Sampling was accomplished by starting at the lower end of the riffle and working upstream using a long handled bottom dredge with a fine mesh net (60 threads per inch). The dredge was raked along the bottom while the substrate was disturbed and loosened upstream allowing the organisms to drift into the net. The nymphs were immediately preserved in 70 percent ethanol.

Water temperature was measured each month with a mercury thermometer. The thermometer was placed in the riffle at a depth of approximately 5 cm. Determinations of dissolved oxygen concentration, bicarbonate alkalinity, and total hardness were carried out with a Hach chemical kit, Model AL-36-WR. The pH was measured with a Corning Model 5 pH meter. The oxygen saturation values were obtained using Rawson's nomogram (Welch, 1948).

Length-frequency distributions were recorded for the nymphs to help determine the duration of the life cycle. Histograms were arranged in 1 mm size groups for each month with the males and females combined. The body length of the nymphs, from the anterior-most tip of the head to the base of the caudal filaments, was measured with a dial Vernier caliper under a dissecting microscope to the nearest 0.1 mm. Head width measurements were used to show the monthly index of growth. The head widths (including eyes) were measured to the nearest 0.01 mm with an ocular micrometer in a Bausch and Lomb dissecting microscope. A population range dia-

gram was used to show the monthly variation in head widths (Hubbs and Perlmutter, 1942). The growth rate of the nymphs (sexes combined) was determined by using the mean monthly head width measurements.

Relative abundance of foregut contents of the nymphs was determined for each month. Five nymphs were selected at random from each month's sample for analysis. Micro-dissecting scissors were used to sever the head and make an incision along the midline of the ventral surface. The foregut was then severed from the intestine and excised. The foregut contents were extruded onto a glass slide and examined under a microscope with a Whipple ocular grid at 430 \times magnification. Five grids or fields were randomly selected to be examined for each nymph. The percentage of composition for each food item was determined by figuring the percentage of small grid squares within each field that contained each of the different food items. Percentage composition was determined for the following food items: (1) plant detritus, (2) diatoms, (3) filamentous algae, and (4) mineral particles.

The sex of the nymphs was determined by the size and shape of the eyes. The eyes of the male are much larger and positioned more closely together than those of the female. The chi-square test was applied to the nymphs to determine any significant departure from the 1:1 ratio at the 0.05 confidence level.

The last instar nymphs collected in April and May were returned to the laboratory for rearing. They were observed closely, and the dates and times of emergence for both the subimagos and imagos were recorded.

The fecundity of *B. bajkovi* was determined by direct egg counts of the adult females using a Bausch and Lomb dissecting microscope. Using micro-dissecting scissors the body cavity was carefully opened with a long dorsal incision. Both ovaries were then carefully excised and the eggs extruded into a culture dish for counting. Size measurements were made on 25 eggs from each female with an ocular micrometer in a dissecting microscope to the nearest 0.01 mm. The external morphology of the eggs was also viewed under a microscope at 100 \times magnification.

RESULTS AND DISCUSSION

Stream Environment. The mean annual water temperature in Beech Fork during the study period was 13.5 C. The monthly ex-

tremes ranged from 3.3 to 23.3 C in January and July respectively. The mean hydrogen ion concentration (pH) was 7.1 with a range of 6.7 to 7.5 in August and December respectively. The mean dissolved oxygen concentration was 8.9 mg/l and ranged from 6.3 to 11.0 mg/l, August and January respectively. The oxygen saturation mean was 83.8 percent and ranged from 73.0 percent in August to 95.0 percent in April. The mean bicarbonate alkalinity concentration was 47.5 mg/l with a range of 30.0 to 65.0 mg/l, February and September respectively. The mean total hardness was 59.6 mg/l with a range of 50.0 to 70.0 mg/l, January and October respectively.

Nymphal Length-Frequencies. Length-frequency histograms of the *B. bajkovi* nymphs are shown in Figure 1. The smallest and earliest nymph was collected in July 1976 and measured 0.76 mm in length. The largest nymph, a female with a length of 10.4 mm, was collected in May 1977. The monthly length distributions, the absence of nymphs in June, and the total absence of mature nymphs in the late summer, fall, and winter months indicates a one year (univoltine) life cycle. Similar findings on the life cycle from other studies in the genus *Baetisca* have been reported by Traver (1931), Berner (1955), Pescador and Peters (1971, 1974), and Lehmkuhl (1972).

Nymphal Growth. Head width measurements of *B. bajkovi* nymphs showing the monthly progression of growth are illustrated with a population range diagram (Figure 2.) Head widths ranged from the smallest nymph in July (0.31 mm) to the largest male (2.67 mm) and the largest female (2.81 mm) in May. Figure 2 also illustrates the univoltine life cycle and shows a definite female size superiority.

The greatest growth rate exhibited at any time during the life cycle was 80.0 percent which occurred from July to August when the mean monthly head width increased from 0.45 to 0.81 mm. The lowest growth rate (1.3%) occurred from April to May when the mean monthly head width increased from 2.32 to 2.35 mm. Nymphal growth rate was also very low (3.5%) from January to February when the lowest water temperatures (3.3 and 4.4 C) were recorded for the study.

Nymphal Food Habits. The relative abundance of foregut contents of *B. bajkovi* is given in Table 1. The nymphs are detritivorous with almost two-thirds (65.3%) of the diet composed of plant and leaf detritus. Diatoms were the next most abundant item (17.1%) in

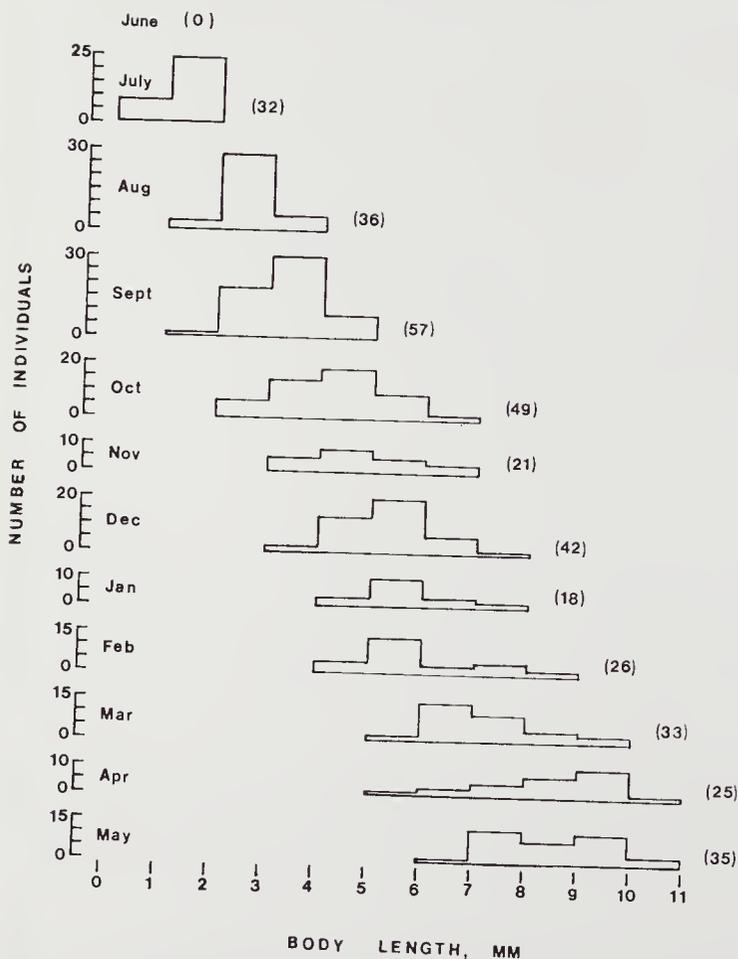


Figure 1. Length-frequency histograms showing monthly distributions of *B. bajkovi* nymphs, Beech Fork of Twelvepole Creek, Wayne County, West Virginia, 1976-77. Number of individuals collected each month is given in parentheses.

the diet. The diatoms most numerous in the foreguts, and in monthly occurrence, were *Navicula* spp., *Cymbella* sp., *Diatoma* sp., and *Synedra* sp. *Navicula* was the only diatom present in the foregut contents every month. The recognizable filamentous algae found in small amounts were *Cladophora* sp., *Spirogyra* sp., and *Ulothrix* sp. Mineral particles were always plentiful, but it is not

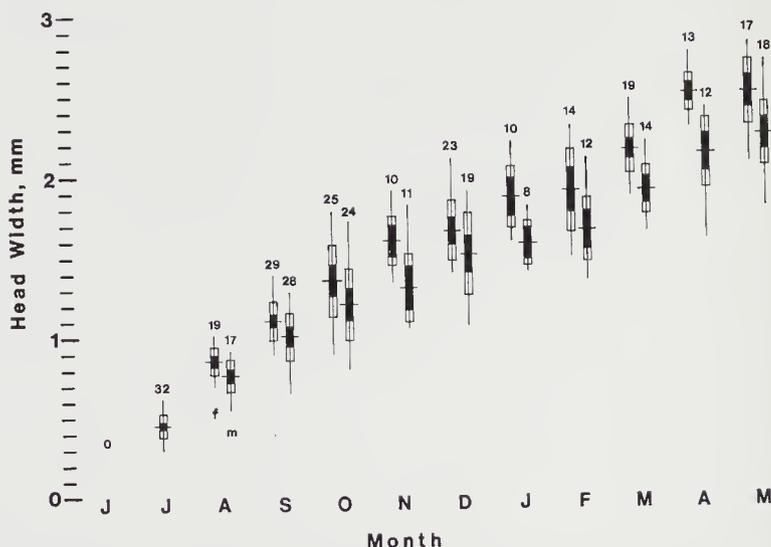


Figure 2. Population range diagram showing monthly head width variations in *B. bajkovi* nymphs, Beech Fork of Twelvepole Creek, Wayne County, West Virginia, 1976-77. Vertical lines = range, horizontal lines = mean, open rectangles = one standard deviation, dark rectangles = two standard errors of the mean, numbers = sample size, f = females, m = males.

known to what extent they may be a part of the regular diet or ingested accidentally along with other food items. The most noticeable monthly variations in diet composition were the increase in plant detritus during the fall months, probably due to the large amount of leaves in the stream, and the increase in the abundance of diatoms in the spring months.

Nymphs of other mayfly species feeding on plant detritus, diatoms, and algae have been reported by Minshall (1967), Pescador and Peters (1974), Richardson and Tarter (1976), and Hamilton and Tarter (1977).

Nymphal Sex Ratio. The chi-square test on *B. bajkovi* nymphs showed no significant departure from the 1:1 sex ratio at the 0.05 confidence level. The test was applied to 163 males and 179 females collected from August through May. The July nymphs were too small to sex.

Adult Stage. Last instar *B. bajkovi* nymphs with wing pads developing were first collected from the stream April 26, and the last

nymph, a female, was collected May 17. They were reared in the laboratory, and the adults emerged from May 2 to May 26. All subimagos emerged between 9:00 AM and 7:00 PM with the imagos emerging 13 to 25 hours later.

Emergence data for other species of the genus *Baetisca* have been reported by other authors. Traver (1931) observed subimagos of *B. carolina* emerging between 8:00 AM and 5:30 PM with the imagos emerging 21 to 30 hours later. Berner (1955) observed subimago emergence of *B. escambiensis* between 9:30 AM and 1:30 PM and found the imagos emerging 40 to 44 hours later. Pescador and Peters (1974), in studying *B. rogersi*, observed subimagos emerging from the stream between 8:30 AM and 2:30 PM, while the laboratory subimagos emerged between 10:00 AM and 8:30 PM. The imagos emerged 12 to 30 hours later.

Ovarian egg counts of 10 adult *B. bajkovi* females ranged from 1508 to 3158 eggs per individual; the mean was 2361. Pescador and Peters (1974) reported that the egg counts for *B. rogersi* ranged from 1500 to 2727 per individual, with the mean being 2168.

The eggs of *B. bajkovi* are subspherical, and the average measurements were 0.15×0.19 mm. The eggs are greenish in color with an

Table 1. Relative abundance of foregut contents of *Baetisca bajkovi* nymphs, Beech Fork of Twelvepole Creek, Wayne County, West Virginia, 1976-77.

Month	Plant Detritus (%)	Diatoms (%)	Filamentous Algae (%)	Mineral (%)
July	66.7	15.3	4.1	13.9
Aug.	68.7	12.9	4.3	14.1
Sept.	71.3	13.6	2.7	12.4
Oct.	72.6	13.2	2.1	12.1
Nov.	70.4	13.1	2.3	14.2
Dec.	63.7	11.8	2.9	21.6
Jan.	57.8	14.7	3.7	23.8
Feb.	59.7	19.3	2.8	18.2
Mar.	63.2	21.2	2.9	12.7
Apr.	63.5	23.5	1.2	11.8
May	59.8	29.9	0.8	9.5
Mean	65.3	17.1	2.7	14.9

adhesive layer present. Chorionic sculpturing was evident but the specific type was not determined.

REFERENCES CITED

- BERNER, L.
1940. *Baetisca rogersi*, a new mayfly from northern Florida. *Can. Ent.* **62**: 156-160.
1955. The southeastern species of *Baetisca* (Ephemeroptera: Baetiscidae). *Quart. J. Fla. Acad. Sci.* **18**: 1-19.
- BURKS, B. D.
1953. The mayflies, or Ephemeroptera, of Illinois. III. *Nat. Hist. Surv. Bull.* **26**: 1-216.
- CHAFFEE, D. L.
1978. Life history and ecology of *Baetisca bajkovi* Neave, in Beech Fork of Twelvepole Creek, Wayne County, West Virginia (Ephemeroptera: Baetiscidae). Unpub. Masters Thesis, Marshall Univ., Huntington, W.Va. 48 pp.
- DAGGY, R. H.
1945. New species and previously undescribed naiads of some Minnesota mayflies. *Ann. Ent. Soc. Amer.* **38**: 373-396.
- EDMUNDS, G. F.
1960. The mayfly genus *Baetisca* in western North America. *Pan-Pacific Ent.* **36**(2): 102-104.
- HAMILTON, D. A. AND D. C. TARTER.
1977. Life history and ecology of *Ephemerella funeralis* McDunnough (Ephemeroptera: Ephemerellidae) in a small West Virginia stream. *Amer. Midl. Nat.* **98**(2): 458-462.
- HILSENHOFF, W. L.
1970. Key to genera of Wisconsin Plecoptera (stonefly) nymphs, Ephemeroptera (mayfly) nymphs, Trichoptera (caddisfly) larvae. *Res. Rep. No.* **67**(3): 18-37. Department of Natural Resources, Madison, Wisconsin.
- HUBBS, C. L. AND A. PERLMUTTER.
1942. Biometric comparison of several samples, with particular reference to racial investigations. *Amer. Nat.* **76**: 582-592.
- LEHMKUHL, D. M.
1972. *Baetisca* (Ephemeroptera: Baetiscidae) from the western interior of Canada with notes on the life cycle. *Can. J. Zool.* **50**(7): 1015-1017.
- MCDUNNOUGH, J.
1932. New species of North American Ephemeroptera II. *Can. Ent.* **64**: 209-215.
- MINSHALL, J. N.
1967. Life history and ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae). *Amer. Midl. Nat.* **78**(2): 369-388.

- MORRIS, W. R.
1976. Ecological life history of *Baetisca* n. sp., Laurel Fork, Mingo County, West Virginia (Ephemeroptera: Baetiscidae). Unpub. M. S. thesis, Marshall Univ., Huntington, W.Va. 44 pp.
- NEAVE, F.
1934. A contribution to the aquatic insect fauna of Lake Winnipeg. Int. Rev. Hydrobiol. 31: 157-170.
- PESCADOR, M. L. AND W. L. PETERS.
1971. The imago of *Baetisca becki* Schneider and Berner. Fla. Ent. 54(4): 329-334.
1974. The life history and ecology of *Baetisca rogersi* Berner (Ephemeroptera: Baetiscidae). Bull. Fla. State Mus. Biol. Sci. 17(3): 151-209.
- RICHARDSON, M. Y. AND D. C. TARTER.
1976. Life histories of *Stenonema vicarium* (Walker) and *S. tripunctatum* (Banks) in a West Virginia stream (Ephemeroptera: Heptageniidae). Amer. Midl. Nat. 95(1): 1-9.
- SCHNEIDER, R. F., AND L. BERNER.
1963. A new southeastern species of *Baetisca* (Ephemeroptera: Baetiscidae). Fla. Ent. 46: 183-187.
- TARTER, D. C., AND R. F. KIRCHNER.
1978. A new species of *Baetisca* from West Virginia (Ephemeroptera: Baetiscidae). Ent. News 89(9-10): 209-213.
- TRAYER, J. R.
1931. The ephemerid genus *Baetisca*. J. N. Y. Ent. Soc. 39: 45-66.
- WALSH, B. D.
1862. List of Pseudoneuroptera of Illinois, contained in the cabinet of the writer, with descriptions of over forty new species and notes of their structural affinities. Proc. Acad. Nat. Sci. Phila. 13: 361-402.
- WELCH, P. S.
1948. Limnological Methods. McGraw-Hill Book Company, New York. 382 pp.

am
in
fig
Ne
g
gen
A
am
ins
Les
gen
com
Le
cor
et a
p
mit
three
Cim
T
H
Su
ce
m
m

DISPERSAL BY MALE DORYLINE ANTS IN
WEST AFRICA*

BY DENNIS LESTON

Agricultural Research and Education Center
University of Florida
Homestead, FL 33031

INTRODUCTION

Sausage-flies, the giant males of Old World doryline ants, are among the more conspicuous forms of tropical insect life, never failing to intrigue the observer by their numbers, size and bumbling flight. If we follow the conventional classification and include the New World Ecitonini within Dorylinae (*cf* Brown, 1973; Gotwald, 1977) there is a large literature—on the group's systematics, biogeography, and behaviour—but little of it quantitative.

At Legon, Ghana, 5°40' N, a 125 watt ultraviolet light-trap was run, the aim primarily to extend an investigation of seasonality in insects commenced earlier at Tafo, a little to the north (Gibbs and Leston, 1970). However, the facts collected on doryline flights fill a gap in our knowledge and can be viewed in several ecological contexts.

Legon was once forested and lies within the 'southern marginal' forest category of the scheme of Hall and Swaine (1976). It is today an area of derived savanna interspersed with gardens and small plots of food crops but some secondary forest survives about six miles distant. Climatological data for Accra, taken for over 30 years three miles south of Legon, are given in the form of a Leston-Gibbs climograph (Fig. 1) (Leston and Gibbs, 1971).

The original data and summary sheets are deposited, together with examples of the species collected, in the British Museum (Nat. Hist.), London.

Sudden heavy rain led to the breakdown of the trap on a few occasions: the missing samples were corrected for by dividing the numbers trapped in each 20-day period by the actual total of sampling days and adding this mean (or a multiple of it) to the total. The

*Florida Agricultural Experiment Stations Journal Series No. 1702
Manuscript received by the editor May 15, 1979.

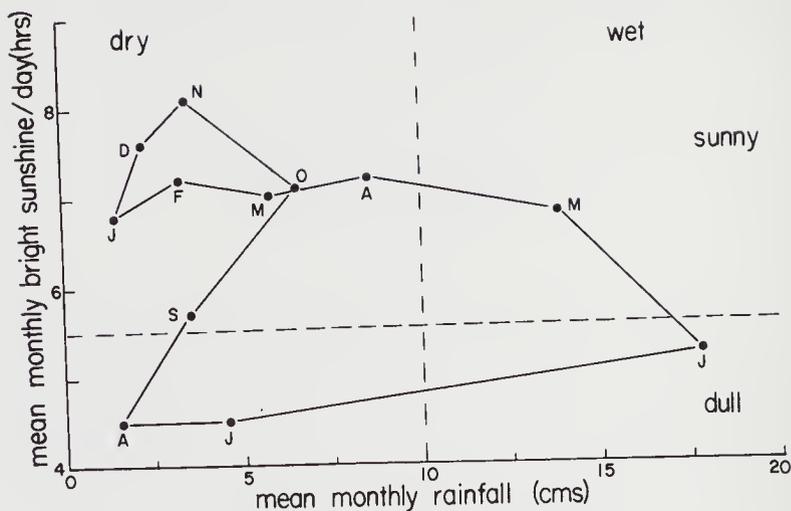


Fig. 1 Leston-Gibbs climograph for Accra, Ghana.

overall results, however, would have been the same even uncorrected.

The insects of this study are Dorylini. Aenictini were also sampled for a while but identification of the eight or nine species, distinguishable only by the male genital structures, was too complex and their study was abandoned.

RESULTS

The trap was run for 400 days (1730 hrs to 0600 hrs). The Dorylini collected are listed together with the corrected number of each:

1. <i>Alaopone atriceps</i> (Shuckard)	2470
2. <i>Typhlopone fulvus</i> Westwood	653
3. <i>Dorylus</i> sp 15	410
4. <i>Rhogmus fimbriatus</i> Shuckard	115
5. <i>Anomma nigricans</i> (Illiger)	88
6. <i>Dorylus</i> sp 14	7
7. <i>Dorylus</i> sp 16	4
8. <i>Dorylus</i> sp 19	3
9. <i>Rhogmus</i> sp 17	2
10. <i>Dorylus</i> sp 6	1
11. <i>Alaopone</i> sp 18	1
Total	3754

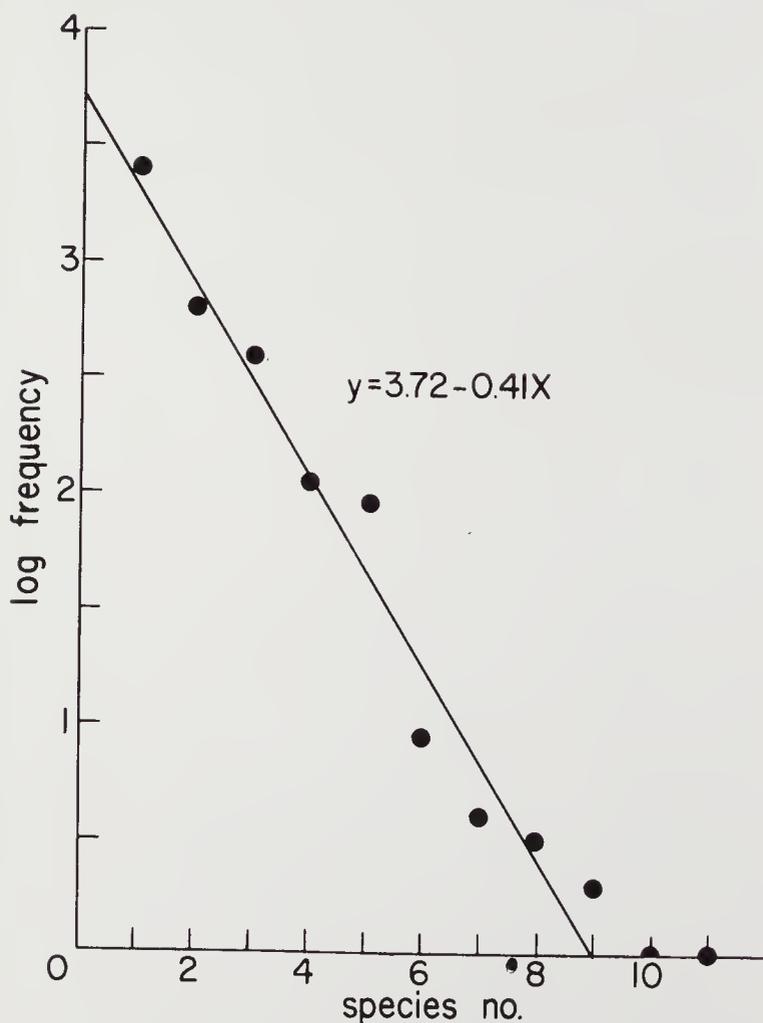


Fig. 2. Log frequencies (y) of the trapped species, species identification number (x) and the regression of y on x .

The number trapped of species 1 through 11 were transformed to logarithms and the regression coefficients calculated for y (frequency) on x (the species' number). (Fig. 2). There is a highly significant agreement with a log distribution hypothesis ($\chi^2 = 0.32$, $DF = 7$, $p > 0.99$).

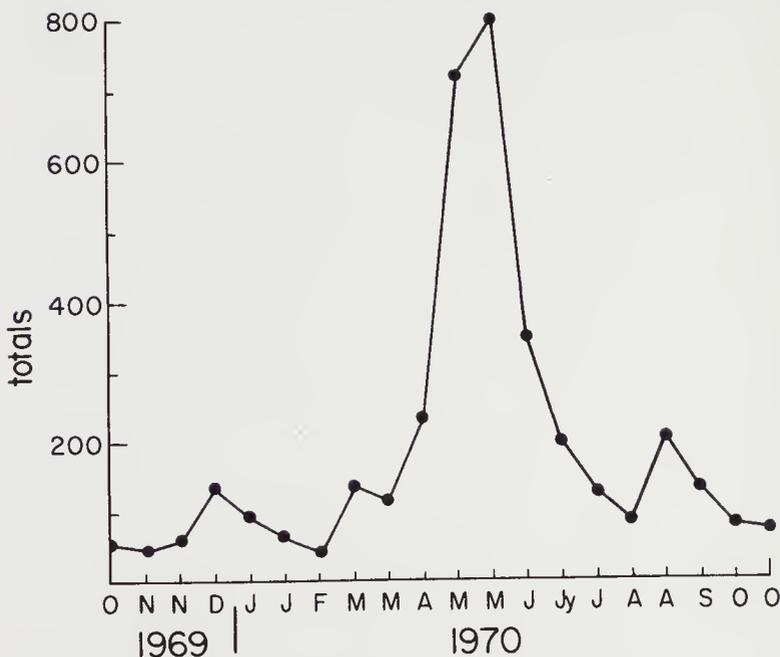


Fig. 3. Totals of male Dorylini trapped by an ultraviolet light trap at Legon, near Accra, grouped in 20-day classes.

The periodicity of the total sausage-flies captured, corrected and grouped in 20-day classes, is shown in Fig. 3. The five most abundant species accounted for over 99.5 percent of the entire catch and the leading four (97.18 percent), when their numbers are plotted (Fig. 4), show markedly similar periodicities. Kendall's index of concordance, W , was calculated, correcting for tied values:

$$n \text{ (number of sampling classes)} = 20$$

$$k \text{ (number of species)} = 4$$

$$W_2 = 0.51$$

$$\chi^2 = 38.76$$

$$DF = 19$$

$$0.01 > p > 0.001$$

The value of p confirms that the similarities could scarcely be due to chance. The fifth species, *Anomma nigricans*, was producing males, as were the first four, more or less throughout the year. However, its peak numbers occurred in mid-September through early October (Fig. 5), and not March to May as in the first four.

Besides the major annual period of abundance the species showed rhythmic pulsations in frequency. In April through June the periodicity was around 29 to 32 days, in December through February around a day or two less. The periodicities were clear cut in *Alaopone atriceps* and *Typhlopone fulvus* (Fig. 6), less obvious—because of the lower numbers taken—in *Dorylus* sp 15 and *Rhogmus fimbriatus*.

The trapped material was assessed in terms of the i^{th} species (Fig. 7). The first ten were amassed rapidly and were present by day 56, in the third sampling period (Fig. 4). However, the eleventh species

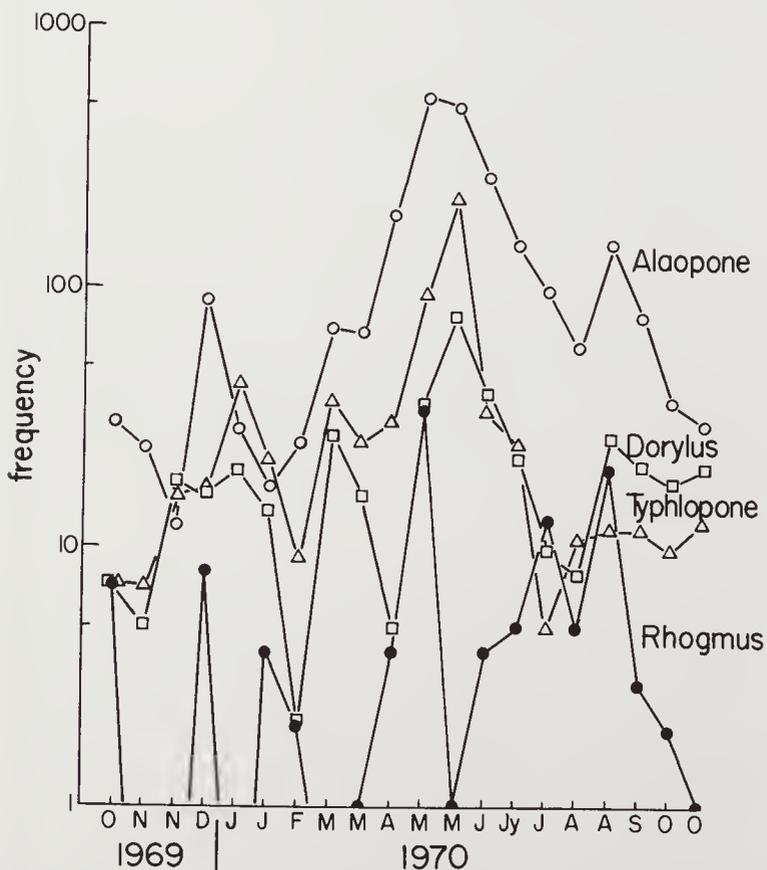


Fig. 4. Totals of the four most abundant species in the Legon samples, logarithmic, grouped in 20-day classes.

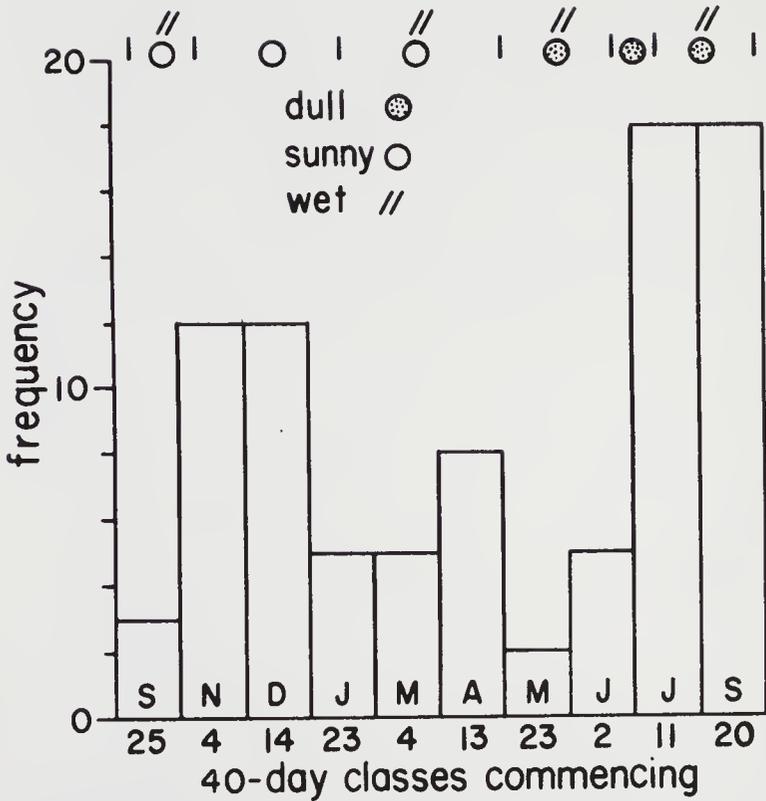


Fig. 5. Totals of *Anomma nigricans* trapped, in 40-day classes; with the seasons in the nearby forest zone indicated.

was caught after the trapping of a far greater number of individuals than extrapolation would have predicted: 3685 as against *c.* 180.

Table 1 gives the monthly rainfall and mean daily hours of bright sunshine per month for the period under review: by bright sunshine is meant sunshine as measured by a Campbell-Stokes' or similar apparatus. The rainfall and monthly totals of *Alaopone atriceps* were compared, using Spearman's rank correlation:

$$\begin{aligned}
 n &= 13 \\
 R &= 317 \\
 p &= > 0.1
 \end{aligned}$$

This confirmed what is suggested by inspection: rainfall and numbers of male dorylines are neither directly nor inversely associated, nor can a lagged correlation be detected.

However, there is a highly significant deviation from a random distribution pattern in the three components of Table 1 (extension of the median test (Siegel 1956): $\chi^2 = 16.15$, $DF = 3$, $p < 0.001$). There is in fact an association of peak numbers, both in *A. atriceps* and overall ant frequencies (Fig. 3), with the period of the year—late April through early June (Fig. 1)—when both mean sunshine and mean rainfall are relatively high. This is obscured in the data of Table 1 by October 1969 and January and February 1970 being wetter than usual.

DISCUSSION

Cyclic phenomena occur in all the New World dorylines studied (Schneirla, 1971, and works cited therein): brood production and a division of activity between well marked statary and nomadic phases are among the events in which regular periodicities are the

Table 1. Bright sunshine, rainfall and numbers trapped of *Alaopone atriceps*, corrected for missing samples and grouped in monthly classes.

	Mean bright sunshine/hrs per day	Rainfall cms	<i>A. atriceps</i> trapped
1969			
Oct	7.9	10.21	34
Nov	8.7	1.12	29
Dec	8.9	0.64	106
1970			
Jan	8.0	7.54	38
Feb	8.1	8.33	57
Mar	8.3	3.76	178
Apr	6.5	6.71	624
May	6.3	25.78	707
Jun	6.3	15.80	237
Jul	5.2	2.49	124
Aug	4.9	0.76	191
Sep	6.5	3.76	104
Oct	7.7	8.46	41

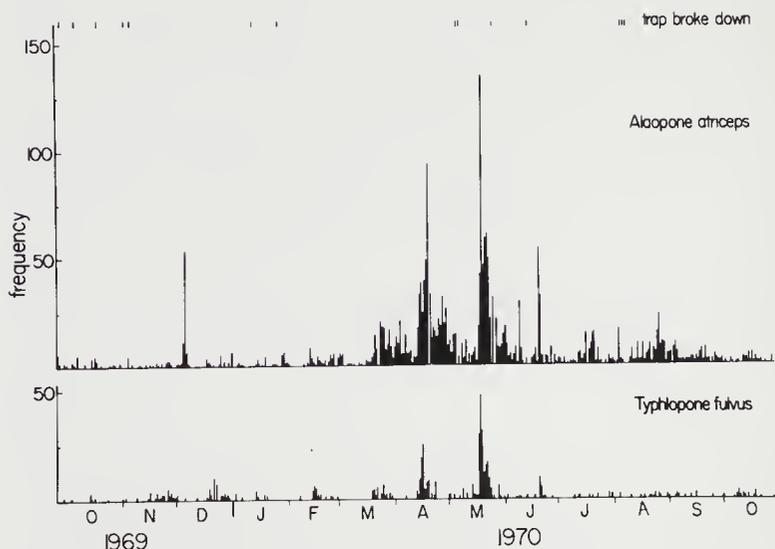


Fig. 6. Daily frequencies of the two most abundant species in the Legon trap samples, with days of missing samples indicated.

rule. However, in the Old World Dorylini examined—mainly in *Anomma*—Raignier and van Boven (1955) denied such cyclic behaviour to be present. My data (Figs. 3, 4) suggest 1) males are produced, at least by the five most common species, throughout the year, 2) there is a regular annual cycle in the timing of male flights, 3) this cycle is synchronous in the four most abundant species (and perhaps in all), 4) males are emitted about every 30 to 32 days between about March through September—around every 28 or 29 days in December through February.

Just as Rettenmeyer (1963) was able to confirm the presence of Schneirla cycles in a wide range of Neotropical and Nearctic Ecitonini species the present figures indicate that such cycles hold true in the Ethiopian Dorylini—and presumably too the Oriental, for they are for the most part congeners. But Raignier and van Boven were correct in noting the production of males throughout the year, confirmed by Haddow *et al.* (1966) through light-trap sampling. The phenomenon is still undetected in Ecitonini. Neither the observations of Rettenmeyer (1963) nor of Kannowski (1969) were conducted during a complete calendar year but the temporal spread of the latter's positive scoring of, for example, alate males of *Labidus*

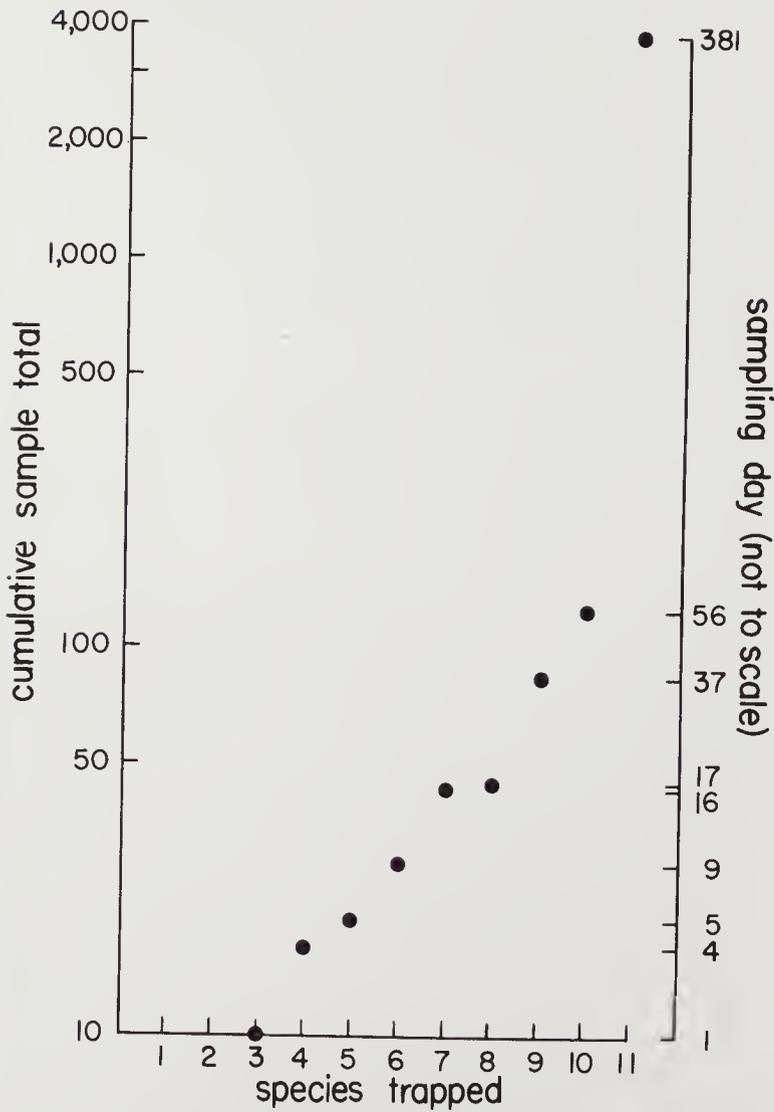


Fig. 7. Arrival days (not to scale), cumulative sample size (logarithmic) and the cumulative species trapped.

praedator (F. Smith)—March 7 to May 30—is suggestive either of the production of more than one sexual brood by the colonies or that each colony is out of step with its conspecifics.

An alternative interpretation of my figures is possible: each colony of a species could be out of phase with its neighbours, in which case each burst of alate males trapped would have come from a distinct colony. Field observations, however, suggest colonies of the surface foraging species—*Typhlopone fulvus* and *Anomma nigricans*—are too widely dispersed to support this hypothesis.

Except for *Anomma nigricans*, the common black driver ant of the forest zone (Haddow *et al.*, 1966), the species concerned are believed to be predominantly non-nomadic—even, it seems, *Typhlopone fulvus*, the common brown driver ant of the forest area (Wheeler 1922). There is no positive evidence at present for the cyclic emission of males to be associated with migratory periodicities, except in *Anomma* species (Raignier and van Boven, 1955).

That the period between peaks in April, May and June (Fig. 5) is longer than in December and January is to be expected: the months December through February are the hottest ones. But are these cycles of about 30 days in the emission of alate males the concomitant of an egg-to-egg cycle in worker brood production?

In their study of *Anomma* Raignier and van Boven (1955) note the period from 1st instar larva to alate adult males to occupy 40 to 52 days, to be followed by a preflight stage of 10 days. They give no information on the duration of the egg stage and their account is somewhat obscured by a confusing larval nomenclature, but they conclude broods of males take twice as long to develop as broods of females and that a colony with male brood remains at one place for twice as long as the normal. This confirms my view that Raignier and van Boven are wrong in denying the existence of cycles in *Anomma*. The data can be interpreted as showing a 30-days cycle to be present, male production occupying two consecutive cycles. That a colony may produce multiple out-of-phase broods is not excluded by this theory.

Comparing the flights of alate male *Anomma* with those of other, non-doryline, species, Raignier and van Boven state of the former '... ces vols ne sont pas des vols nuptiaux mais uniquement des vols de dispersion.' Unless 'dispersion' here means something other than migration or spreading it is impossible to follow this. The only adaptive significance one can accept is the reverse of what these

authors propound: the flights of male dorylines have a genetic role, one that is doubly important in view of the limited dispersal attributes of the flightless females.

The conclusion of Haddow *et al.* (1966), that 'seasonal fluctuations . . . are probably not much greater than the night-to-night variations . . .' is unsupported and results from the defects in their sampling method, noted below. Figs. 3 and 4, to a lesser extent Fig. 5, demonstrate a marked seasonal periodicity in frequencies.

The peak emission of males by Dorylini at Legon during the first wet sunny season of Gibbs and Leston (1970) is concurrent with the production of maximum numbers of alates in the ubiquitous and arboreal-nesting formicine *Oecophylla longinoda* (Latreille) (Leston and Gibbs, 1971) and in the similar nesting but strictly forest-zone myrmicine *Macromischoides aculeatus* (Mayr) (Aryeetey, 1971). The peak in *Anomma* approximates that found in the ground-nesting forest ponerine *Odontomachus troglodytes* Santschi (Gibbs and Leston, 1970); during the second wet sunny season, a season not clearly delimited at Legon but distinct in the nearby forest zone (Fig. 5).

In *Oecophylla* and *Macromischoides* it appears that the ultimate factor is the optimization of conditions for the production of the first broods by the solitary queen (Leston, 1972). After the end of the first wet sunny season there is a dramatic drop in the available prey (Gibbs and Leston, 1970) and a reduction too in mean temperature. However, colonies are not, in Dorylini, founded by a single, claustral queen but by budding. It is suggested the ultimate factor in the production of sexuals in Dorylini is the availability to the parent colony during the beginning of the first wet sunny season, of abundant insects and earthworms, their known prey (Gotwald, 1974).

The annual peak (Fig. 3) falls within the wet sunny period, April through to the end of May (Fig. 1). In the nearby forest zone this wet sunny season is longer and there is, too, a second one later in the year (Fig. 5).

The attempt to fit all biological periodicities in the humid tropics into an alternation of wet and dry 'seasons' still persists. Thus Karr (1976): 'Life history adaptations to seasonal changes in rainfall are well documented.' Karr then lists no fewer than 22 papers in support—including Gibbs and Leston (1970), which says just the reverse! Kanno's (1969) conclusion—'The interface between the wet and dry seasons appears to be the most important time of the

year for army ant nuptial flight activity in the region of Barro Colorado Island'—is in accord with my data, and indicative of this interface being in fact a wet sunny period.

The fauna of Legon is a complex mix of forest relicts, secondary successional species and true savanna forms: investigations have covered such diverse groups as snakes, ponerine ants, hemipters and mantises (Leston, 1972, 1979). In practice it is seldom difficult to categorize a particular animal by habitat. The relative numbers, in a degraded forest habitat, is a function of the degree of deforestation—most species are not directly climate-limited—modified by the varying abilities of savanna taxa to saltate (Leston, 1979).

The traps reported on by Haddow *et al.* (1966) covered both tropical forest and degraded forest but unfortunately the results are given in pooled form, making a numerical habitat comparison difficult: the pooling of data from three traps run at different times of the year makes an investigation of periodicities equally impossible. But overall, despite species differences—which probably reflect an oversplitting taxonomy—there is a marked similarity in the dorylines trapped at Legon, on the edge of the Guinea forest bloc, and that of Entebbe, 3,600 km distant on the edge of the Congo forest bloc.

As at Legon, the most abundant species at Entebbe was an *Alaopone*: these are hypogeic ants of degraded forest habitats. *Typhlopone fulvus*, assumed by Haddow *et al.* (1966) and Wheeler (1922) to be hypogeic, was also numerous at both localities: my field observations show it frequently forages at the surface in forest and degraded forest areas. Some *Dorylus sensu stricto* were frequent at both sampled places: probably for the most part savanna ants which invade degraded forest. *Anomma* species were relatively infrequent at both too: as noted above they are essentially genuine forest dwellers, surface foraging, the 'notorious driver ant' (to cite Haddow *et al.*). *Rhogmus fimbriatus*, about as frequent at Entebbe as at Legon, is a hypogeic, mainly savanna, species.

The similarity of the two faunas over an extensive transcontinental area suggests a widespread pattern of resource partitioning but why the alates should space themselves out in male flights through the hours from dusk to dawn, as Haddow and his colleagues indicate—found too in the American Ecitonini (Kannowski, 1969)—is less easy to interpret in such terms. And the most remarkable feature of the Legon results, the synchrony of the species' cycles,

remains to be placed in an evolutionary context. I cannot accept that synchrony results from a climatic shock bringing the species annually into phase: these are social insects, as adept as other ants in modifying their environment (Leston, 1973), whilst weather-induced synchrony is likely at best to extend over a few weeks only, not over a 400 day period as noted here.

That all Old World dorylines studied—including Aenictini—have nocturnal male flights is indicative primarily, I believe, of high humidity preferenda: after all, these are hypogeic or, at least, ground-nesting species. The diel spacing out of flight times is consistent with this: relative humidity in the wet tropics is minimal around 1500 hrs local time, maximal around 0500 hrs. The immediate post-dusk species are less tied to the highest RH value than are the pre-dawn ones. The species' synchrony, I suggest, has evolved as a mechanism for oversaturation by potential prey. Male dorylines have large flight muscles—protein—and much fat: they are preyed upon by frogs and toads (Wheeler, 1922) and probably a wide range of other nocturnal predators whilst isolated males, once landed, fall victims of the ever-present dominant ants.

The logarithmic relationship in the species' frequencies (Fig. 2) follows the pattern noted for many animals by Williams (1964) and others. It is paralleled in several organisms sampled in Ghana: mist-netted lower-storey birds, field collected snakes, pyrethrum knock-downed non-doryline ants and ultraviolet light-trapped paussid beetles, amongst others (Leston, 1972).

ACKNOWLEDGEMENTS

Field work in Ghana was supported by the Cocoa, Chocolate and Confectionery Alliance (U.K.) and the Ghana Cocoa Growers' Research Association: subsequent help came from the Research Foundation of the University of Connecticut and the Institute of Food and Agricultural Science, University of Florida. Ms. Lyn Garling, Dr. W. H. Gotwald, Jr. and Dr. C. W. Rettenmeyer have kindly read and commented upon the manuscript.

CONCLUSIONS

1. In an ultraviolet light-trap run for 400 days at Legon, Ghana, males of eleven species of doryline ants, in *Dorylini*, were captured.

2. The relative frequencies approximated a logarithmic sequence.
3. The annual peak occurred in the first wet sunny season.
4. Additional to the annual cycle peaks occurred about every 30 days.
5. The more frequent species showed fluctuations in parallel.
6. It is suggested Schneirla cycles were present in the species sampled.
7. The ultimate factor in the annual production pattern is probably the availability of food to the parent colony.

LITERATURE CITED

- ARYEETEY, E. A.
1971. The biology of *Macromischoides aculeatus* (Mayr) (Hym., Formicidae) in Ghana. M.Sc. Thesis. Univ. Ghana, Legon.
- BROWN, W. L.
1973. A comparison of the hylean and Congo-West African rain forest ant faunas, p. 161-185. In B. J. Meggers, E. S. Ayensu and W. D. Duckworth (ed.). Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Institution Press, Washington, D.C.
- GIBBS, D. G., AND D. LESTON
1970. Insect phenology in a forest cocoa-farm locality in West Africa. *J. Appl. Ecol.* 7: 519-548.
- GOTWALD, W. H.
1974. Predatory behavior and food preferences of driver ants in selected African habitats. *Ann. Entomol. Soc. Am.* 67: 877-886.
1977. The origins and dispersal of army ants of the subfamily Dorylinae. *Proc. 8th Congr. Int. Union Study Social Insects, Wageningen 1977*: 126-127.
- HADDOW, A. J., J. H. H. YARROW, G. A. LANCASTER AND P. S. CORBET.
1966. Nocturnal flight cycle in the males of African doryline ants (Hymenoptera: Formicidae). *Proc. Roy. Entomol. Soc. (A)* 41: 103-106.
- HALL, J. B., AND M. D. SWAINE.
1976. Classification and ecology of closed-canopy forest in Ghana. *J. Ecol.* 64: 913-951.
- KANNOWSKI, P. B.
1969. Daily and seasonal periodicities in the nuptial flights of neotropical ants. I. Dorylinae. *Proc. VI Congr. Int. Union Study Social Ins. Bern 1969*: 77-83.
- KARR, J. R.
1976. Seasonality, resource availability, and community diversity in tropical bird communities. *Amer. Nat.* 110: 973-994.
- LESTON, D., AND D. G. GIBBS.
1971. Phenology of cocoa and some associated insects in Ghana. *Proc. 3rd Int. Cocoa Res. Conf. Accra 1969*: 197-204.

LESTON, D.

1972. Insect interrelations in cocoa: a contribution to tropical ecology. Ph.D. Thesis. Univ. Ghana, Legon. 720 p.
1973. The ant mosaic, tropical tree crops and the limiting of pests and diseases. PANS, London **19**: 311-341.
1979. The natural history of some West African insects. Entomol. Mon. Mag. (In press).

RAIGNIER, A., AND J. VAN BOVEN.

1955. Étude taxonomique, biologique biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). Ann. Mus. Roy. Congo belge (N.S. 4° Sci. Zool.) **2**: 1-362.

RETTENMEYER, C. W.

1963. Behavioural studies of army ants. Univ. Kansas Sci. Bull. **44**: 281-465.

SCHNEIRLA, T. C. (ED. H. R. TOPOFF)

1971. Army ants: a study in social organization. W. H. Freeman, San Francisco. 349 p.

SIEGEL, S.

1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York. 312 p.

WHEELER, W. M.

1922. The ants collected by the American Museum Congo Expedition. Bull. Amer. Mus. Nat. Hist. **45**: 39-269.

WILLIAMS, C. B.

1964. Patterns in the balance of nature. Academic Press, London. 324 p.

HABITAT STRUCTURE AND COLONIAL BEHAVIOR
IN *METEPEIRA SPINIPES* (ARANEAE: ARANEIDAE),
AN ORB WEAVING SPIDER FROM MEXICO

BY GEORGE W. UETZ¹ AND J. WESLEY BURGESS²

INTRODUCTION

The topic of social phenomena in spiders has received much attention in the literature recently (Shear 1970; Kullman 1972; Burgess 1976, 1978; Buskirk, in press). Colonial, communal and cooperative behaviors have been observed in a variety of families and genera, mostly from tropical and subtropical regions around the world. Among the species of group-living spiders found in Mexico and Central America is *Metepeira spinipes* F. Pickard-Cambridge, an araneid reported to be the only colonial species in its genus (Levi 1977). We observed large numbers of these spiders in Central Mexico in 1975, and were able to collect some data, which we present here.

METHODS AND STUDY AREA

The site of our observations was Tepotzotlan, Mexico, located 35 km North of Mexico City. The area is an agricultural valley surrounded by mountains (thus the habitat must be considered "disturbed" by the activities of humans). Major agricultural activities include cultivation of corn and maguey (an *Agave sp.* grown to make pulque, a fermented beverage) with open range grazing of cattle, and several feedlots. Our visit took place in late July 1975, during the rainy season. Temperatures were typically warm during the day (20–30° C) and cool at night (5–15° C). It generally rained once a day in the late afternoon 15–17h pm CST).

Metepeira spinipes spiders were studied in 3 sites, all located near the KOA campground where we stayed. One site, a roadside, contained a variety of types of vegetation, including *Agave*, *Opuntia*,

¹Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221.

²North Carolina Mental Health Research, Raleigh, North Carolina 27611 [Present address: Department of Psychology, University of California, Davis, California 95616].

Manuscript received by the editor June 28, 1979

Acacia (?) trees and numerous unidentified shrubs, forbs and grasses. This roadside area was bordered on one side by a large cornfield and on the other by an irrigation ditch. A second roadside area was perpendicular to the first, bordering the same cornfield. This site has a larger irrigation ditch, the sides covered by dense, low growing willows (*Salix sp.*). A third site, a maguey plantation, was located approximately 1.2 km east of the other sites. The area was planted in large (>1.5 m) *Agave* (approximately 5–7 yrs old), interspersed with grasses and occasional trees. The plantation has the appearance of an *Agave* “orchard”, due to the semi-regular dispersion of the large plants. These three areas represent the characteristic habitats where *Metepeira* were found in the Tepotzotlan area.

To assess habitat preferences of *Metepeira*, a series of 6 200 m² quadrats was delineated in the roadside area containing a variety of vegetation types. Within each quadrat, the percent cover and percent volume of each vegetation type was estimated. Frequency of occurrence of *Metepeira spinipes*, (both colonies and solitary individuals) was recorded within each vegetation type.

In both the maguey plantation and the roadside ditch covered by willows, counts were made of spider group size. In addition, measurements of colonial web dimensions and habitat dimensions were made for selected groups.

RESULTS AND DISCUSSION

The web of individual *Metepeira spinipes* is characteristic of the genus, and is a three-dimensional space web/orb web composite with a retreat in the space web (also called a barrier web; Levi 1977) (Fig. 1). Signal threads connect the hub of the spiral and the retreat, where the spider rests (Burgess & Witt 1976). Only the threads of the orb's spiral are sticky, and the orb is the primary prey catching device. Prey are often entangled in the space web and occasionally are caught there. Individuals of *M. spinipes* in Central Mexico usually occur in aggregations, although solitary individuals of this species are also found. Most of the groups we examined consisted of 5–30 individuals, but much larger groups (50–80) were seen. In the groups we observed, individuals had their own retreats and orbs but space webs were joined. Although orbs are usually renewed on a daily basis (spiders rebuild radii and sticky spirals during the night)



Figure 1. *Metepeira spinipes*, compound web. (1) Space web; (2) retreat where spider sits, holding signal threads (4) to (3) catching spiral. Mature females may construct tiers of egg sacs (5). [Courtesy of Dr. Peter N. Witt, North Carolina Division of Mental Health and Mental Retardation Services. Used with permission.]

the colonial space web persists and is elaborated on by the web building activities of numerous individuals. The resultant colonial web is a mass of interconnected individual webs supporting each other, attached at its periphery to the vegetation. The colonies we observed contained adults and immatures of indeterminate age and wide size variation.

Metepeira spinipes colonial webs are usually associated with microhabitats of a somewhat permanent structure: succulents, dead branches, shrubs, man-made objects, etc. In the Tepozotlan area, maguey (*Agave* sp.) plants were the most common site of *M. spinipes* colonies. Habitat preferences of this species were examined in an area containing a variety of microhabitat types. The null hypotheses that spiders are equally distributed in all microhabitat types, or are distributed on the basis of the frequency of occurrence of microhabitat types are rejected based on Chi-square tests (Table 1). These data suggest that *M. spinipes* colonies and/or individuals occur more frequently in *Agave* plants than in other microhabitat sites.

Most of the solitary individuals were found in grasses and forbs, but in frequencies proportionate to the occurrence of that type of microhabitat.

There are several possible reasons why *M. spinipes* exhibit a habitat preference for the maguey plant. *Agave sp.* are perennial, succulent plants with stiff leaves capable of providing strong support for web attachments. These plants have lanceolate leaves with cupped leaf bases, radiating from a basal rosette. Such a leaf arrangement provides much support for the three-dimensional colonial web. Colinvaux (1973) suggests that plants with physiognomy similar to *Agave sp.* (i.e. *Yucca*) are adapted for arid environments, in that their leaf shape reduces heat load, and cupped leaf bases concentrate moisture. Agaves might be a localized source of moisture during the dry season, or even at mid-day during the rainy season when solar radiation is intense and humidity is low. We have observed water accumulating at the base of some plants. There is also some evidence that agaves are sites of high insect activity. Debris from nearby flowering plants and trees and other organic matter sometimes accumulates about the base of these plants. Decomposition of this matter and lower leaves of older agaves attracts flying insects, creating a microhabitat with extremely abundant prey resources.

These findings raise questions about the nature of *M. spinipes* aggregations. Do these spiders exhibit grouping tendencies that may be considered social, or do they exist in fortuitous aggregations associated with habitat resources that are patchily distributed? There is some evidence that these spiders aggregate independently of habitat. The mean colony size of *M. spinipes* in two contrasted microhabitat sites, *Agave sp.* and shrubs is not significantly different (Table 1). Although other *Metepeira* species are associated web sites of a particular architecture (McCook 1889; Kaston 1948; Levi 1977), *M. spinipes* is not. This species occurs in a variety of web sites with widely varying structure. Moreover, the shape of the web colony is flexible, and conforms to that of the web site. This suggests, at least, that coloniality of *M. spinipes* is independent of habitat structure. Spiders brought into the laboratory and released into cages build colonial webs, attaching silk of one animal to silk of another. Moreover, individuals from different colonies, even as far apart as several hundred miles, tolerate each other and build webs together (Burgess 1976). This evidence strongly suggests that *M.*

Table 1. Distribution of *Metepira spinipes* in several microhabitat types.

Microhabitat	<i>Agave</i>	<i>Opuntia</i>	Trees	Shrubs	Grasses + Forbs
percent cover	4.3	1.0	4.6	5.0	85.1
percent volume	4.9	2.3	20.9	7.6	64.4
No. of spiders	691	16	2	96	17
No. of colonies	47	1	0	9	3
\bar{X} colony (± 2 S.E.) size	14.67 \pm 3.38	16.0	—	14.89 \pm 8.1	2.0 \pm 0.0
No. of solitary individuals	2	0	2	2	11

Tests of significance:

<i>no. of spiders</i>	<i>no. of colonies</i>	<i>no. of solitary individuals</i>
H_0 = equal frequencies in all microhabitat types		
$\chi^2 = 2141.8$ $p < .001$	$\chi^2 = 93.7$ $p < .001$	$\chi^2 = 22.12$ $p < .01$

H_0 = frequencies proportionate to percent cover of micro-habitat type

$\chi^2 = 12922.1$ $p < .001$	$\chi^2 = 646.7$ $p < .001$	$\chi^2 = 6.9$.2 < $p < .3$
----------------------------------	--------------------------------	---------------------------------

H_0 = frequencies proportionate to percent volume of micro-habitat type

$\chi^2 = 11188.0$ $p < .001$	$\chi^2 = 551.5$ $p < .001$	$\chi^2 = 3.11$.5 < $p < .6$
----------------------------------	--------------------------------	----------------------------------

spinipes aggregations arise from some kind of interattraction, not from habitat patchiness.

Another means of gathering evidence for or against a social tendency to aggregate is an analysis of the frequency distribution of group size. In a study of web-clumping in *Nephila clavipes*, Farr (1977) compared group size distributions to a Poisson distribution truncated at zero. His data fit the distribution, and he concluded that web clumping by *N. clavipes* is a random process. Using methods described in A. Cohen (1960) and J. Cohen (1971), we attempted this with data on *M. spinipes* group size from two contrasted habitats (the maguey plantation and the willow shrub ditch described in methods). In both habitats, the distribution of spider

group size was significantly different from a zero-truncated Poisson distribution (Tables 2 and 3), indicating a non-random grouping pattern. The distribution did fit a zero-truncated Negative Binomial distribution (Tables 2 and 3), indicating a significant tendency to aggregate. The fact that group size in *M. spinipes* occurs with the same underlying aggregated distribution in such divergent habitat types argues for the existence of a social grouping tendency rather than fortuitous aggregation. While it may be argued that in Agaves, structural habitat resources are concentrated in small patches, this was not the case in the willow shrubs. The willow shrubs appeared to be uniformly dense and of equal height and age. There was no a priori reason to suspect that web site resources for *M. spinipes*

Table 2. Frequency distribution of group size in *Meteteira spinipes* colonies in *Agave* plants.

Group Size	Observed Frequency	Truncated Poisson	Truncated Negative Binom ⁱ	
1	0	.0001	.651	1.46
2	0	.0009	.811	
3	1	.005	.914	1.89
4	2	.017	.977	
5	0	.050	1.010	1.71
6	2	.124	1.010	
7	0	.259	1.010	1.95
8	2	.475	.988	
9	0	.775	.958	1.80
10	0	1.136	.920	
11	0	1.515	.881	1.63
12	1	1.850	.840	
13	2	2.090	.790	1.44
14	1	2.190	.745	
15	1	2.140	.699	1.26
16	0	1.960	.654	
17	1	1.690	.610	1.10
18	0	1.38	.570	
19	1	1.06	.530	6.44
20	0	.78	.49	
>20	7	1.50	5.95	
	21			
		$\chi^2 = 34.06$	$\chi^2 = 11.98$	
		$p < .005$	$.5 < p < .6$	

spiders were aggregated in any way in the willow shrub area, thus a social aggregation hypothesis is supported.

The colonial web of *Metepeira spinipes* is a permanent aggregation of individual prey catching orb webs in a matrix of communal space web. Burgess (1978) has suggested that cooperative behavior of "Social" spiders consists of simultaneous coordination of individual effort on a task, like web-building. In *M. spinipes* the colonial web would appear to arise as the result of simultaneous or sequential (but not coordinated) individual efforts at web building, rather than cooperative behavior. Prey catching orbs are spaced apart and each spider inhabits its own retreat. Although individuals may coexist at short distances, intruders on the spiral are met with agonistic behavior (Web shaking, chasing, etc.). In many solitary and aggregated spider species, maintenance of a personal space or territory by aggressive behavior has been shown (Buskirk 1975 and in press, Riechert 1978, Burgess 1978). The combination of solitary and colonial behaviors exhibited by this species suggests that it represents an intermediate stage in the evolution of social behavior in spiders.

In a colonial web like that of *M. spinipes*, where space webs are three-dimensional and highly interconnected, it is not possible to discern clearly the space web made by one individual vs. another. We measured the dimensions of polygonal colonial webs and counted individuals and orbs in the field, and from these we have estimated how the volume of the colonial web is subdivided by individuals (Fig. 2). The amount of space per individual in a colonial web decreases dramatically as colony size increases from 2-10 individuals. However, in larger colonies, there appears to be a lower limit on the amount of space per individual. The asymptote in figure 2 possibly reflects the minimal individual space requirements of *M. spinipes*. These values are probably underestimates of the actual amount of individual space, since there are often more individuals in a colony than there are orbs. The compressibility of individual space in aggregations of varying size shown by this species indicates a degree of tolerance of conspecifics beyond that expected if individuals' webs were merely attached to one another.

Riechert (1978 and personal communication) has found that territory size in a desert sheet web spider (*Agelenopsis aperta* (Gertsch)) decreases with increased habitat quality over a wide range of areas. The size of the area occupied by an individual *Agelenopsis* spider is

Table 3. Frequency distribution of group size in *Metepeira spinipes* colonies in low willows (*Salix* sp.).

Group Size	Observed Frequency	Truncated Poisson	Truncated Negative Binomial
1	8	0.58	5.16
2	2	.244	3.26
3	3	.686	2.42
4	0	1.44	1.93
5	3	2.42	1.60
6	2	3.39	1.36
7	1	4.080	1.19
8	3	4.285	1.04
9	0	4.000	.93
10	0	3.360	.83
11	0	2.57	.75
12	1	1.00	.68
13	1	1.16	.62
14	0	.69	.57
15	1	—	.53
16	0	—	.48
17	0	—	.45
18	0	—	.42
19	0	—	.39
20	0	—	.36
>20	6		6.06
	31		

$\chi^2 = 79.36$ $\chi^2 = 16.02$
 $p < .005$ $.4 < p < .5$

related to its energy needs and to the accessibility of prey (based on prey abundance and microclimatic stress limits on prey catching time) in a habitat. An energy-based territorial system might be part of a hypothesis generated to explain the evolution of social phenomena in spiders like *M. spinipes*. In habitats where accessibility to prey is high, territory size and inter-individual distance would be reduced, and populations would be large. If available web sites (providing architectural support for a 3 dimensional web as in solitary *Metepeira*) were limited, selection would favor individuals capable of living in an aggregated state. Behaviors favoring group occupation of web sites (increased tolerance of conspecifics, interattraction) would be selected for, although behaviors associated with

maintenance of individual space (web defense etc.) would be retained.

There are many other selective advantages to group living that might also apply to the evolution of coloniality in *M. spinipes*. By locating space webs together, spiders gain additional "knock-down" structures which may serve to increase prey taken. The colonial space web creates a stronger foundation on which to build individual orbs, and may allow energy savings in web maintenance costs. The colonial web also transmits vibrations, and may be an important means of communication of predator attack or prey availability. Prey stealing and web take-over are often seen in *M. spinipes* and other species, and suggest that spiders may benefit from living in an aggregation without building a web. The mate selection process is facilitated by group living, and males may increase their fitness by "attending" a female (we have observed this) before she molts to adulthood. Colonies of spiders like *M. spinipes* can monopolize larger, or better quality web sites, while solitary species

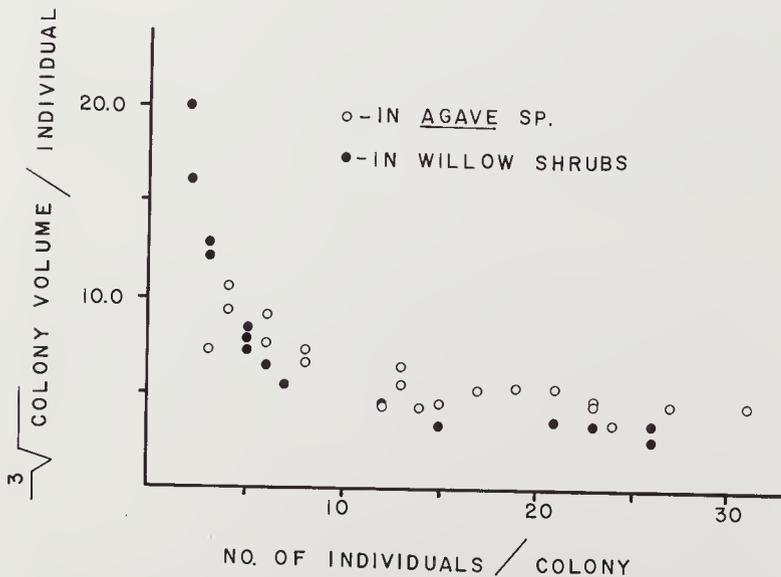


Figure 2. Amount of colony volume per individual *M. spinipes* over a range of colony sizes. (Colony volume in cm^3 is expressed as a cube root for linear comparison with number of individuals.)

may not. (For more detailed discussion see Shear 1970; Kullman 1972; Lubin 1974; Burgess 1978; Buskirk, in press).

Hopefully, future research on this species and other group living spiders will shed more light on the evolution of sociality in an otherwise asocial group of animals.

SUMMARY

Data on habitat preference and group size in *Metepeira spinipes* F. P.-Cambridge, a colonial orb weaving spider from Central Mexico, are presented. *M. spinipes* colonies are associated with microhabitats of permanent structure, and occur most frequently in maguey plants (*Agave sp.*). Colony size appears to be independent of microhabitat structure. Distribution of group size in two contrasted habitats (Agaves and willows) showed a significant difference from a zero-truncated Poisson distribution and a good fit to a zero-truncated Negative Binomial distribution, indicating a tendency to aggregate independently of habitat. Amount of individual space decreased with increased colony size, indicating a tolerance of conspecifics greater than expected if spiders merely attached individual webs together. The combination of solitary and colonial behaviors exhibited by this species suggests that it may represent an intermediate stage in the evolution of social behavior in orb-weaving spiders. Possible selective advantages to group-living in this species and the evolution of coloniality are discussed.

ACKNOWLEDGEMENTS

This research was supported in part by National Science Foundation grant BNS-75-09915-A03 to Dr. Peter Witt. Additional financial assistance by Ms. Colette Croze is gratefully acknowledged. Thanks to Peter Witt and Thomas Kane for reviewing the manuscript. Special thanks to Joan Sattler, who typed the manuscript.

REFERENCES CITED

- BURGESS, J. W.
1976. Social spiders. *Sci. Amer.* 234: 100-106.
1978. Social behavior in group-living spider species. *Symp. Zool. Soc. Lond.* 42: 69-78.
- BURGESS, J. W. & P. N. WITT.
1976. Spider webs: design and engineering. *Interdisc. Sci. Review.* 1: 322-335.

- BUSKIRK, R. E.
1975. Aggressive display and orb defense in a colonial spider, *Metabus gravidus*. Anim. Behav. **23**: 560-567.
in Sociality in the Arachnida. In H. R. Hermann, ed., *Social Insects*, Vol. 11, press. Chap. 7, Academic Press.
- COHEN, A. C., JR.
1960. Estimating the parameter in a conditional Poisson distribution. Biometrics **16**: 203-211.
- COHEN, J. E.
1971. Casual groups of monkeys and men. Harvard Univ. Press, Cambridge, Mass. 175 p.
- COLINVAUX, P. A.
1973. Introduction to Ecology. J. Wiley & Sons, N.Y. 621 p.
- FARR, J. A.
1977. Social behavior of the Golden Silk Spider, *Nephila clavipes*. J. Arachnol. **4**: 137-144.
- KASTON, B. J.
1948. Spiders of Connecticut. Conn. Geol. & Nat. Hist. Surv. **70**. pp. 226-227.
- KULLMANN, E. J.
1972. Evolution of social behavior in spiders (Araneae: Eresidae and Theridiidae). Amer. Zool. **12**: 419-426.
- LEVI, H. W.
1977. The orb weaver genera *Metepeira*, *Kaira* and *Aculepeira* in America North of Mexico (Araneae: Araneidae). Bull. Mus. Comp. Zool. **148**: 185-238.
- LUBIN, Y. D.
1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zool. J. Linn. Soc. **54**: 321-339.
- MCCOOK, H. C.
1889. American spiders and their spinning work. Vol. I. publ. by the author. Acad. Nat. Sci. Phila. 369 p.
- RIECHERT, S. E.
1978. Energy-based territoriality in populations of the desert spider, *Agelenopsis aperta* (Gertsch). Symp. Zool. Soc. Lond. **42**: 211-222.
- SHEAR, W. A.
1970. The evolution of social phenomena in spiders. Bull. Brit. Arachnol. Soc. **1**: 65-76.

RHYTHM VARIABLES AS TAXONOMIC CHARACTERS IN ANTS

BY ELWOOD S. MCCLUSKEY¹ AND SIU-MING A. SOONG²
Loma Linda University, Loma Linda, Ca 92350

A survey of many species of ants in the field indicates a generic difference in the hours of flight and of worker aboveground activity (McCluskey 1973, 1974). Further, species within the same genus may differ consistently (Holldobler 1976; Léviéux 1977; Whitford and Ettershank 1975). Would the same be true if the habitats of the various species were made identical? The present paper reports a beginning laboratory test of this question in worker ants. Secondly, it uses multivariate analysis to examine rhythm and other laboratory-type variables for their potential as taxonomic characters. A preliminary report was given by McCluskey and Soong (1978).

METHODS AND MATERIALS

The species observed were: *Pogonomyrmex californicus* (Buckley), *Pogonomyrmex rugosus* Emery, *Veromessor andrei* (Mayr), and *Veromessor pergandei* (Mayr) in the tribe Myrmicini of Myrmicinae; and *Formica pilicornis* Emery and *Myrmecocystus mimicus* Wheeler in the tribe Formicini of Formicinae. The ants were all collected May 24 and 25, 1973, near Loma Linda or Colton, San Bernardino County, California, at an elevation of about 350 m.

Each group of ants was placed in a clear plastic refrigerator dish 9 cm in diameter by 3 cm deep. Sugar water was provided by a cotton-plugged tube hanging down through the lid, and constant moisture by a wick of dental cotton projecting up from water in a like dish nested underneath. A clear plastic (Tygon) tube 8 cm long led to a dish of the same type to serve as a dry arena. The nest dish was totally covered by heavy black paper, while the tube and arena were fully exposed to the light.

¹Departments of Biology and Physiology; address for reprints.

²Department of Biology; present address, 550 Victoria Road, Baguio Villa, Block 46, 3F, Hong Kong.

Manuscript received by the editor July 5, 1979.

There were five of these nest assemblies per species (except only one for *M. mimicus*), with 30 ants in each. The 26 arenas were lined up side by side, the first replicate of each species, then the second of each, etc. Heating tape was stretched alongside the whole row of arenas so that it was about 1 cm from one side of each arena; it provided constant heat throughout the experiment.

The ants were kept in a constant temperature room. The nest dishes averaged $24.3^{\circ}\text{C} \pm 0.5^{\circ}$. The hot side of the arenas was kept at least $10^{\circ} (\pm 1^{\circ})$ hotter than this. Twelve hours of fluorescent light (2000 lux) was alternated with 12 hours of darkness (the last 2 nights there was dim incandescent light [15 lux] to permit observations).

The ants were installed May 25 and observations began May 27. Each hour during the light periods of May 27-31, and also during the 2 nights beginning May 30 and 31, the number in the hot half of the arena, in the warm half of the arena, and in the tube were counted visually. In addition, the total number active (moving) in tube and arena were counted.

Except where noted, an arc sine transformation was used, treating the count as a proportion of the 30 ants available (Dixon and Massey 1969). Then the transformed counts for the 3 days May 27-29, when the ants were in the best condition, were averaged for each replicate. Finally the hourly observations were fitted to a 24-hour cosine-curve for determination of the best-fit peak (acrophase) and other rhythm parameters.

Variables evaluated

The fitting method used (Halberg et al. 1972) provides the acrophase, the level (average), the amplitude, and the sinusoidality (probability of sine shape) of the fitted rhythm. Each of these four parameters (dependent variables) could serve as a potential character, and each was applied to every one of the following four types of assay (Table 1).

Listed first are the variables related to the total number of ants out (i.e., in tube and arena) at each hour (TOTAL OUT). This would represent choice of an area exposed to alternating light and dark, as well as drier and warmer than the dark humid next dish.

The second type of assay was the number of ants in the hot half of the arena (TEMPERATURE). This represents the extreme distance out from the nest dish, and/or the preference or tolerance of high temperature.

The third, POSITION, was calculated as $(.80 \times \text{total no. out} - \text{no. in tube}) / (\text{total no. out} - \text{no. in hot half of arena})$. It is an index of how far out into the warm (i.e., nearest) half of the arena one would have to go to encompass 80% of the ants which were out of the nest at the time (50% would not work, because too often the 50% line was down in the tube rather than out in the arena). This position assay may be illustrated by sample calculations: If all the ants were in the warm half of the arena, the 80% point would be 80% of the way out through the warm half. If 20% were in the warm half and 80% in the tube, the 80% point would be 0% of the way through the warm half. If 80% were in the warm half and 20% in the hot half, the 80% point would be 100% of the way out through the warm half.

The fourth, ACTIVITY, was the proportion active of the total number out.

The fitting involved above should increase the information content in any given variable. How important is this for taxonomic discrimination? To help answer the question, single "hourly" (i.e., nonfitted) variables were also tested (Table 1), each being simply the value for a particular hour.

Table 1. (see following pages)

Means of variables examined for taxonomic value, averaged over days (May 27-29 except where noted) and replicate nests for each species (abbreviated by initial of genus and species). TOTAL OUT and TEMPERATURE based on arc sine transformation of count; POSITION based on raw count; ACTIVITY based on log of proportion active. *Sinusoidality* represented by log of F statistic, *Acrophase* by clock hour (decimal form: e.g., 15.8 = 3:48 PM; angular avg), and *Level* and *Amplitude* by number of ants (except for POSITION, where *Level* and *Amplitude* represent distance into arena—see text); these first 4 variables under each type of assay are all derived by least-squares cosine-fitting (Halberg et al., 1972). The next 6 variables under TOTAL OUT are: *Shift of Acrophase* (no. of h change in acrophase from May 27 to May 29); *Rise* (h at which count passed up through avg [*Level*] for the day); *Shift of Rise* (no. of h change from May 27 to May 29); *Above Average* (no. of h above avg for the day, May 30-31, when observed all 24 h); *Light-on Difference* (between count immediately after lights on and 2d count several min later, May 28-30); *Fluctuation* (no. of runs, where "run" = series of hourly values each having same sign of change from preceding value). Corresponding to latter is *Fluctuation* under POSITION. Finally, under each type are listed the hourly values, unprocessed except for initial transformation and averaging (ACTIVITY 0700 omitted because could not observe all replicates simultaneously at the moment lights came on). F based on 5,20 degrees of freedom (slightly less for some variables with missing observations); * = $P < .05$, ** = $< .01$, *** = $< .001$.

TABLE I

Variable	Species						F
	P.c.	P.r.	V.a.	V.p.	F.p.	M.m.	
TOTAL OUT							
Sinusoidality	1.79	1.81	1.74	1.62	1.45	1.83	.9
Level	72	83	83	45	65	56	4.8**
Amplitude	25	32	41	28	23	19	1.5
Acrophase	15.8	18.0	.7	22.5	23.4	20.8	23.3***
Shift of acro.	1.4	4.0	.9	.3	2.1	2.8	2.4
Rise	10.7	11.9	18.4	16.0	17.1	14.6	15.1***
Shift of rise	1.3	3.9	.6	-1.0	1.3	2.2	4.0**
Above average	15.0	12.6	12.7	9.2	11.4	13.0	6.4**
Light-on diff.	28.2	40.2	40.8	6.2	41.6	10.5	4.2**
Fluctuation	16.2	15.4	13.0	10.8	18.2	16.0	4.3**
0700	59	62	85	25	60	41	5.6**
0800	60	55	61	22	47	34	2.7
0900	64	61	55	20	44	30	2.9*
1000	70	65	49	20	45	45	2.9*
1100	74	74	48	21	44	41	4.2**
1200	81	84	48	21	43	42	6.4**
1300	89	91	47	23	44	41	8.7***
1400	92	99	45	24	46	50	11.8***
1500	96	106	49	31	52	59	15.0***
1600	97	110	57	45	58	66	11.8***
1700	95	109	67	55	65	66	5.5**
1800	93	111	79	57	70	69	7.0***
1900	86	110	88	61	72	72	4.5**
POSITION							
Sinusoidality	1.78	.92	.79	1.18	.44	.18	9.3***
Level	89	69	70	30	3	59	9.8***
Amplitude	42	12	13	13	14	9	3.9*
Acrophase	20.6	18.7	3.4	11.0	14.5	20.1	5.2**
Fluctuation	19.6	20.6	17.7	11.0	23.7	22.0	6.3**
0700	57	48	74	45	1	2	5.4**
0800	46	60	78	47	0	87	3.4*
0900	52	62	81	31	1	73	3.8*
1000	47	66	60	31	8	41	1.8
1100	49	63	62	43	14	64	1.2
1200	61	70	61	43	9	49	2.2
1300	66	67	58	44	19	54	1.4
1400	77	73	61	46	19	62	2.1

TABLE I (CONTINUED)

1500	109	70	56	40	19	45	4.5**
1600	110	77	55	36	14	60	7.8***
1700	118	78	62	28	18	68	20.7***
1800	116	84	56	24	6	55	12.5***
1900	121	83	62	21	9	90	14.3***
TEMPERATURE							
Sinusoidality	1.72	1.36	.58	.29	.24	1.00	11.9***
Level	31.7	24.5	14.0	11.5	11.7	19.7	5.6**
Amplitude	20.8	14.0	4.1	1.0	.8	9.6	6.9***
Acrophase	19.2	21.8	1.4	1.8	.5	23.1	2.1
0700	14	13	18	13	12	10	.8
0800	12	12	12	12	12	15	.4
0900	14	12	11	10	10	13	3.5*
1000	14	12	10	10	11	10	3.2*
1100	17	11	10	10	11	13	10.8***
1200	23	11	10	10	11	10	20.9***
1300	30	15	11	10	11	10	13.5***
1400	33	17	11	11	11	10	6.3**
1500	49	22	10	12	10	13	13.2***
1600	49	25	11	10	11	20	14.5***
1700	52	29	13	12	13	20	10.3***
1800	51	32	12	11	12	15	9.0***
1900	47	35	12	10	11	31	7.4***
ACTIVITY							
Sinusoidality	.75	.78	.55	.84	.63	.11	1.3
Level	.91	1.09	.93	.53	.94	.60	4.0**
Amplitude	.24	.33	.65	.39	.37	.18	3.0*
Acrophase	20.6	19.7	.4	22.4	.0	12.5	3.4*
0800	77	82	90	49	61	42	.8
0900	71	91	58	18	59	114	2.8*
1000	58	68	26	8	62	79	3.1*
1100	55	84	6	0	75	39	10.7***
1200	88	90	18	0	54	82	9.2***
1300	83	103	29	12	69	84	7.6***
1400	67	111	14	23	50	81	4.9**
1500	103	124	44	43	84	69	4.3**
1600	103	138	103	64	83	85	3.5*
1700	106	142	106	73	92	73	5.5**
1800	103	134	67	50	113	23	8.0***
1900	107	133	73	49	117	80	6.2**

Several miscellaneous variables are also shown in Table 1, such as "shift of acrophase." They and the fitted variables will be referred to as "processed" variables to distinguish them from the "hourly" ones.

Multivariate analysis of variance (MANOVA) and multidiscriminant analysis were used for comparison of species by groups of variables. These methods apply even where variables are highly correlated, which many of those here certainly are. On the basis of known group membership, discriminant analysis emphasizes variables that have a high ratio of among-group to within-group variation. Thus the variables are weighted so as to discriminate optimally between the groups (here species). An introduction to these methods is given by Cooley and Lohnes (1971), and application to behavioral research, by Pimentel and Frey (1978).

RESULTS

Daytime observations

For both species of *Pogonomyrmex* the total number out rose in early midday and remained high through the afternoon (Figure 1). For the other species the number rose in the afternoon and continued rising through the end of the light period.

In *V. pergandei* and *F. pilicornis* few ants ever came out as far as the arena; the rhythmic count was made up largely of those in the tube leading to the arena (Figure 1). In *V. andrei* the proportion in the tube was relatively high at the first and last of the light period. The proportion reaching the hot side of the arena was the greatest in *P. californicus*.

For most of the analyses, only these daytime observations were used.

24-hour observations

After 3 days very dim lights were left on at night, permitting counts then. It was now 6 days after collection from the field, and some of the ants were dead or else came out into the tubes or arenas less frequently. Nevertheless the patterns for the "day" part of the cycle were similar to before. And now it could be seen that all six species were prominently out in the arenas during the night.

That this nocturnal behavior might be explained by the constant high temperature is suggested by field observations, Tevis (1958) found that nocturnal foraging of *V. pergandei* is rare, but could occur if temperatures are higher than normal; Wheeler and Rissing

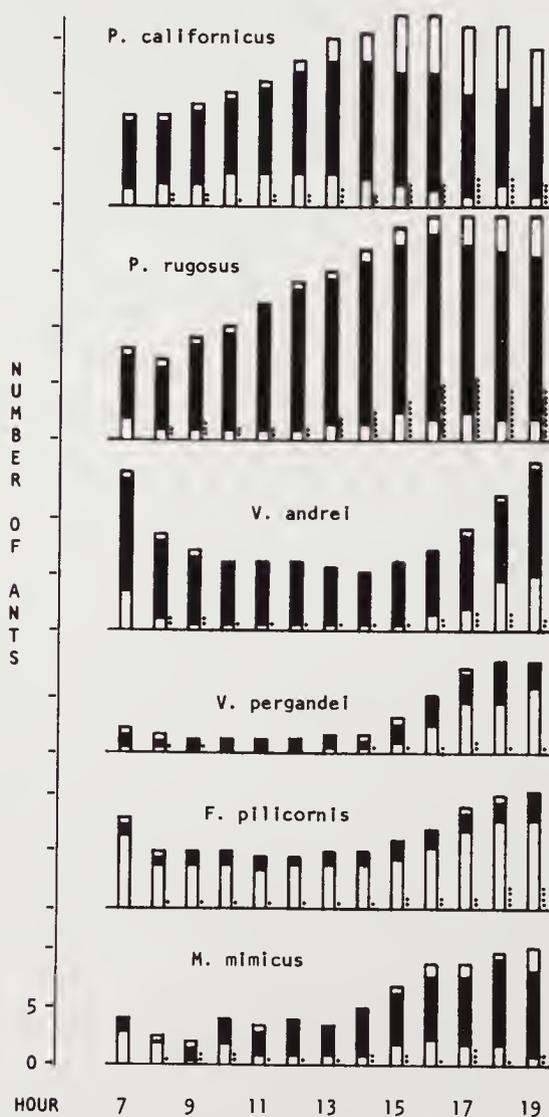


Figure 1. Comparative time patterns during light part of light-dark cycles. Histograms based on raw counts averaged over the 3 days (May 27-29) and 5 replicate nests (1 nest for *M. mimicus*) for each species. Each bar represents total number of ants out at a given observation: bottom part, tube count; middle (shaded), warm half of arena; top, hot half of arena. Dotted line to right of bar represents number active of total number out (omitted for 0700).

(1975) found it to be common in the summer. McCluskey (1963) reported foraging in *V. andrei* on warm nights. *P. californicus* sometimes works at night (Cole 1932), and *P. rugosus* does so when warm (Whitford and Ettershank 1975).

Evaluation of variables as taxonomic characters

By virtue of the replicates it was possible to test each variable for species difference by one way analysis of variance, or in the case of phase variables, by the circular distribution test of Watson and Williams (1956) (Table 1). The differences are significant for 42 of the 51 hourly and 18 of the 23 processed variables, suggesting value as species characters. The hourly variables for the last third of the day are more discriminating than those earlier.

Thus most of the individual variables distinguish species at least in a general way. As a group would they distinguish between the members of each pair of species? Multidiscriminant analysis was used to answer this (somewhat as Brown and Shipp, 1977, did to evaluate wing morphometric characters).

M. mimicus, with only one replicate, was omitted. MANOVA indicates a significant ($P < .01$) difference among the other five species, whether based on processed or on hourly variables. Therefore it is appropriate to use multidiscriminant analysis for further examination of the differences. For the set of processed variables, Figure 2 shows the maximum discrimination possible in two-dimensional space. The replicates are well segregated into their respective species. The same was true if based on either of the two stratified subsets of 17 hourly variables tried (not shown). Further analysis is not attempted here because of small sample size.

The method was checked by deliberately assigning half the replicates initially to incorrect species. The variables then failed to segregate the replicates well into the artificial species, or even to show a significant species difference by MANOVA.

Later experiment

As laboratory projects in a comparative physiology course, the same species of *Pogonomyrmex* and *Veromessor* were compared simultaneously as before, but the conditions were different. Most notably, the season was October instead of May; and the temperature was cycled between 20° C at night and 30° (35° in hottest part of arena) at midday, instead of being held constant.

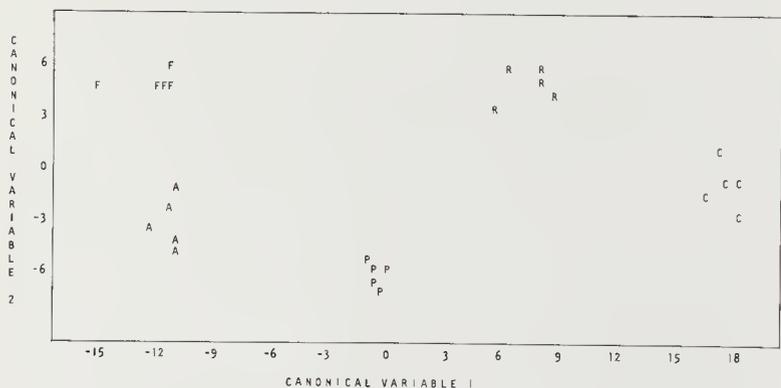


Figure 2. The first two canonical axes, based on all 17 processed variables for which every one of the 25 cases (5 species \times 5 replicates) was represented, and for which (phase variables) distribution was across few enough hours to assume linearity. The first axis represents the greatest possible difference between species, and the second, the greatest remaining difference orthogonal to the first. Output from the BMDP7M program, run so as to bypass the stepwise feature (as recommended by Pimentel and Frey, 1978). A = *V. andrei*; C = *P. californicus*; F = *F. pilicornis*; P = *V. pergandei*; R = *P. rugosus*.

The results again suggest taxonomic differences in rhythm. The cosine-fitted acrophases of number out differed ($P < .01$) among the four species.

DISCUSSION

The study conditions were highly artificial—colony fragments (workers only, and in small number), no soil in the nest, temperature high all 24 hours, etc. The fact that the rhythms were nevertheless striking indicates that at least some of the natural field conditions (e.g., temperature cycle) are not necessary for such behavior.

But the important thing was that the six species were now all under the same conditions. Evidently various species manifest different patterns of rhythm even though in identical habitat; or to put it another way, it is not necessarily differences in field habitat that are responsible for the differences in rhythm. For a laboratory example of phase or pattern difference in another insect group, see Hardeland and Stang's (1973) comparison of 40 species of *Drosophila*.

Many location and activity variables were tested in the six species for their potential as taxonomic characters, including cosine-fitted rhythm parameters as well as simple hourly values (Table 1). For most of them the species difference was significant.

By contrast with the fitted-rhythm and other processed variables, the hourly variables taken singly can indicate only the level (of activity or location) at a given hour. In the aggregate they become more meaningful. For example, scanning the hourly P values in Table 1 indicates one time of day to be more important than another in distinguishing species. Or more formally, a multivariate approach can compare in terms of the whole hourly pattern. MANOVA confirmed the overall species difference, and multidiscriminant analysis made it possible to discriminate each species from the others. It should be noted again that the purpose here is to examine these variables as taxonomic characters, rather than to develop a classification.

Nearly every one of the processed variables was abstracted from all the hourly values of a given type of assay, and hence should have high information content. So it is noteworthy that the groups of hourly variables seemed to distinguish species about as well as the group of processed ones. However, if some of both kinds were included in the same analysis, the most highly weighted were processed variables.

How might the list in Table 1 be compared with catalogues of ant behavior, such as that of Wilson (1976)? In the first place, the variables reported here were population rather than individual phenomena. Secondly, many of them are derived rhythm parameters (e.g., acrophase or amplitude) of certain items of behavior, rather than the behavior itself. The hourly variables, on the other hand, do represent behavior more directly (e.g., the number active or the number in the hot location, at a given point in time). Any comprehensiveness of catalogue (e.g., for choice of heat or light or location in the nest assembly) would require more habitat complexity, and preferably field studies as well. But such comprehensiveness is needed to facilitate behavioral comparisons at species or higher levels (Wilson 1976).

In summary, this study suggests a variety of rhythm-related characters that might be observed in laboratory or field, whether single hourly values, composite hour-by-hour patterns, or fitted rhythm parameters.

SUMMARY

In the field the time of day of certain types of behavior distinguishes various species and genera. Would the same be true if their habitats were made identical? And could rhythm-related variables in general be regarded as taxonomic characters? Groups of workers of *Pogonomyrmex californicus*, *P. rugosus*, *Veromessor andrei*, *V. pergandei*, *Formica pilicornis*; and *Myrmecocystus mimicus* were studied simultaneously in constant temperature and alternating light and dark. A hot dry area and a dark humid area were available in each nest for choice at all hours. This permitted different types of position or activity assays and the calculation of several cosine-fitted rhythm parameters for each. These as well as simple hourly values served as variables. For most of the variables tested there was a significant species difference. With multidiscriminant analysis it was possible to go beyond this general species difference and segregate the replicates of each species from those of other species; either the hourly or the more highly processed variables were adequate here. This study suggests a variety of rhythm-related characters that might be observed in laboratory or field.

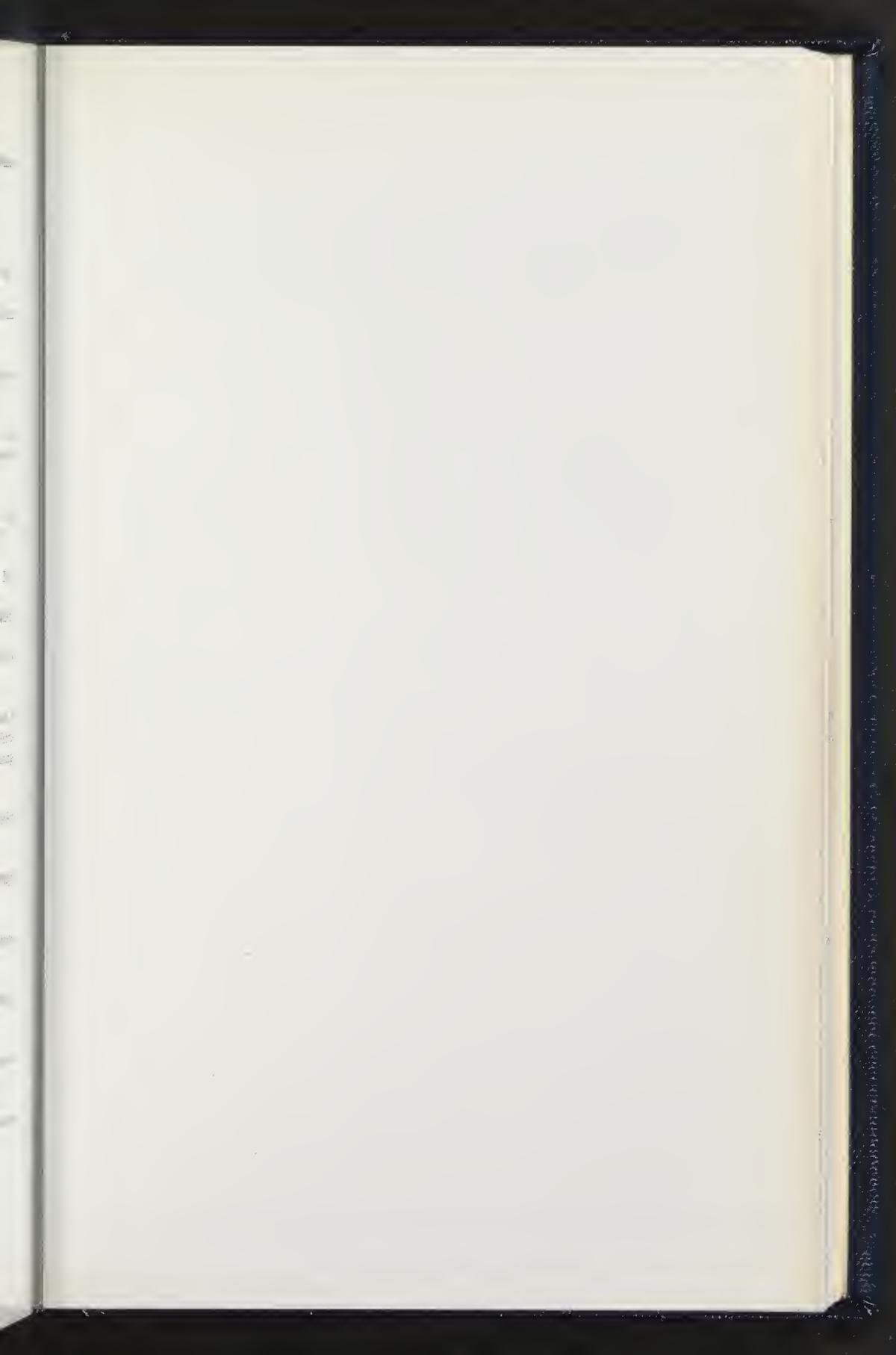
ACKNOWLEDGMENTS

The data on which this report is based are largely from the second author's M.A. thesis research (Loma Linda University, 1975). We thank André Francoeur for determining *F. pilicornis* and Roy Snelling, *M. mimicus*; Glen McCluskey and Duane Zimmerman for programming; Paul Yahiku and Richard Pimentel for statistical help; and Leonard Brand, Conrad Clausen, David Kissinger, Gerald Scherba and Paul Yahiku for reading earlier drafts of the manuscript. Computer time was supported in part by NIH, Grant RR-00276. Also used were BMDP programs developed at UCLA with NIH support.

LITERATURE CITED

- BROWN, K. R., AND E. SHIPP.
1977. Wing morphometrics of Australian Lucilini (Diptera: Calliphoridae). *Aust. J. Zool.* 25:765-777.
- COLE, A. C.
1932. Notes on the ant *Pogonomyrmex californicus*, Buckley (Hym.: Formicidae). *Entomol. News* 43:113-115.

- COOLEY, W. W., AND P. R. LOHNES.
1971. Multivariate data analysis. Wiley, New York.
- DIXON, W. J., AND F. J. MASSEY, JR.
1969. Introduction to statistical analysis, 3d ed. McGraw-Hill, New York.
- HALBERG, F., E. A. JOHNSON, W. NELSON, W. RUNGE, AND R. SOTHERN.
1972. Autorhythmetry—procedures for physiologic self-measurements and their analysis. *Physiology Teacher* 1(4):1-11.
- HARDELAND, R., AND G. STANG.
1973. Comparative studies on the circadian rhythms of locomotor activity of 40 *Drosophila* species. *J. Interdisc. Cycle Research* 4:353-359.
- HOLLDOBLE, B.
1976. The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioral Ecology and Sociobiology* 1:405-423.
- LÉVIEUX, J.
1977. La nutrition des fourmis tropicales: V.—Eléments de synthèse. Les modes d'exploitation de la biocoenose. *Insectes Soc.* 24:235-260.
- MCCCLUSKEY, E. S.
1963. Rhythms and clocks in harvester and Argentine ants. *Physiol. Zool.* 36:273-292.
1973. Generic diversity in phase of rhythm in formicine ants. *Psyche* 80:295-304.
1974. Generic diversity in phase of rhythm in myrmicine ants. *J. New York Entomol. Soc.* 82:93-102.
- MCCCLUSKEY, E. S., AND S. A. SOONG.
1978. Rhythm and other laboratory characters in a taxonomic comparison of ants. In Abstracts of papers of the 144th national meeting 12-17 February 1978 (ed. A. Herschman), p. 134. Amer. Assoc. Adv. Sci., Washington.
- PIMENTEL, R. A., AND D. F. FREY.
1978. Multivariate analysis of variance and discriminant analysis. Chapter 9 in *Quantitative Ethology* (P. W. Colgan, ed), Wiley, New York.
- TEVIS, L.
1958. Interrelations between the harvester ant *Veromessor pergandei* (Mayr) and some desert ephemerals. *Ecology* 39:695-704.
- WATSON, G. S., AND E. J. WILLIAMS.
1956. On the construction of significance tests on the circle and the sphere. *Biometrika* 43:344-352.
- WHEELER, J., AND S. W. RISSING.
1975. Natural history of *Veromessor pergandei*. II. Behavior. *Pan-Pacific Entomologist* 51:202-314.
- WHITFORD, W. G., AND G. ETTERS HANK.
1975. Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environmental Entomology* 4:689-696.
- WILSON, E. O.
1976. A social ethogram of the neotropical arboreal ant *Zacryptocerus varians* (Fr. Smith). *Anim. Behav.* 24:354-363.



The illustration on the front cover of this issue of *Psyche* is a reproduction of the published figure of a myrmicine ant from Bolivia, *Tingimyrme mirabilis*, described by W. M. Mann in *Psyche* (1926, vol. 33, p. 105).

CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room 154, Biological Laboratories, Divinity Avenue, Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

BACK VOLUMES OF PSYCHE

Requests for information about back volumes of *Psyche* should be sent directly to the editor.

F. M. CARPENTER
Editorial Office, *Psyche*
16 Divinity Avenue
Cambridge, Mass. 02138

FOR SALE

REPRINTS OF ARTICLES BY W. M. WHEELER

The Cambridge Entomological Club has for sale numerous reprints of Dr. Wheeler's articles that were filed in his office at Harvard University at the time of his death in 1937. Included are about 12,700 individual reprints of 250 publications. The cost of the reprints has been set at 5c a page, including postage; for orders under \$5 there will be an additional handling charge of 50c. A list of the reprints is available for \$1.00 from the W. M. Wheeler Reprint Committee, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138. Checks should be made payable to the Cambridge Entomological Club.

Psy 6188

ISSN 0033-2615

MUS. COMP. ZOOL
LIBRARY

JUN 25 1980

HARVARD
UNIVERSITY

PSYCHE

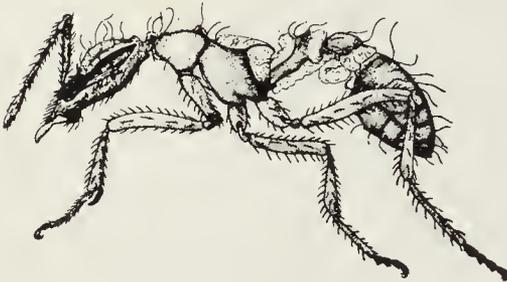
A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 86

June-September, 1979

No. 2-3



CONTENTS

The Natural History of the Flight of Honey Bee Swarms. <i>Thomas D. Seeley, Roger A. Morse, and P. Kirk Visscher</i>	103
Early Warning Cues for Social Wasps Attacked by Army Ants. <i>Ruth Chadab</i>	115
Life History and Behavior of the Case-Bearer, <i>Phereoeca allutella</i> (Lepidoptera: Tineidae). <i>Annette Aiello</i>	125
Seasonal Variation in Egg Hatching and Certain Egg Parameters of the Golden Egg Spider, <i>Nephila clavipes</i> (Araneidae). <i>T. E. Christenson, P. A. Wenzl, and Peter Legum</i>	137
Nesting Behavior of <i>Crabro argusinus</i> and <i>C. hilaris</i> (Hymenoptera; Sphecidae). <i>Robert W. Matthews, Allan Hook, and Joan W. Krispyn</i>	149
Nearctic Species of the Wolf Spider Genus <i>Trochosa</i> (Araneae: Lycosidae). <i>Allen R. Brady</i>	167
Selective Mate Choice by Females of <i>Harpobittacus australis</i> (Mecoptera: Bittacidae). <i>John Alcock</i>	213
Neotropical Butterflies of the Genus <i>Anartia</i> : Systematics, Life Histories, and General Biology (Lepidoptera: Nymphalidae). <i>Robert E. Silberglied, Annette Aiello, and Gerardo Lamas</i>	219
Lower Permian Insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. <i>Frank M. Carpenter</i>	261
The Courtship Call of <i>Chrysopa downesi</i> Banks (Neuroptera: Chrysopidae): Its Evolutionary Significance. <i>Charles S. Henry</i>	291

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1979-1980

<i>President</i>	NORMAN WOODLEY
<i>Vice-President</i>	MATTHEW DOUGLAS
<i>Secretary</i>	HEATHER HERMAN
<i>Treasurer</i>	FRANK M. CARPENTER
<i>Executive Committee</i>	WILLIAM A. NEIL ROGER SWAIN

EDITORIAL BOARD OF PSYCHE

- F. M. CARPENTER (Editor), *Fisher Professor of Natural History, Emeritus, Harvard University*
ALFRED F. NEWTON, JR., *Curatorial Associate in Entomology, Harvard University*
W. L. BROWN, JR., *Professor of Entomology, Cornell University and Associate in Entomology, Museum of Comparative Zoology*
P. J. DARLINGTON, JR., *Professor of Zoology, Emeritus, Harvard University*
B. K. HÖLLDOBLER, *Professor of Biology, Harvard University*
H. W. LEVI, *Alexander Agassiz Professor of Zoology, Harvard University*
R. E. SILBERGLIED, *Associate Professor of Biology, Harvard University*
E. O. WILSON, *Baird Professor of Science, Harvard University*

PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: \$9.50, domestic and foreign. Single copies, \$3.50.

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

Orders for missing numbers, notices of change of address, etc., should be sent to the Editorial Office of Psyche, 16 Divinity Avenue, Cambridge, Mass. 02138. For previous volumes, see notice on inside back cover.

IMPORTANT NOTICE TO CONTRIBUTORS

Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

Authors are expected to bear part of the printing costs, at the rate of \$24.50 per printed page. The actual cost of preparing cuts for all illustrations must be borne by contributors: the cost for full page plates from line drawings is ordinarily \$18.00 each, and for full page half-tones, \$30.00 each; smaller sizes in proportion.

The March, 1979, Psyche (Vol. 86, No. 1) was mailed December 28, 1979

The Lexington Press, Inc., Lexington, Massachusetts

PSYCHE

Vol. 86

June-September, 1979

No. 2-3

THE NATURAL HISTORY OF THE FLIGHT OF HONEY BEE SWARMS

BY THOMAS D. SEELEY,¹ ROGER A. MORSE² AND
P. KIRK VISSCHER²

INTRODUCTION

The flight of honey bee (*Apis mellifera*) swarms is the most spectacular and yet one of the least understood aspects of honey bee social behavior. Over open countryside a flying swarm forms a small cloud, a swirling mass of some ten to twenty thousand individuals, loudly buzzing along at head height en route to a new home. There have been several studies of the behavior of a swarm as it emerges from its nest, clusters at an interim site, and there selects a new nest site (reviewed by Ambrose 1976 and Seeley and Morse 1978), but no one had ever recorded in detail the subsequent events of the long-distance flight to the new nest site. Moreover, a close analysis of honey bee swarm flight held the promise of clearly demonstrating division of labor within an insect society, in this instance between the scouts and nonscouts in honey bee swarms.

The present account treats only the period from agreement upon the new nest site to the entrance of the swarm into its new home. We took special pains to record events simultaneously at the interim cluster site and the new nest site throughout this period. Only in this way could we begin to picture the full complexity of the social organization underlying honey bee swarm flight.

MATERIALS AND METHODS

Study Sites. Most of the study was conducted in August 1979 at the Shoals Marine Laboratory on Appledore Island, Maine. This treeless, 39-ha island lies 16 km offshore and lacks natural nest sites for

¹Museum of Comparative Zoology, Cambridge, Massachusetts, 02138

²Department of Entomology, Cornell University, Ithaca, N.Y. 14853

Manuscript received by the editor November 22, 1979.

honey bees. Thus the swarm of bees we took to the island was forced to adopt the nestboxes we provided, and this simplified observing events at both the swarm's cluster site and future nest site. Besides this island work, we made one preliminary measurement of swarm flight velocity during July 1979 at the Dyce Laboratory, Cornell University.

Swarm Preparation. Artificial swarms were prepared from colonies at Dyce Lab using the standard techniques described by Seeley (1977). The genetic composition of each of these swarms was a mixture of the various honey bee races imported for American apiculture. However, the bees were light brown and so apparently were primarily of *Apis mellifera lingustica* (Italian bee) stock. The swarms weighed about 1400 g and so contained approximately 11,000 bees, a typical size for natural honey bee swarms (Fell *et al.* 1977).

Experimental Layout and Recording Techniques. We positioned the Appledore Island swarm on the island's western shore between Babb's Cove and Pepperrell Cove. We forced the swarm to cluster on a wooden cross (150 cm high with a 46-cm-long cross member) by confining the swarm's queen in a Benton mailing cage for queens, lashing this to the cross, and then releasing the swarm's workers. When they were fully clustered around the caged queen, we uncorked her cage so she could later fly away with the swarm. A 1-liter feeder jar filled with a 50% sucrose solution provided a constant food supply for the swarm.

We observed the island swarm perform two complete flights to a new nest site. Unless stated otherwise, the observations reported below are based on this swarm's second flight. The first flight was to a 5-frame hive placed 350 m away in the storage shed behind the Coast Guard building. After making this flight, the swarm was carried in the hive back to the wooden cross, its queen was recaged, and its workers were repositioned on the cross. The second flight followed the same line as the first, but continued along it for a considerably greater distance, approximately 580 m. The second flight's nest site was a 40-liter bait hive (Morse and Seeley 1978) placed inside a small, lean-to shelter beside Devil's Glen on the easternmost point of the island.

We measured the Appledore swarm's flight velocities by laying out a series of 13 stakes spaced 30 m apart starting from the wooden cross and continuing out along the line leading to the nest sites. This

line of markers was complete for the nearer nest site, but did not reach the farther one. Unbroken stretches of poison ivy shrubs (*Rhus toxicodendron*) prevented us from extending the line of spaced stakes beyond 390 m. We timed the swarm's passing of each distance marker when the swarm cloud's center was over a marker.

Observations at the swarm cluster and nest site were coordinated using walkie-talkies. Because events unfolded very rapidly during swarm flights, we recorded our observations using continuously-running tape recorders.

The flight velocity of the Dyce Lab swarm was measured using a different technique than described above. We placed the swarm on a cross just as already described, but allowed it to select a nest site freely in the woodlands about the laboratory. We measured its flight velocity by sprinting along beneath the flying swarm and periodically jabbing marker stakes in the ground. Time intervals between stakes were recorded by carrying a continuously-running tape recorder and noting aloud the moment of each stake's placement; distance intervals were later measured using a steel tape. Unfortunately, because of fences and tracts of brush, we could not follow the swarm all the way to its nest site.

Labelling Scout Bees. A fraction of the scout bees in the Appledore Island swarm were labelled before the swarm's first flight by painting a blue dot on every bee that danced for our nestbox. The paint was shellac mixed with artist's pigment, as described by von Frisch (1967).

RESULTS AND DISCUSSION

1. *Return of Scouts from Nest Site to Swarm Cluster*

Observations made during studies of nest site hunting by honey bees (Lindauer 1955, Seeley 1977) suggested that once a swarm has decided which nest to occupy, the next step in the swarm movement process is the return of the scouts at the nest site to the swarm cluster. To document this phenomenon we made a count every 30 sec, starting 75 min before the swarm lifted off, of the number of scouting bees visible at the nest site. To simultaneously monitor the accumulation of scouts back at the swarm, we made periodic counts of the number of blue-marked scouts visible on the swarm cluster.

The return of the scouts is clearly shown in Fig. 1. Starting about 30 min before lift-off the number of bees at the nestbox began to decline; the number of marked scouts on the swarm was simultane-

ously increasing. Buzzing runs (*Schwirrlaufen*) performed by some scouts at the nest site apparently triggered this retreat, since their occurrence coincided with the start of the scouts' departures (see Fig. 1). Moreover, buzzing runs have been observed in two other contexts involved in swarming—when a swarm first leaves its nest, and later when a swarm lifts off from its interim cluster site; and in both cases the buzzing runs seem to signal "Let's go!" (Lindauer 1955, Martin 1963).

We counted all buzzing runs performed on the outside of the nestbox during each interval, but probably the majority were performed inside. The behavior of the buzz runners (*Schwirrläuferin*) we observed matched the descriptions of Lindauer (1955), Martin (1963), and Esch (1967) for buzz runners observed during nest departure and swarm lift-off. They made excited zig-zag runs over

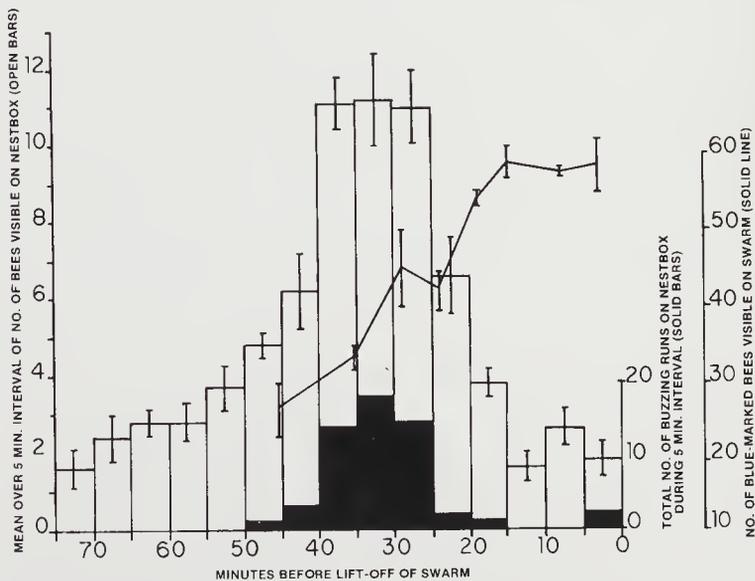


Fig. 1. Mean over 5 min interval of counts each 30 sec of the number of bees visible on the nestbox (open bars, left scale), total number of buzzing runs observed on the nestbox during 5 min interval (solid bars, near right scale), and number of blue-marked scouts visible on the swarm cluster at various times (solid line, far right scale) as time of swarm flight approached. Vertical bars denote plus and minus one standard error. Counts document the return of the scouts from the nest site to the swarm cluster in preparation for the swarm's flight to the nest site. Buzzing runs at the nestsite apparently trigger the scouts' return.

the nestbox surface, punctuated by bursts of wing buzzing. They would butt against individual nestmates and, buzzing steadily, attempt to bulldoze through small clusters of scouts. Esch's (1967) analysis of these movements reveals that when running about a buzz runner produces short pulses of 180-250 Hz wing vibrations, and then shifts to steady blasts of 500 Hz buzzing when contacting other bees.

The importance of the scouts' return to the swarm was revealed when we measured what fraction of the swarm had visited the nest site before the entire swarm flew there. This was done while awaiting the island swarm's first flight by recording over the last 60 min before lift-off the fraction of bees visible at the nestbox that were marked with blue. We marked 143 bees; the percentage of blue-marked bees among the bees observed at the nestbox, based on 130 counts, was $28.9\% \pm 16.3\%$ ($\bar{x} \pm 95\%$ confidence margins). Thus approximately 495 bees from the swarm (95% confidence limits: 316-877 bees), or only about 5% of the swarm, had visited the nest site before lift-off.³ Evidently only a very small minority of a swarm's bees knows the precise location of the new nest site, and it is their task to guide the large majority to the new home. Because the ratio of ignorant to informed (scout) bees is so large, it appears important that as many scouts as possible be back at the swarm when lift-off occurs to guide the swarm to the new nest site.

2. *Lift-off of Swarm*

Upon returning to the swarm, some of the blue-marked scouts sat quietly on the swarm cluster, others resumed their dances advertising the chosen nest site, and still others began performing buzzing runs across the swarm's surface. The first vigorous, distinct buzz runner was sighted 43 min before lift-off, the second at 33 min, the third at 26 min, and by 18 min before lift-off 4 vigorous buzz runners were seen simultaneously scrambling over the swarm. Concurrent with the rise in buzzing run frequency came an increase in the intensity of a much higher-pitched piping sound. We could neither identify which bees were producing this sound, nor had we the means of characterizing it or of quantifying its intensification.

³This 5% estimate is actually an overestimate since only 46 of the 143 blue-marked bees had been painted by the time the proportion counts began at the nest box. Therefore early estimates of the proportion of marked bees were smaller than if all 143 bees had been marked and so, in turn, the net average of 28.9% of the nestbox bees being marked is an underestimate of the fraction of scouts which were painted.

Perhaps this is the 5000 Hz sound which Esch (1967) found superimposed on the 500 Hz wing buzzes generated by buzz runners.

In the final 3 min preceding lift-off, the swarm teemed with buzz runners scrambling over the clustered bees, vibrating their wings and boring through the interlocked nets of hanging bees. A loud humming noise radiated from the cluster, a mixture of the deep wing buzzes and shrill piping sounds. This climaxed as the once solid surface of the swarm appeared to melt as the chains of hanging bees began disintegrating, and within 50 more sec the entire swarm was airborne, filling the air with the roar of 11,000 bees tightly circling just overhead.

3. Cross-Country Flight of the Swarm

The movement of the airborne swarm began very slowly. Fig. 2 shows that in both flights the island swarm traversed the first 30 m with an average velocity of just slightly over 1 km/h. This slow start may reflect the swarm's checking for the airborne presence of the queen, signalled by the odor of (E)-9-oxodec-2-enoic acid (Avitabile *et al.* 1975), or the difficulty of getting the thousands of bees moving en masse in the proper direction, or both. Immediately after lift-off the swarm cloud was circular in horizontal cross-section, with a diameter of about 10 m, as estimated from the 30-m-spaced stakes along the flight path. Its vertical cross-section was roughly circular, though with the bottom somewhat flattened along an imaginary line about 2 m above the open ground.

Not all the swarm's bees stayed with the slow-moving swarm cloud; a few shot out ahead to the nest site where they settled at the nest entrance and began releasing assembly pheromones from their Nasanov glands (reviewed by Wilson 1971, Michener 1974). Fig. 3 shows that there were 2 bees visible and scenting at the nest site 580 m away even before the swarm cloud had crossed the 30 m marker.

By the time the swarm had flown 60 m, its velocity had increased to over 4 km/h and it continued to increase through at least the 210 m mark to 8.5 and 11.0 km/h maximum speeds on the first and second flights, respectively (see Fig. 2). Swarm shape also changed over the first 60 m. The swarm cloud became more flattened top-to-bottom so that its vertical cross-section was ovoid, about 10 m long and 3 m high. The swarm's front was angled upward slightly, with the bottom of the swarm about 1 m above the tops of the bushes,

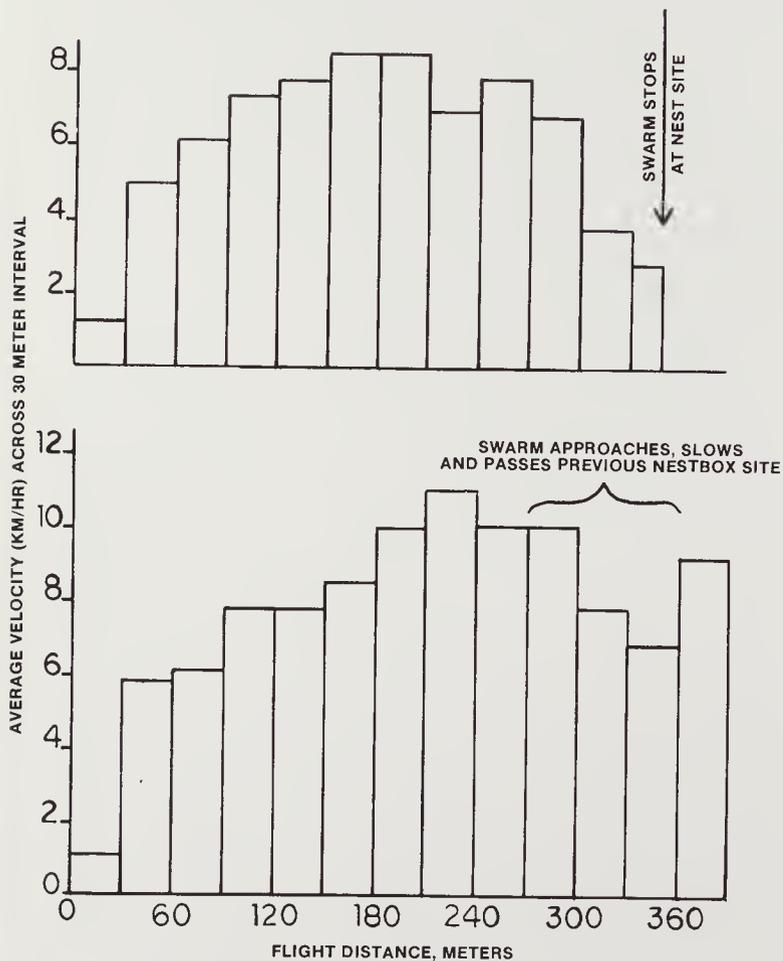


Fig. 2. Swarm flight velocities at various distances along the flight path. First flight (*top plot*) went 350 m and its velocities were measured throughout its flight. Second flight (*bottom plot*) went 580 m which was beyond the range of velocity-recording markers (see text for details). Note the slow start of both flights and the braking over the last 80 m in the first flight. The swarm also slowed upon approaching the first nest site on its second flight, but then again accelerated once past the first nest site.

thus about 3 m above the earth's surface. The bees were dispersed throughout the swarm cloud; although density increased toward the center, there was no tight central cluster.

Even though the two swarm flights observed on Appledore Island involved relatively short distances (350 m and 580 m) the maximum flight speeds stated above may be representative for swarms making much longer flights. The Dyce Lab swarm, which flew more than 2000 m to its nest site, flew between stakes 435 and 605 m from its cluster site with an average velocity of 11.1 km/h. Beyond the 605 m point a fence and a field of brush prevented us from keeping even with the swarm, and so further velocity measurements could not be made. However, we feel that beyond the 605 m point the swarm increased its velocity little, if at all.

One riddle about swarm flight is the mechanism whereby scouts direct the other swarm bees toward the nest site. Lindauer (1955) observed bees streaking through a swarm in the direction of the nest site, and has suggested that these streaker bees are the swarm's scouts pointing the way. We have repeated Lindauer's observation of streakers; a small proportion of the bees in the swarm were moving rapidly in a direction generally oriented toward the nest site, amidst the slower, more wavering flight of their sisters. Avitabile and his coworkers (1975) suggested another mechanism of swarm guidance: scouts somehow lead swarms by releasing Nasanov pheromone. They report leading airborne swarms along zig-zag pathways, though in the general direction they would fly anyway, using an artificial mixture of the Nasanov secretion. One problem with their experiment is that they may have been providing the orientation signal used by swarms at the very end of their flights (see below), and so have influenced the swarms' flight patterns, but without duplicating the principal guidance system of swarms. This could be checked for by testing the orientation ability of a swarm whose members have had their Nasanov glands sealed shut with shellac.

The island swarm ended its two flights with quite elegant braking so that in both cases the swarm's center stopped within 10 m of the nest sites. The velocity plot in Fig. 2 (upper plot) indicates that the braking began at least 80 m before reaching the nest site. However, the mechanism of this braking, like that of the directional guidance, remains a mystery.

4. *Entry in the Nest Cavity*

Within seconds of the swarm cloud's stopping near the nest site,

the number of bees releasing Nasanov pheromone at the nest entrance increased dramatically. Fig. 3 shows that 22 sec after the swarm arrived 5 scenters had appeared at the entrance opening. Within another 35 sec their number had leaped to 35-40. These initial scenters were primarily the swarm's scouts. Of the first 9 bees scenting at the nest entrance, 5 (56%) carried blue marks. Even after over 100 bees, about half of them scenting, were visible at the nest entrance, 25% of the total was composed of marked bees. Because the blue-marked scouts were only 1.3% of the swarm population, it is clear that these scouts were contributing disproportionately in the

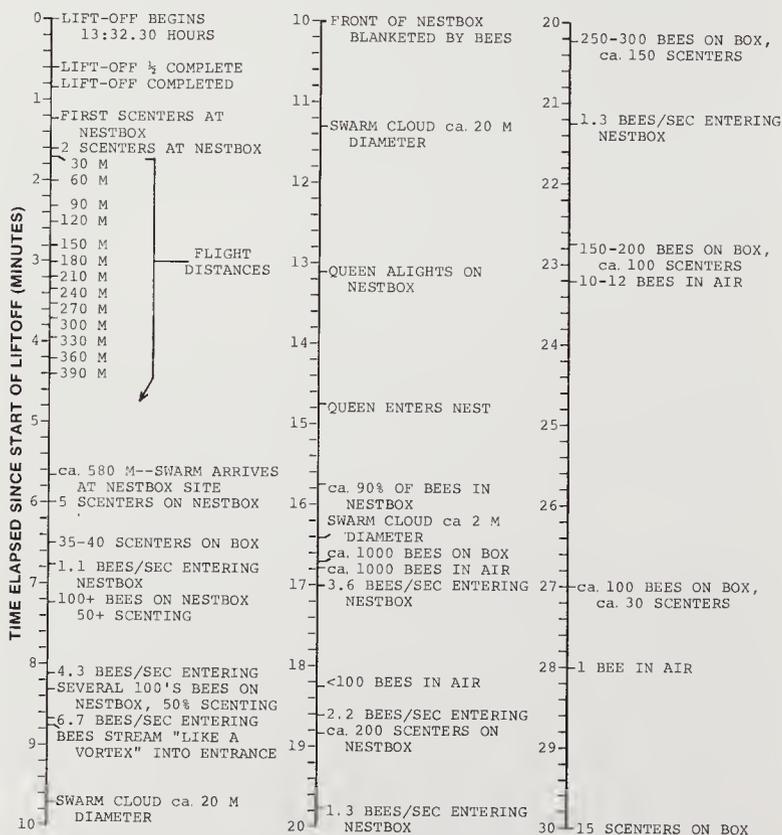


Fig. 3. Time line of events during the flight of a honey bee swarm and its subsequent entry into a new nest site. Note how within 30 min a swarm of about 11,000 bees broke cluster, flew 580 m, and moved completely into a new nest cavity.

earliest stages of signalling the location of the new nest entrance. This is logical, for at first only the scouts know the entrance location, and in nature the entrance opening—a small knothole, a little gap among the roots of a tree, or a narrow crack in a limb—can be quite inconspicuous. Thus, once the scouts had directed the swarm to the vicinity of the new nest site, they dropped out of the swarm cloud to pinpoint the nest's entrance chemically. The early unmarked scouters had probably scouted the nest site, but had not danced at the swarm cluster.

The remaining details of the swarm's entry into the nest cavity are presented in Fig. 3. In general summary, within 3 min of the swarm's arrival, bees had blanketed the nestbox's outer surface and were streaming into the nest cavity at nearly 7 bees/sec, forming a twisting, whirlpool-like swirl of bees flowing into the entrance. In 9 min the queen entered. The bees did not require her presence in the nest to move inside, as they had to fly there. Within 10 min about 90% of the bees had entered, and finally, within 30 min of lift-off, nearly all 11,000 bees were safely inside their new home.

ACKNOWLEDGMENTS

We thank Dave De Jong, Robin Hadlock, Chris Kelley, Richard Nowogrodzki, Ken Ross, Jim Soha, and Lucia Turillo for help in chasing flying swarms. The Shoals Marine Laboratory community kindly tolerated hordes of honey bees zooming across their island. Supported by the American Philosophical Society.

SUMMARY

The social organization of honey bee swarm flight was studied throughout the period extending from completion of nest site selection, through cross-country flight, to entry into the nest cavity. First the scouts, numbering about 5% of the swarm, return from the nest site to the swarm cluster. Thus they are present at lift-off to guide the swarm's flight. Buzzing runs at the nest site trigger their return. Lift-off takes less than 60 sec and is also stimulated by buzzing runs. The airborne swarm forms a circular cloud about 10 m in diameter and 3 m high. The flight starts very slowly, but accelerates to a velocity of 11 or more km/h. Some scouts pilot the swarm, apparently by performing streak flights through the swarm cloud, while others fly ahead to the new nest's entrance and release assembly

pheromones. The swarm halts upon reaching the nest site, whereupon more scouts drop out of the swarm cloud and begin releasing assembly pheromones at the nest entrance to help pinpoint its location. During the next 20 min the bees flood into the nest cavity and so complete the swift, clean process of warm movement.

REFERENCES

- AMBROSE, J. T.
1976. Swarms in transit. *Bee World* **57**, 101-109.
- AVITABILE, A., R. A. MORSE AND R. BOCH
1975. Swarming honey bees guided by pheromones. *Ann. Entomol. Soc. Amer.* **68**, 1079-1082.
- ESCH, H.
1967. The sounds produced by swarming honey bees. *Z. vergl. Physiol.* **56**, 408-411.
- FELL, R. D., J. T. AMBROSE, D. M. BURGETT, D. DE JONG, R. A. MORSE AND T. D. SEELEY
1977. The seasonal cycle of swarming in honey bees. *J. apic. Res.* **16**, 170-173.
- FRISCH, K. VON
1967. *The dance language and orientation of bees*. Belknap Press of Harvard University Press, Cambridge, Mass., 566 pp.
- LINDAUER, M.
1955. Schwarmbienen auf Wohnungssuche. *Z. vergl. Physiol.* **37**, 263-324.
- MARTIN, P.
1963. Die Steuerung der Volksteilung beim Schwärmen der Bienen. Zugleich ein Beitrag zum Problem der Wanderschwärme. *Insectes Sociaux* **10**, 13-42.
- MICHENER, C. D.
1976. *The social behavior of the bees. A comparative study*. Belknap Press of Harvard University Press, Cambridge, Mass., 404 pp.
- MORSE, R. A. AND T. D. SEELEY
1978. Bait hives. *Glean. Bee Cult.* **106**, 218-220, 242.
- SEELEY, T. D.
1977. Measurement of nest cavity volume by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **2**, 201-227.
- SEELEY, T. D. AND R. A. MORSE
1978. Nest site selection by the honey bee, *Apis mellifera*. *Insectes sociaux* **25**, 323-337.
- WILSON, E. O.
1971. *The insect societies*. Belknap Press of Harvard University Press, Cambridge, Mass. 548 pp.

EARLY WARNING CUES FOR SOCIAL WASPS ATTACKED BY ARMY ANTS*

BY RUTH CHADAB

Biological Sciences Group, University of Connecticut
Storrs, Connecticut 06268

Colonies of social insects are well protected from most intruders by stings, bites, defensive chemicals, and nest architecture (Wilson 1971, Jeanne 1975). Army ants of the Neotropical genus *Eciton*, however, prey heavily on a wide variety of ants (Formicidae) and social wasps (Vespidae:Polistinae) (Rettenmeyer 1963, Schneirla 1971). Natural and staged raids observed on Barro Colorado Island, Panama Canal Zone, revealed how army ants break through defensive barriers of insect colonies. Surprisingly, though social wasps are often aggressive and larger than army-ant workers, most showed little or no attempt to defend their colonies and usually abandoned their nests after only brief contacts with the invading ants. Such rapidity of departure suggests 1) that the wasps use some mechanism other than direct contact with the raiding ants to detect the threat, and 2) that the wasps may "recognize" army ants with some specificity. To investigate these two possibilities the social wasp species *Protopolybia exigua binominata* (Schulz) was observed during raids and tested for its ability to detect army ants.

OBSERVATIONS AND TESTS

Protopolybia exigua is a small (length = 5mm) social wasp that makes a flat oval or hexagonal nest 4 to 12 cm long (Fig. 1). The single horizontal comb is attached to the underside of a leaf by several short petioles and is enclosed by a carton envelope having a small entrance near the edge of the upper nest surface. There may be 30 to several hundred adult wasps in a colony. Nests are attached to a variety of plants, usually on leaves one to 4 m above the ground, at sites which are frequently explored by raiding army ants. Colonies of this wasp were observed to be raided by *Eciton burchelli* four times and by *E. hamatum* 10 times during two study periods totaling 19 weeks on Barro Colorado Island.

*Manuscript received by the editor September 3, 1979



Fig. 1 Nest of *Protopolybia exigua* on the underside of a palm leaflet with wasps showing group alarm behavior. Arrows indicate two of many individuals giving alarm.

As soon as army ants approached within several centimeters of a *P. exigua* nest, wasps rushed to the lower nest surface and adjacent leaf. One to several wasps fanned their wings intermittently, and simultaneously produced a buzzing sound. Within seconds other wasps joined in the sound production, and the initial disorganized fanning and buzzing became regular, synchronous pulses. This complex synchronized behavior is termed "group fanning." The buzzing was most likely produced by the vibration of the thoracic skeleton by the indirect flight muscles. Fanning without sound production is a generalized behavior pattern, but fanning with buzzing was observed only in alarm situations.

Not all the wasps in the colony participated in the alarm: the number varied from several to 20 or more, depending in part on the strength of the alarm stimulus. Each buzz was about 0.9 sec long, followed by a 1.3 sec pause, and during its production the tip of the wasp's gaster was pressed to the substrate with head and front legs lifted (Figs. 1, 2). Between pulses the body returned to the normal

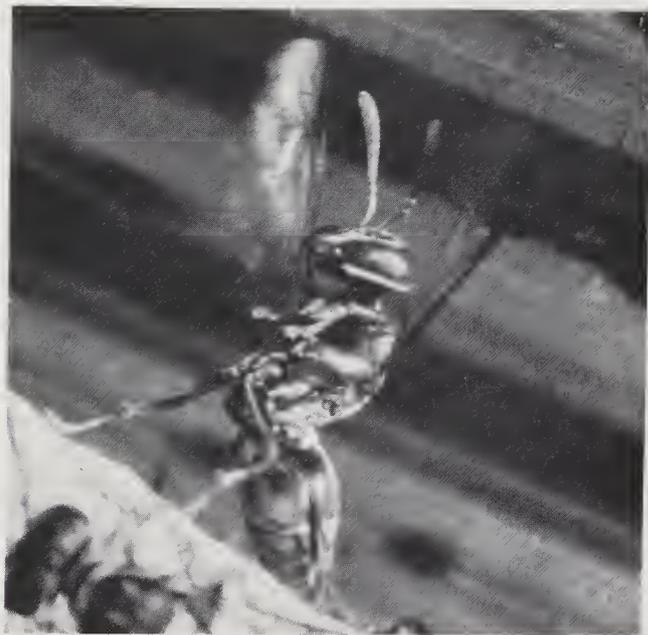


Fig 2 *Protopolybia exigua* participating in group alarm: front legs raised, wings fanning, and gaster pressed to substrate. A few wasps may begin the alarm; others join in.

resting position. Contact between the gaster and carton during the buzzing vibrated the envelope and nest leaf probably communicating alarm to other wasps (West-Eberhard 1969: 16, Naumann 1970: 120). Naumann (1970) described a similar behavior for *Protopolybia acutiscutis* (= *pumila*), but it has not been reported for other polistine genera.

Group fanning continued until the first three or four army ants ran onto the nest. At that point the wasps flew from the nest in unison. In one raid observed, army ants ran back and forth for 10 minutes on the leaf supporting a wasp nest before making actual contact with the wasps; the wasps exhibited group fanning during the entire period.

Clearly, the wasps did not use physical contact to detect the army ants; the form, movement, or odor of the army ants probably alarmed the wasps. The efficacy of a visual cue in eliciting alarm from the wasps was tested by placing a single army ant in a clear, sealed vial and holding it in 30-cm forceps 1 cm from a *P. exigua* nest. Tests were conducted only when there was a minimum of three wasps on the nest surface. As a control the same vial (ant inside) was covered with opaque tape and was tested similarly. During the tests the army ants typically ran back and forth in the vial. A third test was therefore done to investigate the effect of movement of the ant: a dead ant was placed in a clear, sealed vial and tested.

The responses of the wasps were scored in 3 categories: alarm (group fanning), "alert", and no response (Table 1). The moving ant consistently elicited alarm, the dead ant alert, and the control vial no response. These results demonstrate that the movement of the army ant is an important component of the alarm cue. However, numerous other observations on *P. exigua* showed that the wasps' response to a moving army ant was not specific but a generalized alarm response to small moving objects. Phorid flies, spiders and various non-army-ant species elicited alarm when wasps saw them or their shadows through the leaf to which the nest was attached. Tips of forceps elicited alarm when moved rapidly back and forth above a nest leaf but not when held motionless.

To test whether odors of army ants might also elicit alarm from the wasps two procedures were used: 1) single army ants were crushed in forceps, concealed between the tips and held 1 cm from a nest for 2 min, or 2) 10 whole army ants were extracted in 1 ml of solvent (methylene chloride) and 10 μ l of the extract applied to the

Table 1. Response of *Protopolybia exigua* to visual tests of army ants in vials.

Test	Group Fanning	Alert	No Response
moving ant	14	1	0
dead ant	1	5	5
moving ant concealed	0	1	12

end of a strip of paper 1×7 cm which was then held 1 cm from a nest for 2 minutes. Clean forceps and paper strips with $10 \mu\text{l}$ of solvent were similarly tested as controls. For comparison six other ant species were tested, either crushed or extracted, and 3 chemicals known to be components of ant pheromones were tested by applying $0.5 \mu\text{l}$ to a strip of paper and tested as for the ant extracts. Tests of clean forceps and untreated paper strips were controls for those tests. Tests were conducted at a total of 53 nests of *P. exigua*, and the number and order of tests varied at each nest (Table 2).

The wasps were tested for a response to 2 other army ants, *Nomamyrmex esenbecki* and *Neivamyrmex pilosus* in addition to *Eciton burchelli* and *E. hamatum*. Army ants of the former two genera have odors distinct from those of *Eciton* (Rettenmeyer 1963: 295), and though *Nomamyrmex* is known to raid wasps, such raids are probably rare (Chadab 1979). Non-army-ant species used in these tests were *Azteca* sp. and *Monacis bispinosa* (Dolichoderinae), *Camponotus sericeiventris* (Formicinae), *Ectatomma tuberculatum* and *Paraponera clavata* (Ponerinae), all of which are common terrestrial and aboreal scavengers and predators on other insects, but are not known to prey upon wasps.

Chemicals tested were 1) citral, an alarm substance which has been identified from the mandibular glands of 2 ant species in 2 subfamilies (Formicinae, Myrmicinae); 2) formic acid, which occurs in all members of the subfamily formicinae and is sprayed as an offensive-defensive chemical; and 3) 4-methyl-3-heptanone, which "appears to be the most widespread alarm pheromone. . . in the Formicidae" occurring in members of 4 ant subfamilies (Ecitoninae, Myrmicinae, Ponerinae, Pseudomyrmicinae) (Blum 1973 and references contained therein).

The wasps were commonly alerted by the test object, walking on the nest, raising their antennae, and orienting toward the object. Those activities demonstrated an awareness of the test object, but tests were considered positive only if at least 3 wasps participated in

Table 2. Group fanning of *Protopolybia exigua* to odors.

Tests	Trials	Group Fanning	
		N	%
Crushed single ants			
<i>Azteca</i> sp.	15	1	7
<i>Camponotus sericeiventris</i>	23	6	26
<i>Eciton burchelli</i>	40	28	70
<i>Eciton hamatum</i>	14	10	71
<i>Ectatomma tuberculatum</i>	9	0	0
<i>Paraponera clavata</i>	13	0	0
forceps control	27	2	7
Ant extracts			
<i>Eciton</i>	18	12	67
<i>Monacis bispinosa</i>	6	0	0
<i>Neivamyrmex pilosus</i>	8	0	0
<i>Nomamyrmex esenbecki</i>	10	1	10
solvent, methylene chloride	27	0	0
Chemicals			
citral	14	0	0
formic acid	11	8	73
4-methyl-3-heptonone	6	0	0
paper control	44	0	0

group fanning. The data summarized in Table 2 show that of all the crushed and extracted ants, chemicals, and controls tested, only the 2 *Eciton* species, *Camponotus sericeiventris*, and formic acid elicited group alarm in significant numbers of tests ($P < .005$, as determined by chi-square analysis). The response of *C. sericeiventris*, was significantly lower than to the *Eciton* species and the synthetic formic acid ($P < .005$). Most likely, formic acid which occurs in *C. sericeiventris* causes the alarm response of the wasps to that ant species as well. The 0.5 μ l of synthetic formic acid tested falls within the range of a single-ant amount (Stumper 1952), but the odor seemed subjectively stronger than the crushed *C. sericeiventris*. This may explain why the synthetic formic acid evoked group fanning more effectively than the crushed ant.

I conclude that *Eciton* odor is highly effective in eliciting alarm from *P. exigua*. Together, the 8 species of crushed ants and the 3 synthetic ant pheromones tested represent a selection of odors from all 6 Neotropical ant subfamilies (Brown 1973). If the alarm to *C. sericeiventris* is due to formic acid then only one substance other than *Eciton* odor actually evoked alarm. Although *P. exigua* does not respond exclusively to army-ant odor, the odor is a relatively specific alarm cue.

Another indication that the wasps discriminate army-ant odor with some specificity is the use by the wasps of primarily one alarm behavior in response to army ants. *P. exigua* possesses a repertoire of alarm responses: for example, disturbances which simulate a vertebrate predator such as my gently shaking the nest or my approach to the nest caused the wasps to retreat to the space between the upper surface of the envelope and the leaf; a sudden rap on the nest leaf caused the wasps to rush out onto the envelope flipping open their wings; while arthropods flying or walking next to the nest evoked buzzing and fanning by a single wasp and in some instances group fanning. Apparently, the wasps distinguish among types of disturbances and respond appropriately. This specific recognition of predator is similar to the "enemy specification" of the ant *Pheidole dentata* (Wilson, 1975).

Detection of army ants by sight and odor may be adaptive to the wasps for the following reasons. Once army ants discover a nest the wasps are unable to fend off the attack. The wasp brood cannot be rescued, but the adult population can flee and recolonize (Naumann 1975, Chadab 1979). Speed in evacuating the nest is crucial since the ants attack suddenly and in great numbers (Chadab and Rettenmeyer 1975). Using the sight or smell of army ants as a warning cue aids the wasps in preparation for a rapid evacuation: alarm is spread through the colony, the wasps run out of the tiny entrance in single file and spread out on the outside of the envelope. Flight occurs only after contact with the army ants, but the threshold for flight is reached with only one to several army ants. The wasps are able to fly instantly in almost a single wave. In most raids, nonetheless, several adults are seized by the ants because they are trapped inside the nest, become embattled with the first invading ants, or are sluggish tenacious adults. Without an advance warning many more wasps would probably be trapped inside, and the threshold for flight might depend on considerably more direct contact with the ants. The result would be higher mortality of adult wasps.

The adaptive ability of *P. exigua* to detect *Eciton* odor probably resulted from selective pressure exerted by army ants. Since army ants prey upon numerous species and prey colonies are usually cropped rather than destroyed, the effect of army ants on any one species might be considered weak or negligible. However, response of *P. exigua* to army ant predation is evidence that army ants have had a tangible effect on at least that prey species.

I have observed other wasp species leave their nest promptly when besieged by army ants and have found that 16 of 31 other polistines also become alarmed by *Eciton* odors (Chadab 1979). Forsyth (1978) also reported that 3 species of Polistinae responded to army ant odors. Numerous ant prey have also been observed to flee (with their brood in contrast to social wasps) in advance of an army-ant attack (pers. observ., Topoff 1975). Such evidence suggests that the early detection of army ants is common among ant and social-wasp prey and may be an important phenomenon in the invasion of social-insect colonies by army ants.

ACKNOWLEDGMENTS

The author wishes to thank C. W. Rettenmeyer for his advice and comments on the research and manuscript, M. S. Blum for providing chemicals, T. del Beliz for aid in the field, O. W. Richards for identifying the wasp, and C. S. Henry, R. L. Jeanne, M. G. Naumann for commenting on the manuscript. This research was supported by a Smithsonian Tropical Research Institute Visiting Research Student Appointment, NSF Grant BMS 75-03389 (C. W. Rettenmeyer, Principal Investigator), NSF Doctoral Dissertation Improvement Grant 76-11726 and a University of Connecticut Research Foundation Grant #35-902.

LITERATURE CITED

- BLUM, M. S.
1973. Comparative exocrinology of the Formicidae. Proc. VII Congr. IUSI, London, p. 23-40.
- BROWN, W. L.
1973. A comparison of the Hylean and Congo-West African rain forest ant faunas. p. 161-185 in Tropical forest ecosystem in Africa and South America: A comparative review, Betty J. Meggers, et al. eds., Smithsonian Institution Press, Wash. D.C.
- CHADAB, R.
1979. Army-ant predation on social wasps. Unpublished Ph.D. Thesis, University of Connecticut. 260 p.
- CHADAB, R. AND C. W. RETTENMEYER
1975. Mass recruitment by army ants. Science **188**:1124-1125.
- FORSYTH, A. B.
1978. Studies on the behavioral ecology of polygynous social wasps. Unpublished Ph.D. Thesis, Harvard University. 226 p.

JEANNE, R. L.

1975. The adaptiveness of social wasp nest architecture. *Quart. Rev. Biol.* **20**:267-287.

NAUMANN, M. G.

1970. The nesting behavior of *Protopolybia pumila* in Panama (Hym. Vespidae). Unpublished Ph.D. Thesis, University of Kansas. 182 p.

1975. Swarming behavior: Evidence for communication in social wasps. *Science* **189**:642-644.

RETENMEYER, C. W.

1963. Behavioral studies of army ants. *Univ. of Kansas Sci. Bull.* **44**:281-465.

SCHNEIRLA, T. C.

1971. Army ants: A study in social organization. H. R. Topoff, ed., Freeman, Calif. 349 p.

STUMPER, M. R.

1952. Données quantitatives sur la sécrétion d'acide formique par les fourmis. *C. R. Acad. Sci., Paris* **234**:149-152.

TOPOFF, H.

1975. Ants on the march. *Nat. Hist.* **84**:60-69.

WEST-EBERHARD, M. J.

1969. The social biology of polistine wasps. *Univ. Mich. Mus. Zool. Misc. Publ.* **140**:1-101.

WILSON, E. O.

1971. The insect societies. Belknap Harvard Univ. Press, Cambridge, Mass. 548 p.

1975. Enemy specification in the alarm-recruitment system of an ant. *Science* **190**:798-800.



LIFE HISTORY AND BEHAVIOR
OF THE CASE-BEARER
Phereoeca allutella
(LEPIDOPTERA: TINEIDAE)

BY ANNETTE AIELLO*
Smithsonian Tropical Research Institute
P. O. Box 2072, Balboa, Panamá

Phereoeca Hinton and Bradley (1956) is a genus of tropical moths, the larvae of which are casemaking scavengers that feed on animal hair and dead insects. In a communication to Lord Walsingham (1897) a Mr. Schulz wrote of them: "The Amazonian clothes moth [larval and pupal cases] . . . are very frequent in the houses in Para, keeping on the walls of the rooms and are very injurious to clothes." Although common, associated with human dwellings, and known for more than 80 years, little is known concerning their biology or distribution. Specimens are uncommon in collections. Hinton (1956) described the larvae of three species, but the distinctions among these are not clear and the size of the genus remains uncertain.

This paper, the result of studies done during April through August 1978, is a brief report of the life history and behavior of *Phereoeca allutella* (Rebel) on Barro Colorado Island (BCI), Panamá.

HABITAT

Larval and pupal cases (Figure 1) of *Phereoeca* are found on the outside walls and inside non-airconditioned buildings on BCI. They are most abundant under spiderwebs, in bathrooms and bedrooms. (BCI residents refer to them as "bathroom moths.") Adults may be seen flying or resting in these same areas as well.

Speculation as to where *Phereoeca* would live, if buildings were not available, lead to a fruitless search for it in other habitats. They were not seen in three years of BCI berlese sampling of leaf litter (Sally Levings, pers. comm.), or on tree trunks or buttresses. The larval cases would be well camouflaged if they rested on tree trunks;

*Present address: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. U.S. A. 02138

Manuscript received by the editor December 10, 1979

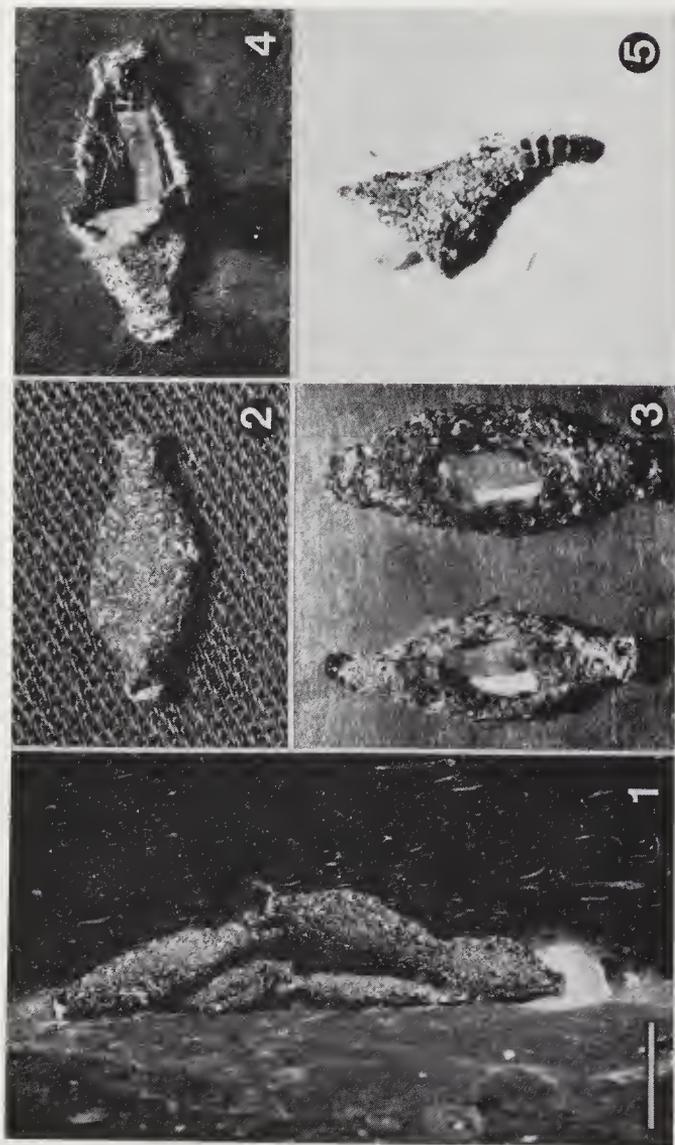
they turn dark when wetted, as does bark, and become light again upon drying. Possibly *Phereoeca* may be associated with mammals other than man. Bat roosts should be checked for the presence of larval cases.

CASE FORM AND FUNCTION

The larval case of *Phereoeca* is flat, spindle-shaped in outline, open at both ends, silk-lined inside, and covered with sand and other small particles outside. It is constructed by the first instar larva soon after hatching, is enlarged by each successive instar, and after special modification, is used for pupation. Fully formed cases are 8–13 mm long and 3–5 mm wide. Once a larva has completed its case, it never leaves; all life functions (feeding, excretion, molting, pupation) take place within the case. When prodded from its case, a larva does not re-enter it, nor does it make a new one. It wanders about, does not eat, and dies in a day or two. Such larvae often walk right over their cases without seeming to recognize them. Larvae occasionally paused upon encountering the inside silk portion of cases which I had split open; however, after a few seconds of exploration, they continued wandering. Larvae placed into cases, through a slit made in one side, repaired the slit and continued to live in the case as if nothing had gone wrong. They also accepted the cases of other larvae as their own.

The case is the same on both sides; it does not matter whether it is flipped over or not. The two openings are also identical, and the larva uses both. The case is widest in the middle permitting easy turn-around inside. Larvae behave as though they don't notice being upside down until they poke their heads out of their cases. If the case is flipped over while the larva is withdrawn, it next appears upside down, withdraws into the case, swivels around inside, and reappears right-side-up.

When disturbed, the larva withdraws into the case and seals it by pulling the bottom-most side up. Presumably this is done using the mandibles. If it is then flipped over, allowed to come out, and disturbed again, it pulls up the "new" bottom-most side (Figure 2). The closed ends are very difficult to open from the outside, but easily pushed open from within. They stay open when pushed open, and closed when pulled closed, because both positions are stable. This phenomenon can be demonstrated by pushing in the ends of a paper tube, such as the core of a paper towel roll.



Figures 1-5. *Pheroeca allutella*. 1. Group of pupal cases attached to wall in a corner. Scale = 6 mm. 2. Larval case with one closed end up (left). 3. Two larval cases with windows. 4. Case slit open to show larva and food (human hair). 5. Larval case cut in half for study of locomotion.

In order to see larval behavior inside the case, I installed windows (Figure 3). A rectangle was cut from one side of each of several cases; a piece of clear lightweight plastic was then glued over each hole. I observed turning movements, feeding, excretion, molting, and pupation through these windows.

To turn around inside the case, the larva withdraws until its posterior end reaches the constriction leading to the opening at the other end, then turns its head to one side and doubles back on itself. When its head has moved past the midpoint of the case, it straightens its posterior end to complete the turn.

Upon encountering food (dead insects, animal hair), the larva chops it into pieces and pulls it into its case. Feeding takes place only within the case. Larvae reared for study were fed dead mosquitoes and my hair (Figure 4). The larva never protrudes its posterior end outside. It defecates inside the case, then turns around inside and pushes the droppings out with its head.

Molting also takes place within the case. The larva retreats into its case and does not emerge again for about 24 hours. After ecdysis, it turns around and pushes the shed skin and head capsule out, using its head.

LOCOMOTION

Pheroeca larvae have two main types of locomotion; one concerned with movement about the habitat while pulling the case behind, the other with movements inside the case.

The prolegs of *Pheroeca* are somewhat reduced, but crochets can be seen under a microscope. That the tenth segment prolegs are used to grip the case when moving was demonstrated by several simple experiments. I cut a case in half transversely so that the larva's head and thorax stuck out of the neck and its posterior end protruded from the large cut end (Figure 5). When it tried to walk and pull its case, the larva went nowhere because it held onto the table with its tenth segment prolegs. When I positioned the loose half of the case against the larval half so that the cut edges came together, the larva held onto the loose half with its tenth segment prolegs, and walked around pulling both halves of the case behind. I then covered the tenth segment prolegs with Elmer's Glue-all® and the larva was no longer able to pull the loose half of the case behind it. However, it

was able to pull the front part of the case, indicating that other prolegs are probably involved as well. The body setae are weak and probably play no role in holding the case.

To move about the habitat, the larva extends the anterior part of its body out of the case, walks ahead with its true (thoracic) legs, then stops and contracts its body to pull the case up behind. When moving at top speed (one pull per second), a larva progresses 1–2 mm per second on a horizontal surface, and only slightly slower on a vertical one.

When moving within the case, the larva uses both true legs and prolegs, plus body extension and contraction, in typical larval fashion.

LARVAE

Larvae chew their way out of their eggs eleven days after oviposition. The head is dark; the rest of the larva is white. From the second instar on, the tergal and pleural sclerites of each thoracic segment are sclerotized and dark, perhaps as protection when the larva reaches out of its case. The final instar larvae of three species of *Phereoeca* were described in detail by Hinton (1956).

Individuals closely monitored during development passed through six larval instars. First instar larvae had head capsule widths of 0.16–0.18 mm. Head capsule width increased with each molt by an average factor of 1.34 (range: 1.22–1.46). Final head capsule widths ranged from 0.66 mm to 0.78 mm. However, these were all males. Larvae of females, collected as final instars, were larger and had head capsules as wide as 1.06 mm. Apparently females either grow more than males from one instar to the next, or attain a seventh instar. Possibly instar number varies among individuals of both sexes.

CASE CONSTRUCTION

Soon after leaving the egg, the larva begins to construct a case of silk and tiny particles such as sand, soil, and insect droppings. It begins by constructing an arch attached at both ends to the substrate. The arch, which consists of silk on the inside and particles on the outside, is gradually extended to form a tunnel within which the larva is concealed. Finally the larva closes the tunnel beneath to

form a tube, open at both ends, and free from the substrate. With the first case complete, the larva is able to move about, pulling its house behind it, in search of food and resting places. This first case is about 1.5 mm long. The smallest individuals initially construct a case that is round in cross section, while the majority of individuals produce a somewhat flattened one. Larvae that fail to make cases never feed, and die within a few days.

CASE ENLARGEMENT

As the larva grows and molts, it enlarges its case to 8–14 mm in length. Beyond the first instar, the case is always flattened, and is spindle-shaped in outline.

In order to determine just how each instar contributes to the formation of the case, I provided two larvae with colored particles for case construction and, during each molt, replaced them with particles of a different color. Three colors were used: red (powdered brick), brown (sand), and black (iron removed from sand with a magnet). The discarded head capsules were collected after each molt to verify the molt and to obtain a measure of growth.

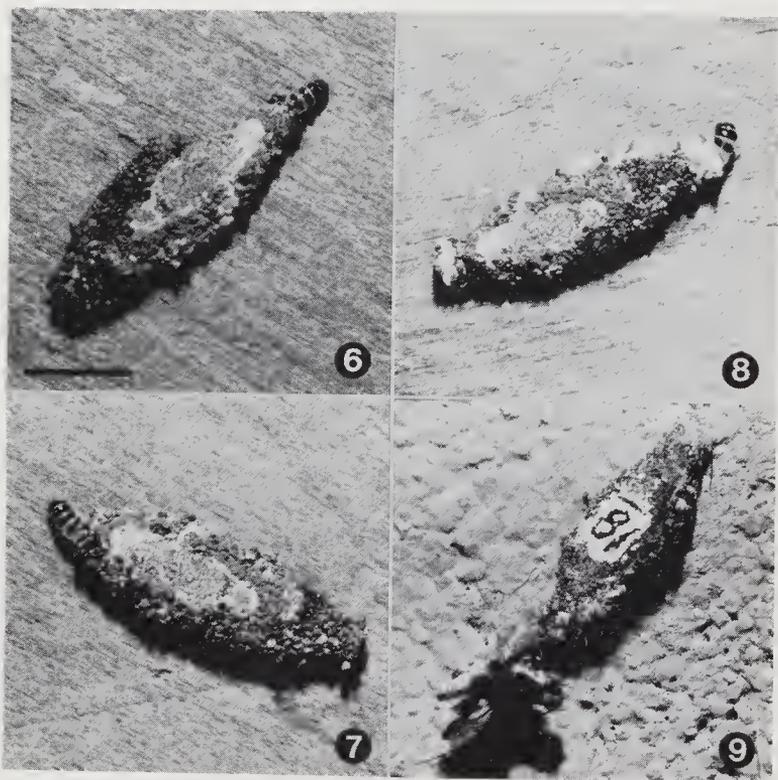
To enlarge its case, the larva first adds a narrow band of new material to both ends. Then, beginning at one end, it slits the case open along one edge for a short distance, and widens it by adding extra silk and new particles which it picks up with its mandibles. The larva continues slitting the case and adding material along one side until it reaches the other end. It then adds extra material to that end and continues the process along the other side of the case (Figures 6–8).

Each instar, from the second through the next to last, adds once to the case as just described. The final instar adds a thin band of new material to both ends of the case, but does not widen it.

MOVEMENTS ABOUT THE HABITAT

In order to follow the daily movements of individual larvae, I numbered the cases of 34 larvae in the bathroom of Barbour House on BCI using typewriter correction fluid (Liquid Paper®), and permanent ink (Figure 9). The cases marked ranged in length from 3 mm to 14 mm. Each was returned to its former location. The positions of these larvae were noted at approximately twelve noon and twelve midnight daily for the following two and a half weeks.

In general, larvae foraged and added to their cases along the floor-wall junctions, or out on the floor at night, and rested at the bases of the walls or up several centimeters on them during the day. Occasionally a larva was seen moving about during the day. Usually each larva returned to, or near to, the spot where it had been recorded the day before. Most stayed within 30–80 cm ranges, with an occasional sudden change from one wall to another. For example, individual “6” was frequently found out on the floor at night, but rested against the wall under the sink by day. After ten days of



Figures 6–9. 6. Larval case (rearing lot 78-5) (25 April 1978) with new material (dark) added to one side and halfway along other side. Scale = 3 mm. 7. Same case (27 April 1978) with enlargement completed. 8. Same case (next instar) (11 May 1978) with further material (white) added to both ends and part way along one side. 9. Individual number “18” eclosing.

this pattern "6" moved into a nearby corner. The greatest minimum distance moved from one day to the next was 228 cm (partly horizontal, partly vertical).

Among eighteen individuals studied in detail, the average distance travelled per 24 hour period was 42.4 cm (range: 13.7–108.7 cm). Nine of these individuals pupated during the study; in each case, pupation was preceded by a horizontal wandering phase of 0.5–2.5 days and a period of vertical movement lasting 0.5–2 days. All nine larvae attached their cases to the wall at heights from 64 cm to 244 cm, and prepared for pupation.

PUPATION

When a larva approaches pupation, it usually walks up a vertical surface and attaches its case firmly with silk at both ends. It then modifies one end of the case by cutting a short slit along both edges of that end. An end thus modified becomes much flatter and is no longer pulled shut by the larva. It acts as a valve; very difficult to enter but easy for the adult to exit through at eclosion.

With its head, the larva next pushes all remaining food and other debris out of the case. A day or two later, it molts to a pupa, pushing the last larval skin and head capsule into the unmodified end of the case (Figure 10).

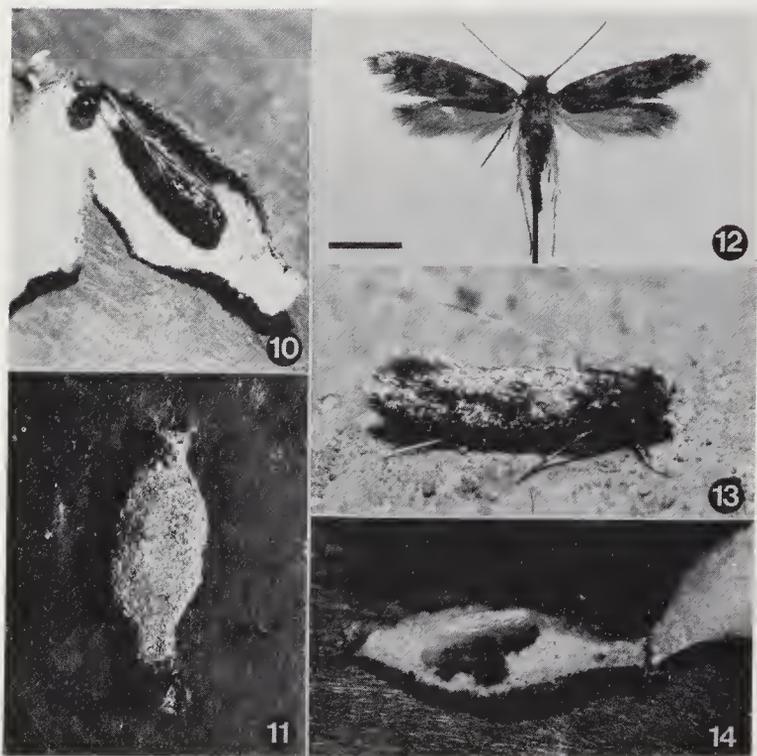
Of 73 abandoned pupal cases examined, the average height from the ground was 87.7 cm (range: 0–214 cm). There was no relationship between the height from the ground at pupation and either case size or sex. Of these, 63 cases were attached vertically, 59 (of the 63) with the head down, and 56 (of the 73) with the ventral side of the pupa towards the wall.

Pupal cases are easily distinguished from cases of resting larvae. The larval case is held very loosely to the wall with several almost invisible silk strands at the upper end; the pupal case is held firmly by a great deal of silk at both ends. After eclosion, the empty pupal skin projects from one end (Figure 11). Most cases seen on walls are actually abandoned pupal cases, but often the pupal skin has been eaten flush with the case by other *Pheroeca* larvae, making it difficult to tell that a case is no longer occupied.

Based on 22 reared individuals, the pupal period averages 15.6 days (range: 11–23 days). The entire cycle from egg to adult averages 74.2 days (range: 62–86 days). Among those reared, males matured before females and outnumbered them 19:3.

ECLOSION

Eclosion takes place during late morning or early afternoon. The pupa wriggles head first part way out of the valve, and the adult emerges from the pupal skin (Figure 9). While the wings are expanding, they are held upwards, perpendicular to the body, but after sufficient expansion and hardening, they snap down over the abdomen.



Figures 10-14. 10. Pupal case slit open to show pupa and cast larval skin. 11. Abandoned case with pupal skin protruding. 12. Adult female (mother of rearing lot 78-99). Scale = 2.5 mm. 13. Wild adult resting. 14. Pupal case slit open to show parasitoid cocoon (Braconidae) and remains of host larva.

ADULTS

Adult females (wingspan: 10–13 mm) (Figure 12) are grey with one to four black spots on the forewings, and a fringe of scales along the posterior margin of the hind wings. Males (wingspan: 7–9 mm) are slightly smaller and have a less distinct wing pattern.

When the adult is at rest, the wings are held tented over the body (Figure 13). The antennae, which are almost as long as the wings, are held back over the body and vibrated constantly.

While adults fly fairly well, they spend much of their time resting on walls, floor edges, or on the webs of theridiid spiders. Adults have reduced mouthparts, and have not been seen to feed.

MATING

During late evening, the newly eclosed female protrudes membranous calling organs from the tip of her abdomen. Males are attracted to “calling” females; their behavior at this time consists of maneuvers for orientation to the female, rather than for courtship. A male flies to a “calling” female, lands near her, runs rapidly about her, then bumps against her abdomen with his head several times before turning suddenly and copulating with her. During copulation, the male ceases antennal vibration, but the female continues it. The pair remains coupled for about thirty minutes.

EGGS

Within several hours of mating, the female begins to lay eggs, cementing them to debris along the bases of walls and in crevices. One female may produce as many as 200 eggs over a period of several days, before dying about a week after eclosion. Unmated females may lay sterile eggs beginning the day after eclosion. Eggs are about 0.4 mm in diameter, pale bluish, and very soft. It is virtually impossible to move them without rupturing them. After ten days, the head of a larva can be seen faintly through the egg wall.

BRACONID PARASITOID

Last instar larvae may be preyed upon by *Apanteles* sp. (Hymenoptera: Braconidae). The larva is killed just before pupation; its case is full-sized, and in most instances has already been modified for pupation. The larval remains can be found inside with the white silk cocoon of the wasp (Figure 14).

DISCUSSION

A number of Lepidoptera and Trichoptera make movable cases during larval life. In the Lepidoptera, movable cases are found in several families (e.g., Psychidae, Tineidae, Mimallonidae, Stenomiidae), and vary among taxa, as to size, shape, and materials. They may be conical, oval, circular, spindle-shaped, dumbbell-shaped, or irregular in outline, and round, flattened, or triangular in cross section. There may be an opening at one or both ends, and the case may have either a definite dorsal and ventral side or the sides may be interchangeable. Construction materials may include soil, frass, twigs, food particles, leaves, or organic debris, but always include silk. Among lepidopterous cases examined, the only ones resembling those of *Phereoeca* belonged to several other species of Tineidae. Of these only *Tinea pellionella* (the case-making clothes moth) has been studied in detail (Réaumur 1737, Marlatt 1898).

The case of *Tinea pellionella* is like that of *Phereoeca* in having two openings and no definite dorsal or ventral side; it differs in being less flattened, in being constructed of food particles (wool), and in the method of case enlargement used. The larva makes a slit along one side of the case from one end to about the middle. It adds a wedge of new material to the slit, and repeats the process on the other side at the far end.

The cases of Trichoptera larvae also are made from silk plus materials collected from the habitat. Hanna (1960) described eight construction patterns used by Trichoptera larvae when making their initial cases. None of these in any way resembles the method employed by larvae of *Phereoeca*.

I thank D. R. Davis (USNM) for determination of the moth, P. M. Marsh (USNM) for determination of the wasp, the Smithsonian Tropical Research Institute for use of facilities, and R. E. Silberglied (MCZ) for helpful criticism of the manuscript and the donation of countless squashed mosquitoes. Specimens of *Phereoeca* have been deposited in the National Museum of Natural History, Smithsonian Institution, and the Museum of Comparative Zoology, Harvard University labeled with the following reference numbers: Aiello lots 77-5, 77-75, 78-4, 78-5, 78-37, 78-53, 78-58, 78-73, and 78-99.

LITERATURE CITED

- HANNA, H. H.
1960. Methods of case-building and repair by larvae of caddis flies. Proc. R. ent. Soc. Lond., (A) 35(7-9): 97-106.
- HINTON, H. E.
1956. The larvae of the species of Tineidae of economic importance. Bull. ent. Res., 47(2): 251-346.
- HINTON, H. E. AND BRADLEY, J. D.
1956. Observations of species of Lepidoptera infesting stored products. XVI: Two new genera of clothes moths (Tineidae). Entomologist, 89(1113): 42-47. [*Phereoeca* Hinton and Bradley, gen. nov.]
- MARLATT, C. L.
1898. The true clothes moths. U.S. Department of Agriculture, Division of Entomology Circular No. 36, second series: 1-8.
- RÉAUMUR, R. A. F. de
1737. Mémoires pour servir à l'histoire des insectes. Vol. 3. xl+532 pp. Paris.
- WALSINGHAM, L.
1897. Revision of the West-Indian micro-Lepidoptera, with descriptions of new species. Proc. zool. Soc. Lond., (1): 54-183. [as *Tineola*.]

SEASONAL VARIATION IN EGG HATCHING AND
CERTAIN EGG PARAMETERS OF THE
GOLDEN SILK SPIDER
NEPHILA CLAVIPES (ARANEIDAE)*

BY T. E. CHRISTENSON, P. A. WENZL, AND PETER LEGUM
Department of Psychology, Tulane University
New Orleans, LA 70118

INTRODUCTION

Little is known about seasonal variation in the reproductive success of spiders. Few field data, for example, are available on temperate egg productivity in relation to the phase of the season in which the female matured and in which the egg clutch was laid. Wise (1976) found that female filmy dome spiders (*Neriene*) who matured early in the summer laid more and lighter eggs than those who matured later. Levy (1970) noted that the early season crab spider (*Thomisus*) egg sacs contained more spiderlings than those laid toward the end of the season. Kessler (1973) noted that under field conditions the first egg sac of the wolf spider (*Pardosa*) contained more eggs than the second; it is probable that some of these late season clutches were the later ones produced by given females.

The present study focuses on the seasonal variation of egg hatching and certain egg parameters of a temperate population of the orb weaving *Nephila clavipes*. Mating occurs from July through September, with a given female mating several times just after her final molt (Christenson and Goist, 1979). Females may copulate after this period, but usually when feeding. Productive females lay their eggs in one to three elaborate egg sacs from mid-August through early December (Moore, 1977; Christenson and Wenzl, manuscript submitted). The female abandons the egg sac after its completion, directing no further attention toward it. Males die by late September and females by mid-December. Second instar spiderlings overwinter in the sac for six to eight months, and emerge under favorable conditions in the spring. The eggs have been described (Moore, 1977), and the functions of the egg sac and major causes of egg and early spiderling mortality have been discussed (Christenson and Wenzl, manuscript submitted).

*Manuscript received by the editor November 27, 1979

In the present study we assessed seasonal variation in spiderling emergence through long term field observation of egg sacs laid throughout the restricted oviposition period. Seasonal variation in causes of failure to emerge, the number of eggs per clutch, individual egg weight, and the total egg clutch weight were also assessed.

METHODS

Study Area

The study area is located 20 km south of New Orleans, La. at the F. Edward Hebert Center of Tulane University. Observations were made within a bottomland hardwood forest cut by drainage ditches and dirt roads. Refer to Christenson and Wenzl (manuscript submitted) for a more detailed description of the study area. Observations were made during the 1975-1978 seasons.

Procedures

To determine if there was seasonal variation in spiderling emergence, we compared spring emergence data from egg sacs formed in early, mid, and late season. Each trimester was about six weeks in length. Throughout the egg laying season a set of pathways we had established in the cleared and forested areas were traversed systematically at least once a week in search of egg clutches. The only criterion for selection was that the egg sac be within 2.5 m of the ground. The approximate date the egg sac was formed was determined by the date of discovery, whether the eggs had hatched, and silk color, since the silk turned from white to gold within a week of being spun. Hatching was determined by gentle palpation of the egg sac. A total of 439 egg sacs were observed throughout the winters of 1975-1978; these accounted for about 60% of the total in the 3 ha study area. The decrease in foliage in winter exposed the egg sacs and facilitated a near total count. Each sac was tagged by placing tape on a nearby twig, and inspected periodically until spiderling emergence, beginning in March. We noted changes in egg sac structure and position, presence of fungus or predators, general condition of the eggs, hatching, and emergence from the sac. The 1975 and 1976 sacs were checked twice a week, the 1977 sacs once a week, and 1978 sacs weekly through January and monthly thereafter. Data from 1978, therefore, are not as complete as those from the previous years.

To determine if there was a seasonal variation in individual egg weight, number of eggs per clutch, and total egg clutch weight, we collected and examined 63 egg sacs in 1977 and 93 in 1978. Egg clutches were removed from mid-August through early December. In 1977 weekly samples were taken from a thoroughly examined 1500 sq mt area within the hardwood forest. Only those egg sacs that appeared to contain yellow eggs were collected. In 1978 weekly samples were taken from a thoroughly examined 600 sq mt area of the hardwood forest bordering a cleared drainage ditch. Half of the egg sacs found in the latter area were randomly chosen for removal and examination, and half for observation throughout the winter in the field. The egg sacs brought into the laboratory were placed in Petri dishes, the inside covers of which were mist sprayed with water every other day. A normal day-night cycle and a temperature of about 22°C were maintained in the laboratory. About four days after collection the silk was removed from the sac, and the egg mass was weighed. The delay in handling was designed to minimize damage to the eggs, since they are particularly fragile for a few days after oviposition. The egg mass was carefully broken apart and the eggs counted. Within two days of counting a random sample of 10 yellow eggs was drawn from each clutch; each egg was weighed separately on a Mettler analytic balance.

RESULTS

Field observations revealed a seasonal variation in the emergence of spiderlings; they were less likely to emerge from egg sacs laid later in the season (Table 1). The numbers in Table 1 and under twig

Table 1. Percentage of egg sacs from which no spiderlings emerged in the spring according to the trimester of the season in which the egg sac was formed. Each trimester represents about six weeks. Estimated numbers of failures are in parentheses; see text for explanation of estimate. Trimester effect analyzed by Chi square test; data were collapsed across years.¹

Trimester:	%—Early	%—Mid	%—Late
1975	26.6(20.8 of 78)	60.5(29.0 of 48)	72.3(8.7 of 12)
1976	29.8(26.6 of 89)	94.5(44.4 of 47)	100.0(10.0 of 10)
1977	35.3(16.6 of 47)	10.0(1.7 of 17)	78.4(7.8 of 10)
1978	31.3(16.6 of 53)	42.0(8.4 of 20)	75.0(6.0 of 8)

¹ $X^2_2 = 62.45$, $p < .001$

breakage in Table 2 are estimates based upon the fact that 84.2% (16 of 19) of the egg sacs that were found after falling to the ground failed to produce spiderlings. The three successful clutches fell within one month prior to the normal time of spring emergence. We estimated the number of failures by multiplying the number of egg sacs that fell by .84. We feel this is a correct estimate since several clutches that were never found fell shortly before the normal time of emergence.

One major cause of mortality was egg inviability, distinguished by the hard and blackened nature of the eggs. There was a seasonal variation in inviability; it caused most of the late but few of the early season failures (Table 2). Its exact causes are not known, although fungus was not found on inviable eggs and no parasites emerged

Table 2. Causes of spiderling failure to emerge from the egg sac according to the trimester of the season in which the egg sac was formed. Actual numbers for the egg inviability and miscellaneous categories, and the estimates for twig breakage are in parentheses.¹

CAUSES OF FAILURE

Year and Trimester:	% Egg Inviability ²	%Twig Breakage	% Misc. ³
1975			
Early	19.3 (4)	56.6 (11.8)	24.1 (5)
Mid	55.1 (16)	17.4 (5.0)	27.5 (8)
Late	57.6 (5)	19.4 (1.7)	23.0 (2)
1976			
Early	48.9 (13)	28.5 (7.6)	22.6 (6)
Mid	72.1 (32)	18.9 (8.4)	9.0 (4)
Late	80.0 (8)	0	20.0 (2)
1977			
Early	0	75.9 (12.6)	24.1 (4)
Mid	0	100.0 (1.7)	0
Late	89.3 (7)	10.7 (.8)	0
1978			
Early	24.1 (4)	75.9 (12.6)	—
Mid	59.8 (5)	3.4 (4)	—
Late	100.0 (6)	0	0

¹See text for explanation of estimate.

²Includes the cases in which the twig fell after the eggs hatched.

³Misc. includes immobility (3), loss of leaf canopy (3), damage to the silk surrounding the eggs (2), fungus (10), and predation (7). The 1978 egg sacs were not observed as often as those in previous years; therefore, causes under this category can not be assessed with the accuracy possible for the previous years.

from samples brought into the laboratory. There was also seasonal variation in the second major cause of mortality, twig breakage; early season sacs fell more frequently than those formed later (Table 2). Twig breakage resulted in the eggs falling to the ground, and subsequently rotting or being preyed upon. No seasonal variation, however, was noted in the frequency of failures caused by immobility of the egg sac after lodging on a branch, loss of the leaf canopy over the eggs, damage to the silk covering the eggs, fungus, or predation (Table 2).

Seasonal variation in certain egg parameters were also noted. Individual egg weight in clutches laid early in the season was significantly greater than in those laid later (Table 3). The same was true for total egg weight. The early 1978 clutches also contained significantly more eggs (Table 3), but no significant relationship was found between individual egg weight and number within a clutch. The Pearson correlations between these two parameters in 1977 and 1978 were $r = +.068$ $F_{1,42} = .20$, $p > .05$ and $r = +.202$ ($F_{1,82} = 3.44$, $p > .05$), respectively.

DISCUSSION

Seasonal variation in spiderling emergence may be due, in part, to climatic factors. Clutches laid early in the season are exposed for a longer period of time to wind and rain which, in turn, may increase the likelihood of those clutches falling to the ground. Moreover, the early part of the egg laying season coincides with the peak of the hurricane and rainy season which may cause a higher frequency of twig breakage, the major cause of failure among early season clutches.

Climatic factors may also contribute to the increase in egg inviability of clutches laid later in the season. For example, the cooler temperatures later in the season may significantly delay hatching, similar to that found in temperate *N. edulis* (Austin and Anderson, 1978). Christenson and Wenzl (manuscript submitted) have shown that *N. clavipes* eggs are particularly vulnerable to some causes of mortality during the three week period prior to hatching. Cooler temperatures may also reduce the amount of prey available to adult females, thereby hampering egg production.

The seasonal variation in inviability could also be due, in part, to the maturation of the adult. Some of the late season clutches are probably the later ones produced by given females. Horner and

Table 3. Variation in certain parameters of the egg and egg clutch according to the trimester of the season in which the clutch was laid.

Trimester	Early			Mid			Late		
	n	\bar{x}	\pm	n	\bar{x}	\pm	n	\bar{x}	\pm
Egg weight (mg)									
1977	(9)	.96	.06	(18)	.80	.05	(21)	.79	.08 ¹
1978	(26)	.98	.09	(29)	.92	.01	(28)	.90	.09 ²
Egg number									
1977	(24)	443.4	118.0	(17)	390.1	167.0	(19)	338.3	117.8 ³
1978	(26)	585.8	249.0	(29)	385.1	151.9	(28)	390.2	132.4 ⁴
Clutch weight (g)									
1977	(24)	.56	.18	(17)	.41	.14	(21)	.37	.15 ⁵
1978	(26)	.63	.28	(33)	.40	.17	(30)	.38	.14 ⁶

¹ $df_{2,45}$ $F = 21.53$, $p < .01$ ² $df_{2,80}$ $F = 4.08$, $p < .05$ ³ $df_{2,57}$ $F = 2.36$, $p > .05$ ⁴ $df_{2,80}$ $F = 10.51$, $p < .01$ ⁵ $df_{2,59}$ $F = 4.27$, $p < .05$ ⁶ $df_{2,90}$ $F = 14.10$, $p < .01$

Starks (1972) and Jackson (1978) found that eggs of the second clutch of *Metaphidippus* and *Phidippus*, respectively, hatch with a lower frequency than those from the first clutch. Gametic inviability, infertility due to sperm depletion, and the production of "trophic" eggs as food for the first few instars could, in part, explain the lower frequency of late season hatching (Jackson, 1978). The timing of maturation may also relate to inviability. From their study of temperate *N. maculata*, Thakur and Tembe (1956) suggest that some females may mature late in the season after the disappearance of males. Eggs laid by these females, therefore, could be infertile and inviable. This assumes that parthenogenesis does not occur in *N. clavipes*; an assumption that has yet to be evaluated. The timing of male maturation may also be significant; males maturing on their own orbs toward the end of the season may be less healthy and vigorous due to reduced prey availability. Some males who mate at the end of the season may be older and incapable of normal spermatogenesis. We are presently assessing the relationship of egg inviability to sperm depletion, seasonal variation in male vigor, and the extent to which females mature after the males have disappeared. We are also attempting to determine if parthenogenesis occurs in our population.

Wise (1976) has noted that *Linyphia* egg weight may be adapted to the temperate ecology of his population. He suggested that eggs laid later in the season were heavier as an adaptation to the reduced amount of prey available to spiderlings who mature late in the summer. Similarly, the seasonal variability of *N. clavipes* egg weights may be an adaptation to the length of the overwintering period. Since eggs laid early in the season must overwinter one to two months longer than those laid afterwards, spiderlings from early clutches may require additional yolk to maintain themselves during this period. If we assume a relationship between egg weight and spiderling weight at emergence, then large early season egg size may minimize the chances that early spiderlings would be at a competitive disadvantage upon emergence in the spring (Kessler, 1971). To understand the role of egg weight as an adaptation to a temperate ecology, we must examine its relationship not only to egg number, discussed below, but also to the possibility that siblings may prey and/or feed upon one another during the overwintering period. We are currently examining the relationships between these variables and spiderling survival.

The decreased weight of individual eggs laid near the end of the season may be due to reduced female prey intake as a function of prey availability at this time. Turnbull (1962) and Kesler (1971) have noted that prey intake can, in part, determine egg weight in *Linyphia* and *Pardosa*, respectively. This could explain why the egg sacs we collected in 1978 appeared to contain heavier eggs than those collected in 1977. In 1978 eggs came from an area of the forest bordering a cleared drainage ditch near which many adult females maintained orbs. During the mating season the biomass of flowering plants and prey seemed much greater and the females relatively larger in this area. In contrast, 1977 clutches were collected from within the forest, where the biomass of prey and female size seemed restricted. We obviously need to do more sampling. Habitat can, however, influence egg productivity. Kessler (1973) noted that the variance in the number of eggs produced by *Pardosa* in different localities was greater than that noted in the same locality from year to year.

Reduced prey intake by the female near the end of the season may also reduce the number of eggs in later clutches. Kessler (1971) noted that in some species of *Pardosa* decreased food intake resulted in fewer eggs per clutch. This decrease in egg number could also be explained, in part, by the observation that successive clutches contain fewer eggs in *N. maculata* (Bonnet, 1930) and in a variety of other genera (*Phidippus*—Jackson, 1978, and Gardner, 1965; *Tegenaria*—Mikulska and Jacunski, 1968; *Achaearana*—Valerio, 1976; *Enoplognatha*—Seligy, 1971; and *Chiracanthium*—Peck and Whitcomb, 1970). In *Linyphia* female size is related to egg number in that clutches of the larger early maturing females contained more eggs than those of smaller later maturing females (Wise, 1976).

In an interesting discussion Jackson (1978) suggested that female *Phidippus* may invest more of their energy in the first clutch as an adaptation to the increased risk of desiccation and reduced prey availability experienced by spiderlings from later clutches. Early season *N. clavipes* might invest more of their reproductive energy, in terms of egg number, in the first clutch as an adaptation to the possible detrimental effects of cooler late season temperatures. We suspect that the number of spiderlings in a clutch determines, in large part, how successful the siblings are at constructing a succes-

sion of normal communal webs, and maintaining group integrity during the communal phase prior to dispersal. We are currently examining the relationship of egg and spiderling numbers to the behavior and success of spiderlings after emergence from the egg sac.

It has been suggested that individual egg weight might be reduced to produce more eggs, or vice versa (Kessler, 1973; Jackson, 1978). Individual female *N. clavipes* do not adopt such a strategy. Examination of several clutches produced by our population indicate that these two parameters do not vary systematically with one another. The relationship between egg number and egg weight may be useful, however, when applied to differences between well defined populations or closely related species.

Nephila is primarily a tropical genus that has expanded into temperate climates, which we suspect results in seasonal variation in egg productivity and probably individual reproductive success. In the tropics less seasonal variation would be expected, since climate and prey availability are more stable, and since adults may mature, mate, and oviposit throughout the year. Individual tropical *Nephila* eggs may be relatively light, since after hatching the spiderlings probably remain in the egg sac for a shorter period, and require less yolk. If this were the case, tropical clutches might also contain more eggs than temperate clutches. We calculate from data presented by Robinson and Robinson (1976) that tropical *N. maculata* eggs weigh about .49 mg, while we have shown that temperate *N. clavipes* eggs weigh about .89 mg. It also appears that tropical *N. maculata* clutches contain about six to eight times the number of eggs as those of temperate *N. edulis* (Austin and Anderson, 1978) and *N. clavipes*. The comparative study of *N. clavipes* under temperate and tropical conditions would contribute to our understanding of reproductive strategies as adaptations to ecological conditions.

ACKNOWLEDGEMENTS

The authors wish to thank Allison Shack, Robert Moore, Mike Sheltzer, and George Ehringer for their help in the field, and Kenneth Goist for his comments on the manuscript.

REFERENCES

- AUSTIN, A. D. AND D. T. ANDERSON
1978. Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae:Araneae). Aust. J. Zool. **26**: 501-518.
- BONNET, P.
1930. Les araignees exotiques en Europe II. Elevage a toulouse de la grande Araignee fileuse de Madagascar et considerations sur l'Araneiculture. Bull. Soc. Zool. France **55**: 53-77.
- CHRISTENSON, T. E. AND K. C. GOIST, JR.
1979. Costs and benefits of male-male competition in the orb weaving spider, *Nephila clavipes*. Behav. Ecol. Sociobiol. **5**: 87-92.
- CHRISTENSON, T. E. AND P. A. WENZL
1979. Egg laying of the golden silk spider, *Nephila clavipes* L. (Araneae, Araneidae): Functional analysis of the egg sac. Manuscript submitted.
- GARDNER, B. T.
1965. Observations on three species of *Phidippus* jumping spiders (Araneae: Salticidae). Psyche **72**: 133-147.
- HORNER, N. V. AND K. J. STARKS
1972. Bionomics of the jumping spider *Metaphidippus galathea*. Ann. Entomol. Soc. America **65**: 602-607.
- JACKSON, R. R.
1978. Life history of *Phidippus johnsoni* (Araneae, Salticidae) J. Arachnol. **6**: 1-29.
- KESSLER, A.
1971. Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia **8**: 93-109.
- KESSLER, A.
1973. A comparative study of the production of eggs in eight *Pardosa* species in the field (Araneae, Lycosidae). Tijdschrift voor Entomologie **116**: 23-41.
- LEVY, G.
1970. The life cycle of *Thomisus onustus* (Thomisidae:Araneae) and outlines for the classification of the life histories of spiders. J. Zool. Lond. **160**: 523-536.
- MIKULSKA, I. AND L. JACUNSKI
1968. Fecundity and reproduction activity of the spider *Tegeneria atrica* C. L. Koch. Zool. Pol. **18**: 97-106.
- MOORE, C. W.
1977. The life cycle, habitat and variation in selected web parameters in the spider, *Nephila clavipes* Koch (Araneidae). Amer. Midl. Nat. **98**: 95-108.
- PECK, W. B. AND W. H. WHITCOMB
1970. Studies on the biology of a spider *Chiracanthium inclusum* (Hentz). Agr. Expd. Sta., Div. Agr., Univ. Arkansas Bull. No. 753.
- ROBINSON, M. H. AND B. ROBINSON
1976. The ecology and behavior of *Nephila maculata*: A supplement. Smithsonian. Contrib. Zool. **218**: 1-22.

SELIGY, V. L.

1971. Postembryonic development of the spider *Enoplognatha ovata* (Clerck) (Araneae: Theridiidae). Zool. J. Linn. Soc. **50**: 21-31.

THAKUR, M. K. AND V. B. TEMBE

1956. Bionomics of the giant wood spider, *Nephila maculata* Fabr. J. Bomb. Nat. Hist. Soc. **53**: 328-334.

TURNBULL, A. L.

1962. Quantitative studies of the food of *Linyphia triangularis* Clerck (Araneae: Linyphiidae). Can. Entomol. **94**: 1233-1249.

VALERIO, C. E.

1976. Egg production and frequency of oviposition in *Achaearanea tepidarium* (Araneae, Theridiidae). Bull. Br. Arach. Soc. **3**: 194-198.

WISE, D. H.

1976. Variable rates of maturation of the spider, *Neriene radiata* (*Linyphia marginata*). Amer. Mid. Nat. **96**: 66-75.

NESTING BEHAVIOR OF *CRABRO ARGUSINUS* AND
C. HILARIS (HYMENOPTERA: SPHECIDAE)

BY ROBERT W. MATTHEWS, ALLAN HOOK¹ AND
JOAN W. KRISPYN
Department of Entomology
University of Georgia
Athens, Georgia 30602

INTRODUCTION

The Crabroninae comprise over 1200 species of small to large solitary wasps which exhibit considerable behavioral diversity (Bohart & Menke 1976). The Holarctic genus *Crabro* includes 85 species with 47 found in the Nearctic region (Bohart 1976). Males of about 3/4 of these species possess a rather bizarre tibial "shield" thought to function in courtship, a hypothesis which awaits confirmation. Nesting information is recorded for members of 6 of the 10 species groups recognized by Bohart, but few detailed studies have been made. Kurczewski and Acciavatti (1968) reviewed the biology of the Nearctic species listing a number of behavioral generalizations applicable to *Crabro*. All known species are relatively uniform in their nesting behavior, compared to the diversity of behaviors found in other sphecid genera of comparable size. Evans et al. (1979) have recently extended our knowledge of Nearctic *Crabro* with observations on 7 species.

The 2 species reported here, *C. argusinus* Packard and *C. hilaris* F. Smith, are "typical" members of the genus although each belongs to a different species group. This is the first record of nesting for *C. hilaris*; *C. argusinus* was studied briefly by Evans (1960) and again in 1970 (Evans et al. 1979) in New York.

With the exception of one population briefly observed on the mainland 11 mi E of Midway, Georgia, all observations were made on St. Catherine's Island, GA, a coastal island situated about 30 miles south of Savannah. The study spanned three seasons 1976-1978. Principal island study sites are located in Fig. 1.

¹Present address: Department of Zoology and Entomology, Colorado State University, Ft. Collins, CO 80523

Manuscript received by the editor November 13, 1979



Figure 1. St. Catherine's Island, Georgia, with study sites where populations of *Crabro hilaris* (sites 1 and 2) and *C. argusinus* (sites 3, 4 and 5) nested.

Crabro hilaris F. Smith

This previously unstudied species was discovered on October 29–30, 1977 when several nests were found at two inland localities. A check of the same localities on October 5, 1978 failed to turn up any *C. hilaris*, which suggests that this species is a late season nester. Intensive collecting on the island throughout the summers of 1977 and 1978 and the early spring of 1978 also failed to turn up any specimens suggesting that the species is univoltine.

The majority of our observations were made along a plowed strip of sandy loam soil extending across a grassy clearing of about 100 m. The habitat (Fig. 2) had been created earlier in 1977 (late July) as a firebreak approximately 1 m wide. We counted about 30 active nests along this firebreak. Another smaller aggregation of about 15 nests was found in sandy soil adjacent to a road several km away.

Eight nests were successfully excavated. These contained from 1–5 cells per nest. Burrows descended nearly vertically (Fig. 3); cells were situated 5–8 cm to the side of the main burrow and averaged 28 cm deep (ranges 25–38 cm; n=14). Two measured cells were 7.5 × 14 mm and 6 × 20 mm. Cells contained an average of 9 flies (range 4–14; n=13). Prey were identified as follows:

Sciomyzidae:	<i>Dictya</i> sp. -1
Syrphidae:	<i>Allograpta obliqua</i> (Say) - 4
	<i>Toxomerus geminatus</i> (Say) - 1
Muscidae:	<i>Coenosia</i> sp. - 6
Calliphoridae:	<i>Cochliomyia macellaria</i> (F.) - 1
Sarcophagidae:	<i>Camptops unicolor</i> Aldrich - 3
	<i>Sarcophaga</i> sp. - 1
Tachinidae:	<i>Ceracia dentata</i> (Coquillett) - 1
	<i>Spathimeigenia spinigera</i> (Coq.) - 1

One female was observed to initiate a new nest only 1 cm away from her previous nest. Soil was loosened with the mandibles and forelegs and pushed backwards with the assistance of the mid and sometimes the hind legs. As she digs the female slowly rotates through 360° while penetrating the surface and she was very soon completely hidden by the accumulating mound. Nest entrances were surrounded by a conspicuous tumulus of unleveled soil averaging about 5 cm diam. Burrow diameter was 4–5 mm.



Figure 2. Plowed "firebreak" where *Crabro hilaris* nested in 1977 (site I in Fig. 1).

Nest entrances are left open during periods of active provisioning and closed at night. Prey-laden females typically approach from about 2/3 m above their entrance and then slowly descend nearly vertically into the open entrance. Flight is silent and prey is held venter up by the middle legs. Provisioning appeared to occur throughout the day. Departing females were often observed to rest motionless with their head blocking the nest entrance for several minutes before departure.

Parasitism by miltogrammine flies was 26.7% overall with maggot-infested cells found in nests from both aggregations. As many as 6 maggots were found in a single cell. Those reared were identified as *Senotainia* sp. or *S. trilineata* (Wulp).

Three adult wasps were successfully reared from cocoons maintained at room temperature. A male emerged the following February and a female emerged in mid-April, followed by another in May.

Miller and Kurczewski (1976) have made observations on two other members of the *hilaris* species group.

Crabro argusinus Packard

This species was clearly bivoltine, having both a spring and a fall generation on St. Catherine's Island. In late April, 1978 it was without question the "dominant" species of solitary wasp, occurring ubiquitously over the island. We studied it principally at 3 localities (Fig 1). One was at the northern end of the island where it nested in steep eroding sand cliffs and blowouts adjacent to the ocean (Fig. 4) that we termed the "north beach site". Another was termed the Wamassee Creek site and was located on the western edge of the island. Here the wasps nested sparsely over a large area of sand bank exposed by the meandering Wamassee Creek. The third study site was called the "boiler site" because of its proximity to an abandoned oyster boiler (Fig. 5). This locality was considerably more protected than the north beach area and the Wamassee Creek site was surrounded on three sides by salt marsh. In contrast to the nearly vertical nesting surfaces at the other sites, nests at the boiler site were constructed in flat, more or less open sandy soil having a surface of crushed oyster shells. High tide level came to the edge of the nest area with the highest of the spring tides occasionally briefly inundating the entire nest site. The nesting population at the boiler site was rather localized, consisting of about 50 nests concentrated in an area of about 2 × 8 m. Nests at the north beach and Wamassee

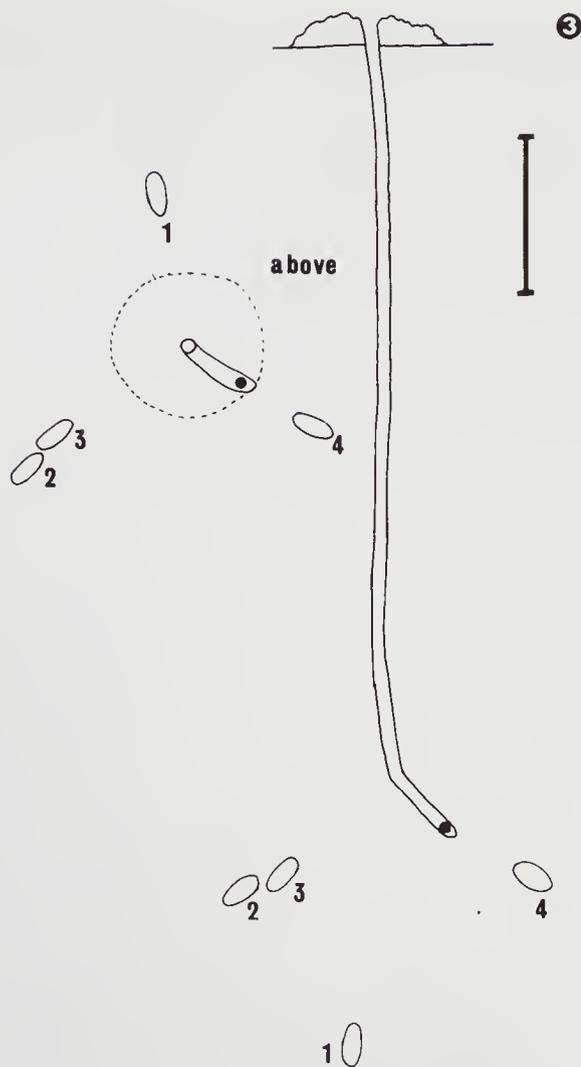


Figure 3. Profile and top view of a typical nest of *Crabro hilaris*. Black dot indicates burrow storage site of flies prior to placement in cell. Cells are numbered according to apparent order of construction based upon larval development. Scale bar is 5 cm.



Figure 4. "Cliff" at the north beach site (site 3 in Fig. 1), containing numerous nests of *Crabro argusinus* scattered throughout the middle portions of the cliff. Females hunted prey along the high tide line among the washed-up debris (mostly *Spartina* reeds).

Creek sites were scattered over a much larger area, with over 100 nests estimated to be active in each area. In early October, 1978 we also excavated a few nests from a sandy road which led to the boiler site about 100 m away. Evidently we were too early for most of the fall nesting season, since, despite extensive searching, no *C. argusinus* were nesting at the other sites at this date and all nests found on the road were fresh and the population seemed to be greatly increased on the last day of our visit.

Table 1 summarizes data obtained from 31 nest excavations of this species according to date and locality. At all sites burrows entered the soil obliquely at roughly a 60° angle to the surface and contained from 1–7 cells situated 3–5 cm from the sides of the tunnel end (Figs. 6–7). Prey accumulate in the bottom of the burrow and are later transferred to the cell. Eggs are attached to the throat of one of the largest flies situated venter up, head in-first, farthest into the cell. Burrow diameter was 4–5 mm and on level soil a distinct unlevelled tunnel of soil accumulated around the entrance. The 16 cells measured fell into 2 clusters, smaller cells 5×10 mm – 6×14 mm and larger cells 7×15 mm – 8×17 mm.

Considering the 2 main study localities (north beach and boiler site), comparisons of the different populations from the same season as well as comparisons of populations from different seasons at the same site reveal some rather striking differences (Table 1). Fall populations at the north beach site constructed nests with cell depths averaging 16.1 to 17.0 cm (2 successive seasons). Cells contained an average of 11.2 to 14.6 prey (2 successive seasons). Spring populations nesting at the same site constructed significantly deeper burrows, with cell depths averaging 28.9 cm and provisioned with a much larger number of flies ($\bar{x} = 30.9/\text{cell}$).

Comparing populations of the two main localities at the same season (spring 1978) also revealed important differences. Spring nests at the boiler site were significantly shallower and cells were provisioned with fewer flies per cell (Table 1). Prey preferences also differed somewhat, possibly reflecting differences in hunting habitats. The north beach population lacked ready access to salt marsh and appeared to hunt mainly along the beach. Even so, 12 of 32 prey species were represented in cells at both sites (Table 2). Ephydriidae and Dolichopodidae were preferred prey at both sites.

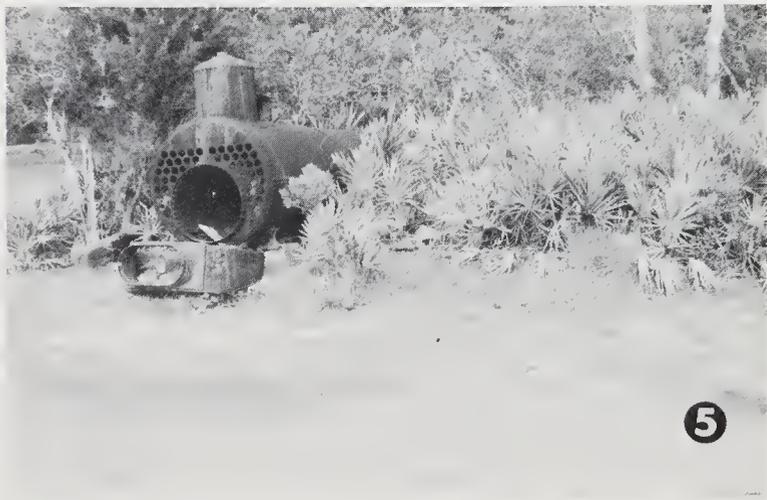
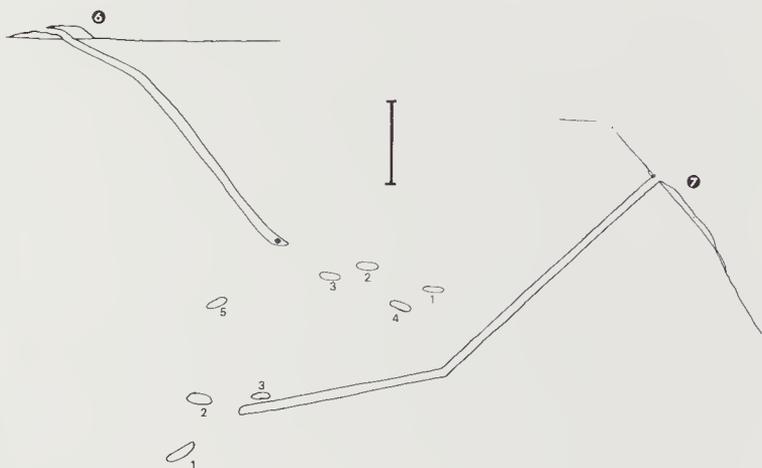


Figure 5. Boiler site (site 5 in Fig. 1); *Crabro argusinus* nested in the flat area in the foreground. Back Creek runs adjacent to this site on the left, and an extensive area of salt marsh extends behind the viewer. High tides occasionally barely covered the nest area.



Figures 6-7. Profiles of typical *Crabro argusinus* spring nests from (6) the boiler site, and (7) the north beach site. Cells are numbered according to apparent order of provisioning based upon larval development. Black dot indicates point where prey flies were stored in burrow prior to transfer to a cell. Scale bar is 5 cm.

Hunting behavior and prey capture was observed on several occasions at the north beach site. Females flew slowly into the wind along the high tide line where salt marsh reeds and other debris had accumulated along the base of the cliffs. Prey appeared to be detected visually as they rested on the white sand as wasps were frequently seen to dart at small dark pebbles of the same size as the flies. Upon spying a potential prey item the wasp hovered momentarily about 10 cm downwind of it and 6-8 cm above the substrate, then suddenly it darted forward very quickly and pounced upon the prey in an attack aptly described as "hit and run". It was possible to walk alongside of individual females for several meters as they flew slowly along pouncing on one object after another until they were finally successful in capturing a prey item. In contrast to the majority of other species of *Crabro*, *C. argusinus* prey were clearly paralyzed and not necessarily killed.

In addition to the physical differences between these two study localities, differences in the abundance of parasites were also striking. At the more localized and protected boiler site miltogrammine flies were excessively common and reflecting this, the incidence of

Table 1. Summary of data for 31 *Crabro argusinus* nests from different sites and different seasons on St. Catherine's Island, Ga.

Locality	Date	No. nests examined	No. cells per nest	Cell Depth (cm)	No. Prey Per Cell	Percent Parasitism
North Beach	5 Nov. 1976	7	1-2	$\bar{x}=17.0$ range: 15-18 (n=8)	$\bar{x}=14.6$ range: 8-16 (n=7)	0
North Beach	29-30 Oct. 1977	4	1-3	$\bar{x}=16.1$ range: 15-18 (n=5)	$\bar{x}=11.2$ range: 5-19 (n=6)	0
North Beach	21-23 Apr. 1978	8	1-3	$\bar{x}=28.9$ range: 19.5-37.5 (n=13)	$\bar{x}=30.9$ range: 9-92 (n=8)	0
Boiler Site	21-23 Apr. 1978	6	3-7	$\bar{x}=18.7$ range: 12.5-26 (n=26)	$\bar{x}=19.9$ range: 18-43 (n=24)	16.7
Road to Boiler	7-8 Oct. 1978	5	1-5	$\bar{x}=11.0$ range: 8-13 (n=11)	$\bar{x}=14.9$ range: 9-28 (n=11)	0
Wamassee Creek	10 June	1	7	$\bar{x}=35.9$ range: 32.5-40.5 (n=7)	$\bar{x}=13.7$ range: 7-25 (n=4)	0

parasitized cells was 16.7% in April, 1978. Miltogrammine flies collected or reared from the boiler site belonged to two genera, *Senotainia* spp. and *Sphenometopa* sp. At north beach no miltogrammine flies were seen and no parasitized cells were found. Possibly the strong and persistent winds blowing along the north beach cliffs dispersed the parasites. Also, it may simply be that it was less "profitable" for the flies to invest time and energy battling the winds to locate the widely dispersed nests. At the road site in October, 1978, parasite flies were common, but no parasitized cells were found. Two flies collected here were *Senotainia trilineata* (Wulp) and *Sphenometopa tergata* (Coquillett).

Perhaps correlated with the presence or absence of parasites, the behavior of provisioning females differed strikingly. Prey-laden females returning to open nests at the boiler site made a distinctive approach flight in which they would approach the nest entrance and then slowly drift backwards away from the nest. Some females were observed to retreat as much as 3 m in a rather pulsating flight about 6–10 cm above the substrate. This conspicuous flight behavior usually attracted 1 to several miltogrammine flies who followed in close synchrony with the movement pattern of their potential host (hence the very apt common name = satellite flies). Having lured the parasites off some distance, the female suddenly and unpredictably zoomed forward in a "bee line" plunging headlong into her open entrance and leaving the flies behind, somewhat disoriented. The same behavior was observed on the mainland site, a flat expanse of sandy soil constituting a turnaround area at the end of a dirt road. Several miltogrammine flies were sighted at this area. Comparable behavior was never seen in females nesting at north beach or Wamassee Creek, and may therefore represent a response to increased parasite pressure at the boiler and mainland sites. Evans (1960) records the same behavior for this species when pursued by miltogrammines. Closely similar anti-parasite provisioning behavior has also been described for an unrelated sphecid, *Philanthus crabroniformis* F. Smith by Alcock (1974).

On at least one occasion a *Senotainia* was observed to follow a female wasp into her burrow. Nests were typically left open during provisioning, but at least two females made weak temporary outer closures between provisioning trips and "crashed" directly into their nests upon returning. This behavior may have been a response to parasite pressure. Several parasitized cells contained more than one

Table 2. Summary of 520 prey taken by *Crabro argusinus* from different sites and at different seasons on St. Catherine's Island, Georgia.

Prey Species	North Beach Site		Locality and Date		Road Site	Wamassee Creek
	Nov. 1976	Oct. 1977	April 1978	Boiler Site		
TABANIDAE						
<i>Chrysops fuliginosus</i> Wiedemann			1			
THEREVIDAE						
<i>Psilocephala</i> sp. prob. <i>latifrons</i> Cole			1			
EMPIDIDAE						
<i>Hilara</i> sp.			3			
<i>Rhamphomyia pectoris</i> Coquillett			2			
DOLICHOPODIDAE						
<i>Chrysotus</i> sp.		1	2			
<i>Dolichopus alacer</i> Van Duzee		15	7			
<i>Gymnopternus vetitus</i> Melander		6				
<i>Hypocharassus gladiator</i> Mik		4	9			
<i>Hypocharassus pruinosus</i> (Wheeler)			5			
<i>Nanomyia litorea</i> Robinson		1				
<i>Paraclius filifer</i> Aldrich		1	2			
<i>Paraclius claviculatus</i> Loew		1	2		3	
<i>Paraclius pumilio</i> Loew					11	
<i>Pelastoneurus angulatus</i> Robinson					1	
<i>Pelastoneurus abbreviatus</i> Loew		1	6		1	
<i>Pelastoneurus</i> spp.			16		7	4

Table 2 (continued)

<i>Thinophilus frontalis</i> Van Duzee					10
<i>Thinophilus semipallidus</i> Robinson					
<i>Thinophilus ochrifacies</i> Van Duzee	2	1	2		
SYRPHIDAE					
<i>Toxomerus marginatus</i> (Say)	7				
OTITIDAE					
<i>Chaetopsis apicalis</i> Johnson			1		
<i>Euxestia</i> sp.			1		
TETHINIDAE					
<i>Tethina albula</i> (Loew)	1	1			
MILICHIIDAE					
<i>Phleomyia</i> n. sp. nr. <i>indecora</i> (Loew)	3				
CANACIDAE					
<i>Canace snodgrassi</i> Coquillett	1				
EPHYDRIDAE					
<i>Cirrula fuscifemur</i> (Steyskal)	1		2		4
<i>Ephindra subopaca</i> Loew	1	1			
<i>Dimecoenia fuscifemur</i> Steyskal		1	1		1
<i>Lamproscatella</i> n. sp.	1				
<i>Lipochaeta slossonae</i> Coquillett	1	1			
<i>Notiphila bispinosa</i> Cr.		1			5
<i>Notiphila</i> sp.	1				
<i>Paradrya quadrinuberculata</i> Loew					1

Table 2 (continued)

Prey Species	North Beach Site			Locality and Date		Wamassee Creek
	Nov. 1976	Oct. 1977	April 1978	Boiler Site	Road Site	
<i>Paradrya unituberculata</i> Loew		1		12		
<i>Polytrichophora</i> sp.				1		
<i>Scatella obsoleta</i> Loew			43	2		1
<i>Scatella picea</i> (Walker)		1				
<i>Scatella</i> sp. prob. new			6	2		
<i>Setacera pilicornis</i> (Coquillett)			52	58		
<i>Chersidromia inusitata</i> Melander		1				
<i>Paralimna decepiens</i> Loew		2				
ANTHOMYIIDAE						
<i>Hylemyia platura</i> (Meigen)		6				
<i>Fucellia tergina</i> (Zetterstedt)	92	5	1			
MUSCIDAE						
<i>Coenosia</i> sp.		3				
<i>Lispe albitarsis</i> Stein			2	2		
CALLIPHORIDAE						
<i>Cochliomyia macellaria</i> (F.)		1				
SARCOPHAGIDAE						
<i>Tricharaea simplex</i> (Aldrich)	3					
<i>Sarcophaga</i> sp.		1				
TACHINIDAE						
<i>Leucostoma simplex</i> (Fallen)		1				
<i>Myiophasia</i> sp.		1				
TOTALS	95	89	144	145	37	10

maggot. Total development time for one of the *Sphenometopa* reared was 22 days. One cocoon excavated during April, 1978 was found to contain unidentified nematode worms.

On sunny warm days females appeared to construct 2 cells per day. A period of intense provisioning activity occurred in the late mornings with a majority of nests closed from within during the middle part of the day. Late in the afternoon there would again be a period of intense provisioning activity. Observations of individual females revealed that flies were brought in at the rate of 1 fly every 3 to 4 min during peak activity. A summary of all prey is given in Table 2, and includes over 50 species from 15 families. Brine flies (Ephydriidae) and Dolichopodidae are the preferred prey, but in the late fall the anthomyiid *Fucellia tergina* constituted the primary prey at North Beach. Evans (1960) recorded 15 species of prey from his New York study which also were predominantly Dolichopodidae and Ephydriidae.

Males were seldom seen. However, on October 7, 1978, 2 males were observed investigating freshly dug burrows at the road site adjacent to the boiler site. This date was clearly early in the fall nesting season, for no nests had been initiated at the boiler site nearby nor were any found at north beach, and during the subsequent 2 days several new nests were initiated at this site. Another male was taken on November 4, 1976, dug from a "sleeping" burrow 5 cm deep found among an aggregation of nests in a blowout area at north beach. On May 11, 1978 2 males were observed searching about nest entrances in a small sand pile at the mainland site.

Males of about 3/4 of Nearctic *Crabro* possess an enlarged shield-like projection on the front tibia. Bohart (1976) suggested a clasping role for the male tibial shield, but pointed out that "this does not explain the great variety and ornamentation of the shield according to species" which may also serve a "display function" in courtship. In an attempt to learn the possible role of the male tibial shield, on 28 May 1978 two reared males were placed in a plexiglass observation cage (76 cm × 60 cm × 36 cm) with a reared female known to be unmated. One male repeatedly hovered 3–5 cm above the female as she crawled up the container sides and pounced on her several times. Males are not very discriminating; it was not unusual for one male to hover and pounce on the other several times before searching elsewhere. However, several mounting attempts were observed in which the male placed his shields over the eyes of the female, but the

female was apparently not receptive and no copulations were observed. Evans (pers. comm.) suggests that *Crabro* females recognize their species specific pattern when their eyes are covered by these distinctively marked male tibial shields. Light passing through such thin, partially transparent shield cuticle could transmit a characteristic pattern which might alter female receptivity.

Several cocoons of *C. argusinus* were obtained during the course of this work and one of them is shown in Fig. 8. Developmental data were obtained for a few cells transferred to rearing tins during the spring of 1978. One egg laid April 22 developed to mature larva which spun its cocoon on April 26-27 and emerged as an adult on May 20. It seems likely that there is at least a partial second generation in the spring. During our visit in late April nesting seemed to be at a peak at all localities. The boiler site colony was still active on 12 May when we returned, but activity ceased about 20 May and *Oxybelus sericus* Robertson became the dominant species at that site. The last nest was dug on 10 June 1978 at the Wamassee Creek site where only a few active nests remained at that date.

Searching females were repeatedly observed to dart at the sides of depressions in the substrate. At the road site females showed a decided bias for nest sites situated in depressions as compared to surrounding flat sand. For example, a horse hoof print had 4 closely spaced nests initiated in the angle formed by the sides and base of the print within 24 hr. Such a close spacing of nests is unusual. Evans (1960) never found active nests closer than half a meter. His study site was an erosional bank of a draw, most similar to our

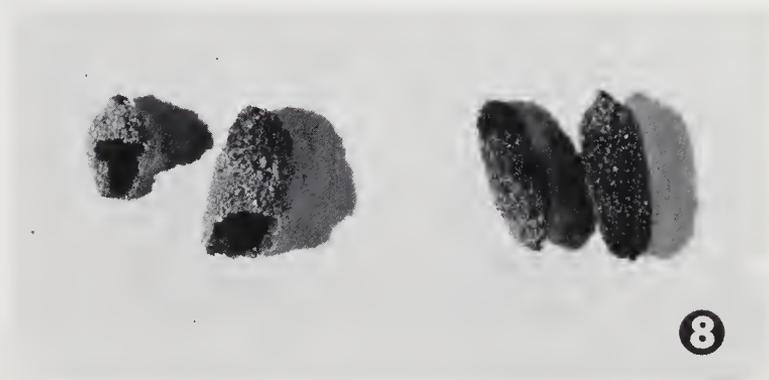


Figure 8. Cocoons of *Crabro argusinus*. Length of right cocoon is 7 mm.

north beach site where nests were also typically widely spaced. Since time did not permit following the above 4 nests to completion, all were excavated late in the day that they were initiated. In every case the burrow excavation was still incomplete and no prey had yet been stored. This indicates that *C. argusinus* requires at least one day to excavate the main tunnel.

DISCUSSION

Like all known *Crabro*, *C. hilaris* and *C. argusinus* nest in sandy soil and prey upon a variety of Diptera. *C. hilaris* prefers stockier-bodied flies, primarily muscoids whereas *argusinus* utilizes a wide diversity of prey, but prefers ephydriids and dolichopodids. *C. hilaris* inhabits inland protected locations in flat soil, whereas *C. argusinus* characteristically nests in close association with water and prefers to nest in slopes or in the sides and "corners" of depressions in relatively flat open sand.

Striking differences in the behavior and nest parameters of the two populations of *C. argusinus* studied at the same season may be due to differences in both biotic factors (available prey and parasite pressure) and physical factors (erosion, wind, etc.). The larger number of prey stocked per cell at the north beach site may in part reflect the absence of parasites and in part a preference for smaller sized prey. It may also reflect different hunting habitats, beach versus salt marsh; larger flies may be more accessible in the marsh. At the boiler site, the presence of strong parasite pressure may have caused wasps to finish provisioning sooner. The greater depth of cells at north beach possibly reflects the relative instability of that habitat where erosion continually whittled away at the cliff bank. In contrast, the boiler site has probably changed very little in the many years since the boiler was abandoned. However, reasons for the much greater depth of spring nests as compared to that of fall nests at north beach are unknown. The road site where the shallowest nests were found was very compacted sand with innumerable roots which caused nests at this site to be very contorted. It may be that digging behavior is genetically controlled and shut off after a predetermined amount of energy is expended which would vary between localities and seasons.

In overall biology these two species fit the typical *Crabro* pattern on all traits enumerated by Kurczewski and Acciavatti (1968) and summarized by Bohart and Menke (1976). Nevertheless, variation

between populations nesting in different habitats at the same season and between populations nesting at the same sites at different seasons demonstrates a rather larger amount of behavioral plasticity than might have otherwise been anticipated.

ACKNOWLEDGEMENTS

We would like to dedicate this paper to Professor Howard E. Evans on the occasion of his 60th birthday. This paper is a part of a comparative study of sand wasp behavior undertaken on St. Catherine's Island with the support of the Edward John Noble Foundation in cooperation with the American Museum of Natural History. For prey and parasite identifications we are indebted to the following specialists: R. J. Gagne (Muscidae, Calliphoridae and Sarcophagidae); L. Knutson (Sciomyzidae and Empididae); W. N. Mathis (Ephydriidae and Canacidae); C. W. Sabrosky (Milichiidae and Tachinidae); G. Steyskal (Anthomyiidae, Tethinidae and Otitidae); F. C. Thompson (Tabanidae, Syrphidae and Dolichopodidae); and W. W. Wirth (Therevidae). R. M. Bohart confirmed the identities of the *Crabro*. Voucher specimens are deposited in the University of Georgia P. W. Fattig Museum.

REFERENCES

- ALCOCK, J.
1974. The behaviour of *Philanthus crabroniformis* (Hymenoptera: Sphecidae). *J. Zool. (London)* **173**: 233-246.
- BOHART, R. M.
1976. A review of the Nearctic species of *Crabro* (Hymenoptera: Sphecidae). *Trans. Amer. Ent. Soc.* **102**: 229-287.
- BOHART, R. M. AND A. S. MENKE.
1976. *Sphecid Wasps of the World*. University of California Press, Berkeley, 695 pp.
- EVANS, H. E.
1960. Observations on the nesting behavior of three species of the genus *Crabro* (Hymenoptera: Sphecidae). *J. N. Y. Ent. Soc.* **68**: 123-134.
- EVANS, H. E., F. E. KURCZEWSKI AND J. ALCOCK.
1979. Observations on the nesting behavior of seven species of *Crabro* (Hymenoptera: Sphecidae). (in preparation)
- KURCZEWSKI, F. E. AND R. E. ACCIAVATTI.
1968. A review of the nesting behavior of the Nearctic species of *Crabro*, including observations on *C. advenus* and *C. latipes* (Hymenoptera: Sphecidae). *J. N. Y. Ent. Soc.* **77**: 152-170.
- MILLER, R. C. AND F. E. KURCZEWSKI.
1976. Comparative nesting behaviors of *Crabro rufibasis* and *Crabro arca-diensis* (Hymenoptera: Sphecidae: Crabroninae). *Florida Ent.* **59**: 267-285.

NEARCTIC SPECIES OF THE WOLF SPIDER
GENUS *TROCHOSA* (ARANEAE: LYCOSIDAE)*

BY ALLEN R. BRADY
Department of Biology, Hope College
Holland, Michigan 49423

This is the first in a projected series of systematic studies of the Nearctic Lycosidae described in the genera *Trochosa* and *Lycosa*. One important aspect of the proposed series of revisions will be an attempt to delimit generic taxa within the Lycosidae, with special reference to Nearctic species. Over 50 species of North American *Lycosa* have been described and most of the medium to large-bodied wolf spiders are included in this genus at present. However, preliminary studies indicate that several distinct species groups, which may well represent different genera, have been assembled under *Lycosa*. Before undertaking the larger and more complicated task of delimiting genera within the *Lycosa* complex, it seemed logical to gain some idea of generic limits—to develop a yardstick whereby the species groups of *Lycosa* could be measured. *Trochosa* is represented by a small, relatively well-defined, widespread group of species. This genus might well serve as a model and yardstick for the study of *Lycosa* and I thought it practical to begin here.

The genus *Trochosa* is represented by five species in the Nearctic Region. One of the species, *T. terricola*, is quite common in Western and Central Europe (Locket and Millidge 1951, Engelhardt 1964, Fuhn and Burlacu 1971) and very likely occurs throughout the temperate parts of the Holarctic Region. The other four species comprise a distinct group that is probably restricted to North America. *Trochosa avara* occurs from the eastern coast westward to the 100th parallel, while *Trochosa gosiuta* is found in the southwestern United States (Map 2). *Trochosa shenandoa* occurs along the Atlantic and Gulf coasts and extends inland in the central United States as far as Kansas and possibly Illinois (Map 3). *Trochosa parthenus* appears in the southeastern United States and is the only species found in the Florida peninsula (Map 3).

North American species of *Trochosa*, with the exception of *shenandoa*, have been relegated to the genus *Lycosa* at one time or

*Manuscript received by the editor November 16, 1979.

another. They do share some features with certain members of that large aggregate, but can be grouped together and distinguished from other lycosids on the basis of characteristics delineated in the preliminary diagnosis of the genus and the discussion of species groups.

Trochosa C. L. Koch

Trochosa C. L. Koch, 1848: 95; 1851: 33. Type species by original designation *Arenea ruricola* DeGeer, 1778. Keyserling 1877: 610. Scudder 1882: 328. Marx 1890: 564. McCook 1894: 90, 100, 107, 112, 118. Montgomery 1904: 300. Banks 1905: 319. Petrunkevitch 1928: 250.

Trochosina Simon, 1885: 10 (subgenus of *Trochosa*). Type species by original designation *Trochosa terricola* Thorell, 1856. Roewer 1954: 302 (raised to generic status).

Varacosa Chamberlin and Ivie, 1942: 36 (subgenus of *Trochosa*). Type species by original designation *Trochosa avara* Keyserling, 1877. Roewer 1954: 304 (raised to generic status). NEW SYNONYMY.

Allohogna (part). Roewer, 1954: 212.

Allotrochosina Roewer, 1954: 213. Type species by monotypy. *Lycosa maunganuiensis* Berland, 1925 (misspelled *mananganuiensis* by Roewer).

Diahogna Roewer, 1954: 239. Type species by monotypy *Lycosa martensii* Karsch, 1878.

Trochosomma Roewer, 1954: 304. Type species by original designation *Trochosa annulipes* L. Koch, 1875.

Discussion. For a more complete listing of synonyms of *Trochosa* by European authors refer to Bonnet (1959: 4698-4699). *Trochosina* Simon, *Allotrochosina* Roewer, and *Diahogna* Roewer were synonymized by Guy (1966) and his findings are supported here. *Trochosomma* Roewer was synonymized by McKay (1979).

Characteristics. Small to medium size spiders (total length 5.8 to 13.0 mm). Carapace length 3.2 to 5.9 mm; width 2.4 to 4.3 mm.

Color brownish yellow to dark brown with a lighter submarginal stripe on each side of the carapace and a broad median light stripe as in Figures 1-6. Within the light median stripe appears a pair of dark short stripes or dashes as in Figures 1, 2, 3, 5, 6. *Trochosa gosiuta* (Fig. 4) is the only species that does not show these dashes so characteristic of the genus. With this exception the dorsal pattern is similar throughout the genus. Abdomen yellowish brown to brown ground color with darker brown or black markings; sometimes with indistinct chevrons, but mostly mottled as in Figures 1-6.

Eyes: Anterior median eyes (AME) larger than anterior lateral eyes (ALE). Posterior median eyes (PME) larger than posterior

lateral eyes (PLE), both much larger than anterior eyes. Eye arrangement: anterior eye row slightly procurved, equal or subequal (less than 0.02 mm difference) to PME width. PME width less than PLE width. PME width greater than length of posterior ocular quadrangle (POQ).

Cephalothorax relatively flat when viewed from the side, tapering downward slightly in cephalic region.

Legs relatively short when compared to carapace length (ratio derived by dividing length of leg IV by carapace length 2.4 to 3.2 in females and 2.6 to 3.3 in males). Order of leg length IV-I-II-III. Order of length of segments: patella-tibia IV—metatarsus IV—patella-tibia I in *avara* group; patella-tibia IV—patella-tibia I—metatarsus IV in *terricola*. *Trochosa terricola* males have patella-tibia I longer than patella-tibia IV.

Posterior cheliceral teeth 3-3 in *avara* group, variable in *terricola* (Map 1 and Table 1).

Epigynum of female with median septum (*ms*) in shape of inverted "T" (Fig. 25). The longitudinal piece (*lp*) broad and flat in *terricola* (Fig. 13) or narrow with a bulbous white structure (*b*) filling most of the atrium in the *avara* species group (Fig. 27). In the latter species the transverse piece (*tp*) of the median septum has the ends curved anteriorly.

Palpus of male with palea (*p*) partly sclerotized (Fig. 46) or heavily sclerotized with prominent distal knob (Fig. 40). Embolus (*e*) arising on distal or prolateral margin of palea with long intromittent part curled distally into a loop (Fig. 30) or with broad pars pendula (*pp*) and a short intromittent part angled distally (Fig. 45). Conductor (*c*) prominent, broad, and concave (Fig. 42). Median apophysis (*ma*) well developed, conspicuously enlarged and directed ventrad in some species (Fig. 43).

Diagnosis. As described above, representatives of the genus *Trochosa* differ from those of other lycosid genera primarily in the distinctive color pattern of the carapace. In addition the first eye row, which is essentially equal in width to the PME row, the low carapace that slopes downward anteriorly, and the relatively short legs are features that distinguish *Trochosa* from other lycosid genera. The relative dimensions of the eye rows compared to one another, and the carapace dimensions compared to leg length are

quite similar in *Trochosa* species; and once known for all genera of North American lycosids these ratios may help to set apart *Trochosa*, as well as other genera.

Although the ecology and behavior of North American species of *Trochosa* have not been well studied, there is enough information to indicate similarities in habitats and phases of life history. All North American species of *Trochosa* inhabit edge of woods or open woodland habitats (as do a number of their Palaearctic relatives). None of the American *Trochosa* are burrowers, such as *Geolycosa* and many species of *Lycosa*. Both *Trochosa terricola* and *avara* are often found under logs or stones, where they presumably molt and construct egg cases. These ecological and behavioral features also serve to separate species of *Trochosa* from many other lycosids.

Species Groups. The structure of the male palpus and the female epigynum are often diagnostic at the generic level in spiders. In the case of *Trochosa* the genitalia delimit two species groups: *uricola*, *robusta*, *spinipalpis*, and *terricola* on the one hand; and *avara*, *gosiuta*, *shenandoa*, and *parthenus*, on the other hand. In *Trochosa terricola* the male is recognized by the long, thin embolus forming a loop at its distal end (Fig. 30) and the female by the broad inversely "T-shaped" epigynum (Figs. 13, 14, 16). *Trochosa uricola*, *robusta*, and *spinipalpis* of Europe are very similar to *terricola* in genitalic structure (see Locket and Millidge 1951, Engelhardt 1964, Fuhn and Burlacu 1971). In North America *terricola* is the lone member of the *uricola* species group and is easily differentiated from other species of *Trochosa* in this region by genitalic structure.

Trochosa avara females are recognized by the epigynum which has the ends of the transverse piece directed anteriorly (Figs. 20, 21). This feature is characteristic of females of the *avara* group (Figs. 18, 23, 25, 27) and separates them from all other North American Lycosidae. A unique feature of the males in the *avara* group is the embolus which expands into a broad flattened, semi-transparent plate as it curves beneath the palea and then narrows to form a filament that coils into the concavity of the conductor (Figs. 34, 36, 39, 42, 45). The twist at the tip is reminiscent of the embolus in *terricola*. Despite the differences in structure of the male and female genitalia of *terricola* when compared with representatives of the *avara* group, the close correspondence in color patterns, particular morphological features, and certain ecological characteristics warrant their inclusion in a single genus.

Species Excluded from *Trochosa*

The following North American species have been placed in *Trochosa* by previous authors, but they do not belong in this genus as it is diagnosed here.

Lycosa animosa Walckenaer, 1837. Placed in *Trochosa* by Simon (1864) = *Anahita animosa* (Walckenaer)

Trochosa cherokee Chamberlin and Ivie, 1942 = *Lycosa cherokee* (Chamberlin and Ivie)

Lycosa contestata Montgomery, 1903. Placed in *Trochosa* by Montgomery (1904) and synonymized by Chamberlin (1909) with *Lycosa pratensis* Emerton, 1885 = *Lycosa contestata* Montgomery

Lycosa frondicola Emerton, 1885. Placed in *Trochosa* by Montgomery (1904) = *Lycosa frondicola* Emerton

Lycosa similis Banks, 1897. Synonymized by Banks (1916b) with *Lycosa pratensis* Emerton, 1885 = *Lycosa similis* Banks

Lycosa animosa Walckenaer was transferred to the genus *Anahita* of the Family Ctenidae by Chamberlin and Ivie (1942). John Abbot's Figure 81, the figure upon which the name *Lycosa animosa* is based, in the *Spiders of Georgia* (1792) is not *Trochosa*. Chamberlin and Ivie are probably correct in their diagnosis. The female holotype of *Trochosa cherokee* Chamberlin and Ivie from the American Museum of Natural History (AMNH) was examined. It belongs to the *Lycosa gulosa* species group. The holotype of *Lycosa contestata* Montgomery from the AMNH was examined. It is an immature female belonging to the *Lycosa helluo* species group. Numerous specimens of *Lycosa frondicola* were examined, samples were measured, and detailed drawings made for comparison to species of *Trochosa*. I concluded that *frondicola* is best placed in *Lycosa* at present. The holotype of *Lycosa similis* Banks from the Museum of Comparative Zoology (MCZ) was examined. It is an immature female belonging to the *Lycosa helluo* species group. In addition to the above species, type specimens of *Lycosa abdita* Gertsch from the AMNH and *Lycosa acompa* Chamberlin from the MCZ were examined because of certain Trochosoid characters they possessed. They do not belong in *Trochosa* as it is conceived here.

METHODS

Spider systematists, in general, employ many of the same techniques and methods in their study of materials. Basically a number of measurements of bodily components are made and characters of taxonomic importance are illustrated. These measurements and drawings characterize the species under investigation and aid in their identification and separation from closely related forms. Some idea of the phylogenetic relationships of species can be gained from this information as well.

It is often taken for granted by the specialist that others outside his field know about the techniques and methods employed and the rationale behind them. Since this is not necessarily true, and since this is the first in an anticipated series of systematic revisions on the Lycosidae, I decided to explain some of the details involved in the study. The methods and rationale set forth here will be a basis for future investigations. The subheadings below include the components explored in the analysis of each species.

Discussion. Under this subheading an attempt is made to clarify the nomenclatural history of the species in question as well as explain the rationale for certain conclusions regarding names.

Figures and Color Descriptions. The color descriptions and illustrations are based on fresh alcoholic specimens in most cases. Well-preserved specimens of *Trochosa* in which the hairs have not been rubbed off are very similar to the living spiders and were utilized where possible. The differences in live and freshly preserved lycosids is produced by shrinkage in alcohol, which disrupts the abdominal color pattern; wetting, which makes the specimen darker than in life; and rubbing off of appressed hairs which make up some of the color pattern. Where discrepancies in color between live and preserved specimens have been observed, they are noted.

Color descriptions and illustrations were made under low power (16X) of a dissecting microscope, with the spider illuminated by a microscope lamp. Where variation is great, the range of color patterns representative of the greatest number of specimens is described. A given specimen may not fit the general description in all details.

For each species a dorsal view of the female was drawn, with an additional drawing of *T. terricola* to indicate the range of variation. The dorsal color pattern is one of the distinctive features of the

genus *Trochosa*. At least two drawings of the female genitalia were made for each species: a ventral external view of the epigynum after all the hair had been removed (often revealing some internal structure through the integument) and a dorsal view with the separated genitalia submerged in clove oil for clearing. The female genitalia of all species are drawn to the same scale. Two views of the male palpus were drawn for each species: a ventral view and a retrolateral view. The left palpus of the male was drawn after gentle removal of hair to reveal the palpal sclerites. All palpi are drawn to the same scale. The female genitalia and the male palpus are classically used in identifying spider species and they are of considerable importance in *Trochosa* for that purpose.

Measurements. All measurements listed are in millimeters. Two net micrometers (0.5mm, 1.0mm) were used in an ocular (16X) with a combination of low (1X) and high (4X) power objectives for making measurements. The higher power combination was used in measuring the eye rows and was determined to be accurate to 0.2 units of the micrometer grid or 0.025mm. The lower power combination was used to measure the body dimensions and leg lengths and was determined to be accurate to 0.2 units of the micrometer grid or 0.1mm. A measurement when retaken always read within two units of the original measurement with either of the micrometer grids, e.g., an original measurement of 6.5 micrometer units when retaken would read 6.3–6.7 units. In all cases the greatest dimension of the structure was recorded, e.g., patellea-tibia length was measured as the greatest distance from a line tangent to the most proximal part of the patella to a line tangent to the most distal part of the tibia.

The segments of leg I were measured from the prolateral aspect, as was patella-tibia II. The segments of leg IV were measured from the retrolateral aspect, as was patella-tibia III. This method was found to be accurate and resulted in fewer broken legs than others that were tried. Total body length was estimated by measuring the abdomen and adding this figure to carapace length. Although the anterior end of the abdomen tends to overlie part of the cephalothorax, the abdomen usually shrinks in alcohol, reducing its size. Measurements of total body length in this fashion can be reproduced more accurately, and since this dimension is highly variable, its primary function is for general recognition, not definition of the species.

A set of 10 specimens of each sex was measured to give some idea of the range of variability within a species. A series of 19 different measurements was made of selected specimens of all species. Since eastern and western populations of *Trochosa terricola* differ in the number of posterior cheliceral teeth (Map 1) and in color and were described as different species, it seemed best to treat them separately for comparison. Six additional measurements of *T. terricola* epigyna, used by Locket and Millidge (1951) to separate female specimens of European *Trochosa*, were also made to compare North American populations of *terricola* with European populations. The range and mean for the more significant measurements are recorded for each species. The measurements should prove useful not only to identify certain species of North American *Trochosa*, but to help distinguish this genus from others as the study progresses. Preliminary measurements of other lycosids indicate that both the eye arrangement and ratio of leg length to carapace width or length are useful in distinguishing genera.

Diagnosis. The species under investigation is compared to its closest relative(s) and differences that distinguish them are noted.

Natural History. In discussing methods (in a broad sense) it is appropriate to emphasize the importance of routine observations in the field. It is not the province of the systematist to explore and record detailed elements of the ecology and behavior of each species he studies, nor is it practicable from the standpoint of time, but it behoves him to note the habitat where certain species are found and any peculiar behavioral traits associated with the species. This kind of information is often as valuable to the systematist as that concerning morphological features and should be incorporated into decisions about species relationships.

Distribution. The geographic range of the species is given.

Records. Includes only those specimens examined. Collecting localities for Canada are listed by city or town and separated by a semicolon. Multiple records for the United States are listed by county and separated by a semicolon. Collection records at the periphery of the species range are given in detail. The lower case "o" represents immature specimens.

ACKNOWLEDGMENTS

This study was made possible by the loan of large numbers of specimens from the Museum of Comparative Zoology, Cambridge,

Massachusetts, the American Museum of Natural History, New York City, and the Canadian National Collection, Ottawa, Canada. I wish to thank sincerely the curators of these collections, Dr. H. W. Levi, Dr. N. I. Platnick, and Dr. C. D. Dondale respectively, for the use of these materials. The study of type specimens on loan from the Museum of Comparative Zoology and the American Museum was an essential part of this investigation.

Special thanks are extended to Dr. C. D. Dondale who kindly consented to review the manuscript and offered constructive criticism and friendly advice. Thanks also go to Dr. J. Reiskind who supplied important specimens from the University of Florida collection. Dr. Torbjorn Kronstedt sent critical European specimens for examination and supplied information about the syntypes of *Trochosa terricola* Thorell. I am grateful to Mr. F. R. Wanless for sending specimens of *Trochosa avara* Keyserling from the L. Koch collection maintained in the British Museum (Natural History).

Finally a word of appreciation and recognition is given to Dr. W. J. Gertsch, Dr. H. K. Wallace, the late Dr. A. M. Chickering, and the late Mr. W. Ivie for their efforts in collecting many of the specimens examined.

Initial support was provided during the summers of 1975 and 1976 by the Andrew W. Mellon Foundation under the program for faculty development at Hope College. National Science Foundation grant DEB-7803561 helped defray expenses of this investigation.

Key to Females

- 1a. Posterior margin of cheliceral fang furrow with three teeth 2
- 1b. Posterior margin of cheliceral fang furrow with two teeth *terricola*
- 2a. Longitudinal piece of median septum of epigynum narrow, with lateral ends of transverse piece directed anteriorly (Figs. 8, 9, 18, 20, 21, 23, 25, 27) 3
- 2b. Longitudinal piece of median septum of epigynum broad, with transverse piece straight (Figs. 10, 13, 14, 16) *terricola*
- 3a. Longitudinal piece of median septum with blunt, posterior median process and with lateral ends of transverse piece extending only slightly anteriorly (Figs. 20, 21). Eastern United States (Map 2) *avara*

- 3b. Longitudinal piece of median septum without blunt, posterior median process and with lateral ends of transverse piece extending considerably anteriorly (Figs. 8, 9, 18, 23, 25, 27) 4
- 4a. Color pattern of carapace with two dark, elongate spots or short dashes within light, broad median stripe (Figs. 3, 5, 6) 5
- 4b. Color pattern of carapace without dark spots or dashes within light, broad median stripe (Fig. 4). Western United States (Map 2) *gosiuta*
- 5a. Width of transverse piece of epigynum less than twice length of longitudinal piece (Figs. 18, 23, 25) *shenandoa*
- 5b. Width of transverse piece of epigynum more than three times length of longitudinal piece (Figs. 8, 9). Primarily restricted to peninsular Florida and adjacent regions (Map 3) *parthenus*

Key to Males

- 1a. Posterior margin of cheliceral fang furrow with three teeth 2
- 1b. Posterior margin of cheliceral fang furrow with two teeth *terricola*
- 2a. Embolus of palpus long and thin with tip curled to form characteristic loop or "pig-tail" (Figs. 28-31) ... *terricola*
- 2b. Embolus of palpus with broad flattened subterminal area and short, thinner tip forming hook but not loop (Figs. 32-37, 39, 40, 42, 43, 45, 46) 3
- 3a. Total body length 5.7-7.6 mm. Primarily restricted to peninsular Florida and adjacent regions (Map 3) ... *parthenus*
- 3b. Total body length 7.5-8.4 mm. Occurring outside peninsular Florida 4
- 4a. Palea of palpus with prominent distal knob (Figs. 34-37, 39, 40, 42, 43) and proximal pair of retrolateral macrosetae of tibia I stout and elongate (Figs. 38, 41) 5
- 4b. Palea of palpus without prominent distal knob (Figs. 45, 46) and proximal pair of retrolateral ventral macrosetae of tibia I not as stout or elongate (Fig. 44). Western United States (Map 2) *gosiuta*
- 5a. Median apophysis of palpus greatly enlarged and directed ventrad (Figs. 36, 37, 39, 40). Proximal retrolateral ventral macroseta of tibia I not extending more than one-half distance along shaft of median retrolateral macroseta (Fig. 38) ...
..... *avara*

- 5b. Median apophysis of palpus not as large (Figs. 34, 35, 42, 43). Proximal retrolateral ventral macroseta of tibia I extending more than one-half distance along shaft of median retrolateral macroseta (Fig. 41) *shenandoa*

Trochosa terricola Thorell

Figures 1, 2, 10–16, 28–31. Map. 1. Table 1.

- Lycosa trabilis*: C. L. Koch 1836: heft 134, pls. 19, 20; 1840: 410; 1847: 229. Not *Lycosa trabilis* Clerck according to Thorell 1856.
- Trochosa trabilis*: C. L. Koch 1848: 141. Not *Lycosa trabilis* Clerck according to Thorell 1856.
- Lycosa agretyca*: Blackwall 1842: 407. Not *Lycosa agretyca* Walckenaer according to Pickard-Cambridge 1874.
- Trochosa terricola*: Thorell 1856: 171. Syntypes (2♂♂:3♀♀) from Uppsala, Sweden, in the Natural History Museum, Stockholm, Sweden, not examined, but see below. Pickard-Cambridge 1874: 332. Bonnet 1959: 4713.
- Lycosa terricola*: Westring 1861: 529.
- Tarentula terricola*: Collett 1875: 255.
- Trochosina terricola*: Simon 1885: 10.
- Lycosa pratensis* Emerton, 1885: 483, pl. 46, figs. 4, 4a, 4b, ♀♂. Two female syntypes from Salem, Essex Co., Massachusetts, in the Museum of Comparative Zoology, examined. Emerton 1884: 422, pl. 3, fig. 4, ♀; 1902: 69, figs. 168–170, ♀; 1913: 156; 1914: 118; 1920: 328; 1921: 108; 1924: 123, 124; 1928: 46; 1930: 168. Marx 1890: 563. Banks 1892: 64; 1895: 91; 1900: 483; 1907: 57; 1910: 57; 1916a: 71; 1916b: 80. Harrington 1897: 191. Slosson 1898: 248. Britcher 1903: 191. Ruthven 1906: 101. Bryant 1908: 85. Chamberlin 1908: 225, 261, pl. 21, fig. 3, ♀. Petrunkevitch 1911: 565. Comstock 1913: 638, fig. 720a, ♀; 1940: 649, fig. 720b, ♀ Barrows 1918: 314. Holmquist 1926: 410. Crosby and Bishop 1928: 1067. Worley and Pickwell 1931: 94. Banks and Newport 1932: 31. Elliot 1932: 423. Worley 1932: 55. Procter 1933: 272. Chickering 1933: 516. Crosby and Zorsch 1935: 39. Kaston 1938: 184.
- Lycosa terricola pallida* Nosek, 1904: 4. First synonymized by Bonnet 1949: 4716.
- Tarentula pratensis*: Strand 1906: 466.
- Lycosa orophila* Chamberlin and Gertsch, 1929: 108. Female holotype from Montpelier, Bear Lake Co., Idaho, in the American Museum of Natural History, examined. Chamberlin and Ivie 1933: 50. First synonymy by Gertsch 1934: 1.
- Alopecosa terricola*: Denis 1937: 167.
- Trochosa pratensis orophila*: Chamberlin and Ivie 1947: 24. Hackman 1954: 78. Lindroth 1957: 104.
- Trochosa pratensis*: Kaston 1948: 330, figs. 1092–1094, 1117–1118, ♀♂; 1953: 147, fig. 371. Bonnet 1959: 4706.
- Trochosa terricola pratensis*: Hackman 1954: 78. Lindroth 1957: 104. Fox and Donale 1972: 1914.
- Trochosa terricola*: Dondale 1971: 67. Kaston 1972: 198, fig. 446; 1978: 188, fig. 478.

Discussion. The synonymy for European *Trochosa terricola* given here follows that of Bonnet (1959). In most cases, only the initial

usage of the various synonyms by European authors is given. For more complete synonymy of the European populations refer to Bonnet (1959: 4713-4716).

Gertsch (1934) reported that Reimoser (1919) considered *Lycosa pratensis* Emerton a synonym of *Trochosa robusta* Simon, but when Gertsch compared *L. pratensis* Emerton with European species of *Trochosa* he found that "it is more closely related to *Trochosa terricola*, of which it is scarcely more than a variety." Hackman (1954), Lindroth (1975), and Fox and Dondale (1972) regarded *pratensis* as a subspecies of *terricola*. Dondale (1971) was the first American to use *Trochosa terricola* Thorell for the species that has long been known under the name of *T. pratensis* (Emerton) and Kaston (1972, 1978) followed suit.

To clarify the matter I requested the holotype of *T. terricola* from the Swedish Museum of Natural History, Stockholm, for comparison with *T. pratensis*. Mr. T. Kronstedt informed me that Thorell had not designated any type, but he did list (Thorell 1856: 171) *terricola* among species found in the Swedish province of Uppland. Kronstedt reported: "There is in our museum a collection of dry pinned spiders belonging to Thorell. In this collection are preserved other species which Thorell described as *new* in the above publication, so the original *terricola* specimens should be there too, and there are three males and four females. Two males and three females bear the label 'Ups.', which means Uppsala in the province of Uppland. The three dry males in the collection are all *terricola* in the present sense. They have the terminal loop in the embolus, characteristic of this species and also present in *pratensis*." Kronstedt felt it would be risky to send pinned specimens through the mails and I agreed. Instead he sent three males and one female from the type locality in preservative for examination. In addition a male, which survived the transatlantic crossing in the mails, arrived alive and was observed for one week before preserving. These specimens together with 33 other European specimens of *terricola* that I've examined agree in most details with *pratensis* and I cannot distinguish them. The males and females in the Swedish Museum of Natural History bearing the "Uppsala" label are considered syntypes.

Chamberlin and Gertsch (1929) described *Lycosa orophila* from Idaho and Utah as new. They reported that, "This species is indistinguishable from *Lycosa pratensis* Emerton except in the fact that the

lower margin of the chelicerae is armed with two rather than three teeth." Gertsch (1934) listed *L. orophila* as a junior synonym of *L. pratensis* and reported upon the geographic distribution of the number of teeth on the lower cheliceral margin. Chamberlin and Ivie (1947) later compromised by relegating *orophila* to subspecies status, presumably because of the difference in number of teeth on the posterior cheliceral margin. The geographic distribution of the character in over 1300 specimens is shown by Map 1 and Table 1. Since a single symbol on the Map 1 may indicate from one to 50 specimens a more accurate distribution of actual numbers is given by province and state in Table 1. From these data it is clear that subspecies of *T. terricola* in North America cannot be delineated by the number of posterior cheliceral teeth present in certain populations. Measurements of selected specimens from the eastern and western United States indicate a slightly larger average size for those in the East. However, there is considerable overlap in size and none of the other anatomical characters measured allows separation of these populations into subspecies (compare *Measurements* of eastern and western populations). It is possible that biochemical, ecological or behavioral studies may help clarify the relationships of the populations of *T. terricola* in Europe and the eastern and western United States. Until more information is forthcoming, I find it difficult to recognize subspecies of *T. terricola*.

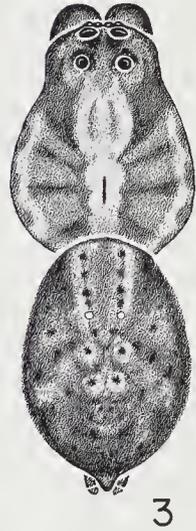
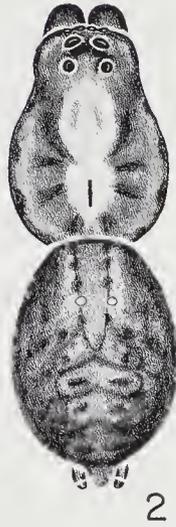
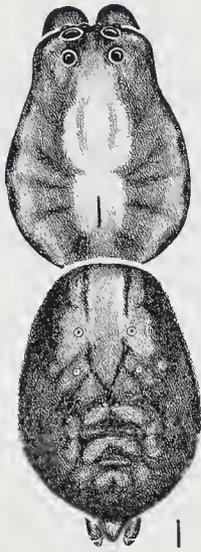
Color. Eastern Females. Face dark orange-brown. Chelicerae darker, reddish brown. Condyles orange-brown. Eyes with black nacelles.

Carapace dark orange-brown with broad median stripe of pale yellow-orange; with paired short stripes of a darker color inside median stripe as in Figure 1, and with yellow-orange submarginal stripes.

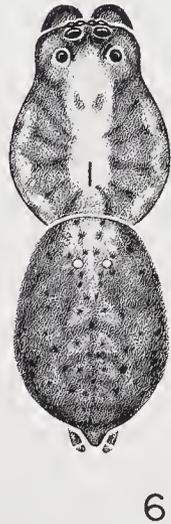
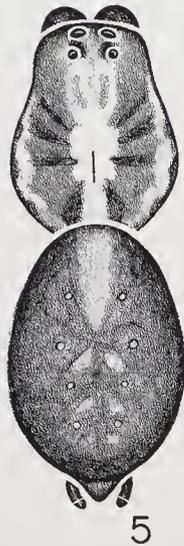
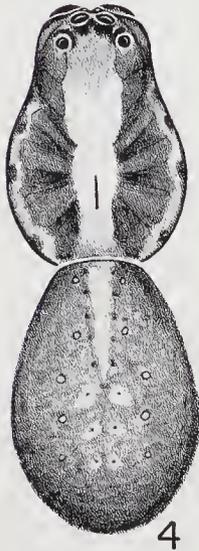
Dorsum of abdomen brown in appearance, with yellow-orange base mottled with dark brown forming pattern as in Figure 1. Venter of abdomen yellow to pale yellow-orange, with darker mottling along sides.

Legs yellow to pale yellow-orange; with few dusky markings dorsally, but without distinct bands. Distal region of tibiae, metatarsi, and tarsi brown.

Labium and endites orange-brown with distal ends paler, yellowish. Sternum light orange-brown.



1 mm



Color. Western Females. Face yellow to brownish yellow, lightest along lower edge of clypeus. Chelicerae darker, orange to brownish orange. Condyles lighter, yellow. Eye nacelles black.

Carapace yellow-brown with broad, yellowish median stripe enclosing pair of darker short stripes anteriorly as in Figure 2; with pale yellowish submarginal stripes.

Dorsum of abdomen pale yellow to brownish yellow with irregular spots of dark gray or brown as in Figure 2. Cardiac area even colored, pale brownish yellow to tan. Venter of abdomen cream to pale brownish yellow, without darker markings.

Legs yellow to pale brownish yellow, without darker markings, lighter ventrally.

Labium and endites yellowish brown to orange-brown; with distal ends cream to pale yellow. Sternum yellow to light brownish yellow.

Color. Eastern Males. Face dark orange-brown to brownish yellow at lower edge. Chelicerae dark reddish brown. Cymbium of palpus orange-brown.

Carapace dark orange-brown with broad yellow-orange median stripe, and with paired short dusky median stripes as in female. Yellow-orange submarginal stripes not as distinct as in female.

Dorsum of abdomen appearing gray-brown—color produced by background of brownish yellow finely reticulated with gray. Cardiac area pale yellowish brown. Venter of abdomen yellow to brownish yellow; sides mottled gray.

Legs with femora yellow, darker brown distally, with patella-tibiae, metatarsi, and tarsi brown.

Labium and endites brownish orange with distal ends yellowish.

Figs. 1-2. *Trochosa terricola* Thorell. 1. Female from Ridgefield, Fairfield Co., Connecticut, 9 May 1965. 2. Female from Fruitland, Payette Co., Idaho, 10-25 Sept. 1943.

Fig. 3. *Trochosa avara* Keyserling, female from Ramsey, Bergen Co., New Jersey, 24 Sept. 1934.

Fig. 4. *Trochosa gosiuta* (Chamberlin), female from Timpanogos Park, American Fork Canyon, Salt Lake Co., Utah, 13 June 1941.

Fig. 5. *Trochosa shenandoa* Chamberlin and Ivie, female holotype from Shenandoah National Park, Virginia, 5 July 1933.

Fig. 6. *Trochosa parthenus* (Chamberlin), female from Alachua Co., Florida, 8 Feb. 1934.

Sternum yellow to light brownish yellow.

Color. Western Males. Face yellow to brownish yellow, lightest along lower edge of clypeus. Chelicerae orange to brownish orange. Eye nacelles black. Cymbium of palpus brownish yellow to light brown.

Carapace yellow-brown, with broad pale yellow median stripe enclosing pair of darker stripes in the cephalic region; with lighter pale yellow submarginal stripes.

Dorsum of abdomen pale yellow to light yellow-brown with darker brown or black spots that sometimes coalesce to form pattern. Cardiac area uniformly brown with slight reddish tinge. Venter pale brownish yellow to cream without darker markings.

Legs light brownish yellow to yellow dorsally, pale yellow to cream ventrally. Distal segments darker.

Labium and endites yellow-brown with distal ends yellow to cream. Sternum yellow.

Measurements. Ten females and ten males from New Hampshire, Vermont, Connecticut, and Massachusetts representing eastern populations formerly known as *Trochosa pratensis* (Emerton).

Females (Eastern):					
	Mean	Range		Mean	Range
Ant. Eye Row	.919	.86- .98	Femur I	3.02	2.8- 3.4
PME	.925	.88- .98	Pat.-Tibia I	3.88	3.5- 4.3
PLE	1.289	1.19- 1.38	Meta. I	2.06	1.8- 2.3
POQ	.822	.79- .88	Tarsus I	1.29	1.2- 1.4
			Total I	10.18	9.2-11.4
Carapace					
Width	3.56	3.2 - 3.9	Femur IV	3.42	3.0- 3.8
Carapace					
Length	4.89	4.5 - 5.4	Pat.-Tibia IV	4.12	3.8- 4.4
Body Length	10.36	9.2 -11.2	Meta. IV	3.51	3.2- 3.8
Pat.-Tibia II	3.41	3.0 - 3.8	Tarsus IV	1.47	1.4- 1.6
Pat.-Tibia III	3.00	2.8 - 3.3	Total IV	12.48	11.4-13.3

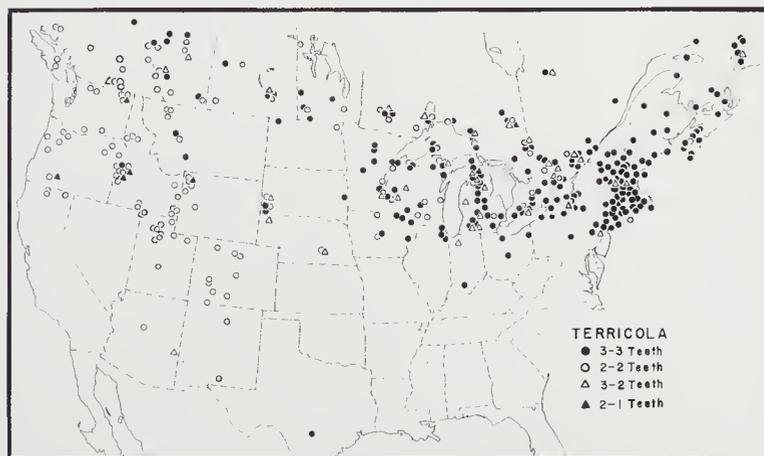
Males (Eastern):					
	Mean	Range		Mean	Range
Ant. Eye Row	.818	.71- .88	Femur I	3.12	2.8- 4.0
PME	.830	.74- .89	Pat.-Tibia I	4.15	3.7- 4.6
PLE	1.122	.90- 1.25	Meta. I	2.67	2.4- 3.1
POQ	.744	.64- .88	Tarsus I	1.56	1.4- 1.8
			Total I	11.40	10.0-13.4

Carapace					
Width	3.24	2.8 - 3.6	Femur IV	3.30	2.9- 3.8
Carapace					
Length	4.44	3.8 - 4.9	Pat.-Tibia IV	3.94	3.5- 4.4
Body Length	8.55	7.2 - 9.6	Meta. IV	3.54	3.2- 3.9
Pat.-Tibia II	3.44	3.0 - 3.8	Tarsus IV	1.48	1.4- 1.6
Pat.-Tibia III	2.94	2.6 - 3.4	Total IV	12.27	10.9-13.6

Measurements. Ten females and ten males from Fruitland, Payette Co., Idaho, 14 Sept. 1943, representing western populations formerly known as *Lycosa orophila* Chamberlin and Gertsch.

Females					
(Western):	Mean	Range		Mean	Range
Ant. Eye Row	.835	.74- .95	Femur I	2.74	2.4- 3.3
PME	.829	.75- .95	Pat.-Tibia I	3.39	3.0- 4.2
PLE	1.121	1.02- 1.29	Meta. I	1.86	1.5- 2.2
POQ	.731	.66- .80	tarsus I	1.17	1.0- 1.4
			Total I	9.20	7.9-11.0
Carapace					
Width	3.20	2.8 - 3.8	Femur IV	3.14	2.8- 3.6
Carapace					
Length	4.40	3.8 - 5.2	Pat.-Tibia IV	3.65	3.2- 4.3
Body Length	9.34	8.2 -11.8	Meta. IV	3.08	2.7- 3.6
Pat.-Tibia II	3.02	2.5 - 3.7	Tarsus IV	1.39	1.1- 1.7
Pat.-Tibia III	2.70	2.4 - 3.2	Total IV	11.30	9.8-13.0
Males					
(Western):	Mean	Range		Mean	Range
Ant. Eye Row	.725	.66- .78	Femur I	2.63	2.4- 2.9
PME	.732	.69- .78	Pat.-Tibia I	3.52	3.2- 4.0
PLE	.969	.88- 1.09	Meta. I	2.24	2.0- 2.6
POQ	.649	.60- .71	Tarsus I	1.38	1.2- 1.4
			Total I	9.76	8.8-10.8
Carapace					
Width	2.82	2.6 - 3.2	Femur IV	2.88	2.6- 3.2
Carapace					
Length	3.84	3.4 - 4.4	Pat.-Tibia IV	3.43	3.2- 3.9
Body Length	7.74	6.7 - 9.4	Meta. IV	2.98	2.8- 3.4
Pat.-Tibia II	2.90	2.6 - 3.2	Tarsus IV	1.34	1.2- 1.5
Pat.-Tibia III	2.52	2.3 - 2.8	Total IV	10.64	9.9-11.7

Diagnosis. *Trochosa terricola* is like other Nearctic species of *Trochosa* in color pattern (compare Figs. 1, 2 with 3-6) and morphological features such as the eye arrangement and relative length of legs compared to carapace length. Males of *terricola* differ from other Nearctic species of *Trochosa* in structure of the palpus (compare Figs. 28-31 with Figs. 32-37, 39, 40, 42, 43, 45, 46). The most distinguishing feature of the palpus in *terricola* is the loop at the distal end of the embolus (Fig. 30). Females of *terricola* differ from other Nearctic species of *Trochosa* in structure of the epigynum. The transverse piece of the epigynum in *terricola* does not have the ends curved anteriorly as in *avara*, *gosiuta*, *shenandoa*, and *parthenus* (compare Figs. 10-16 with Figs. 7-9, 17-27). *Trochosa terricola* forms together with *spinipalpis*, *robusta*, and *ruvicola* of Europe a close-knit species group. There is a great anatomical similarity among these species and a definitive study of the middle European species of *Trochosa* (Engelhardt 1964) did not reveal any ecological, seasonal, or ethological isolation mechanisms present. These four species occur sympatrically throughout western and central Europe. In spite of morphological, ecological, and behavioral similarities, no hybrids could be produced in the laboratory. Engelhardt suggests that physiological mechanisms (pheromones) may prevent hybridization between these species.



Map 1. Collection localities for *Trochosa terricola* showing distribution of posterior cheliceral teeth. Alaskan and northern Canadian localities not on map are listed under *Records* and marked with asterisks.

Table I
 Posterior Cheliceral Teeth—*Trochosa terricola**

State or Province	3-3	3-2	2-2	2-1
Alaska			15	
Newfoundland	8	1		
Prince Edward Island	1			
Nova Scotia	102	1	1	
New Brunswick	22			
Quebec	39	3	1	
Ontario	147	19	97	1
Manitoba	5		7	1
Saskatchewan	1	1	4	
Alberta	8	6	35	
British Columbia	1	1	62	
Maine	19			
New Hampshire	28	1		
Vermont	28	1		
Massachusetts	68			
Rhode Island	1			
Connecticut	22	1		
New York	56	1	2	
New Jersey	18	1		
Pennsylvania	5			
Ohio	5			
Michigan	43	8	9	1
Indiana	2	1		
Wisconsin	10	2	7	
Illinois	4			
Minnesota	16	1	9	
Iowa	8		3	
North Dakota	1		1	
South Dakota	5	1	2	
Texas	1			
Montana	2			
Idaho	1		192	2
Wyoming			33	1
Colorado			9	
Utah			33	
New Mexico			3	
Arizona		1	1	
Washington			65	1
Oregon			14	1
California			12	
TOTALS	677	51	617	8

*Geographic distribution of *Trochosa terricola* with reference to number of posterior cheliceral teeth. Geographical sequence is from North to South and East to West.

Of the above three species *terricola* appears to be most closely related to *spinipalpis*. Males of *spinipalpis* can be identified by macrosetae on the ventral side of the palpal tibia. These macrosetae are absent in *terricola*. According to Locket and Milledge (1951) the females of the two species can be separated by color and certain anatomical proportions. For example, the number derived by dividing the width of the transverse piece of the epigynum by the width of the sternum between coxae II ranges from .30-.33 in *terricola* and .24-.29 in *spinipalpis*. In addition European specimens of *terricola* (93%) have 2-2 posterior cheliceral teeth while *spinipalpis* (66%) tend to have 3-3 posterior cheliceral teeth. For a thorough analysis of comparative anatomy of the Middle European *Trochosa* see Engelhardt (1964).

In North America *Trochosa terricola* shows considerable variation in the number of cheliceral teeth and in color. In general, eastern populations tend to be darker in color and tend to have 3-3 posterior cheliceral teeth and western populations tend to be lighter in color and have 2-2 posterior teeth. The geographic pattern of the number of posterior cheliceral teeth in specimens examined is shown in Map 1 and Table 1. Because a single symbol on this map may represent anywhere from one to 50 specimens it tends to exaggerate the variability of this character. Table 1 is a list of the actual number of specimens examined from each locality. These data indicate that populations of *Trochosa terricola* in North America cannot be separated into distinct geographic races upon the basis of cheliceral teeth number. It remains to be seen whether or not additional information concerning the ecology, behavior, or genetic mechanisms of the eastern and western populations will support recognition of subspecies.

Natural History. Kaston (1948) reports this species running over dead leaves of forest floors, and beneath stones in fields. I have found this species in Michigan under logs and in leaf litter of deciduous woods. It occurs most often at the edge of woods. Males have been captured in pitfall traps in an old field.

According to Engelhardt (1964) Central European populations of *terricola* have spring and fall mating seasons. Males may live up to two years and females longer, with those of the autumn generation surviving almost three years. The habitat of *terricola* in Europe resembles closely that of American populations. The skirts of forests

where medium humidity and little shadow prevail offer preferred situations.

The comparative study of Central European *Trochosa* by Engelhardt (1964), covering the morphological, ethological, and autecological characteristics of *robusta*, *ruricola*, *spinipalpis*, and *terricola*, provides a wealth of detailed information.

Distribution. Temperate areas of the Holarctic Region (Map 1).

Records. *ALASKA. Haines, 20–25 Aug. 1945, ♂ (J. C. Chamberlin); Ketchikan, 29 Aug. 1922, ♀ (R. Marshall); Kodiak, 22–25 Aug. 1958, 3♀♀ (C. Lindroth); Matanuska, 26 May 1944, 3♀♀; 23 May 1945, ♂♀ (J. C. Chamberlin); Palmer, 31 Aug. 1959, ♀ (A. B. Krom); Wasella, 11 Oct. 1959, ♂♀ (A. B. Krom); Wrangell, 1–20 Sept. 1951, ♂ (B. Malkin).

CANADA. *Northwest Territory. Mackenzie Dist.: 40 mi. NW of Enterprise, 15 Aug. 1965, ♀ (J., W. Ivie). *Labrador. Natashquan River, 1912, ♀ (T. W. Townsend). Newfoundland. Bay of Islands, Aug. 1912, ♀ (Lung); 4 July 1927, ♀ (O. L. Austin); Deer Lake, 19 June 1915, ♀ (G. K. Noble); Humber River, Sept. 1912, ♀ (G. C. Shattuck); *St. John's, 20 May 1958, ♂, 31 Aug., ♀; Spruce Brook, Aug. 1912, ♂♀♀ (Lenz); Bay St. George, Stephenville Crossing, July 1912, ♀♀ (Engelhart). Prince Edward Island. Malpeque Bay. Nova Scotia. Barrington; Beaconsfield; Bridgewater; Canard; Cape Breton Island; Digby; Gasperaux; Glenora Falls; Granville Ferry; Graywood; Kentville; Sable Island. New Brunswick. Fredericton; Green River, N of Edmundston; Priceville. Quebec. Anticosti Island; Bagotville; Breckenridge; Entry Island; Fort Coulonge; Freightsburg; Kingsmere: Gatineau Park; Montreal; Mt Orford; Natashquan; St. Agathe; Sherbrooke; Vaudreuil. Ontario. Algonquin Provincial Park; Ameliasburgh; Ancaster; Batchawana; Bear Island, Lake Temagami; 9 mi. N of Bloomfield; Brion Island; Chatterton; Cochrane; 30 mi. E of Dryden; 20 mi. E of Dryden; 2 mi. N of Dryden; Fitzroy; Grundy Lake Provincial Park; Ingersoll; 70 mi. E of Kenora; 20 mi. E of Kenora; Lake Superior Provincial Park; Lake Temagami; 15 mi. W of Marathon; Maynooth; Mazinaw Lake; Mer Bleue, near Ottawa; New Liskeard; 17 mi. W of Nipigon; Odessa; Ottawa; 10 mi. NW of Ouimet; Oxford Mills; 3 mi. S of Porquis Junction; Port Credit; Raith; 3 mi. N of Ramore; Rednersville; Ridgetown; St. Thomas; 7 mi. E of Smooth Rock Falls; 19 mi.

*Not on Map 1.

S of Temagami; 7 mi. S of Temagami; Tillsonburg; Toronto; Trout Creek, Parry Sound District; Turkey Point; Wallacetown; Walsingham; Warsaw; Wawa. *Manitoba*. Birtti; 15 mi. S of Deloraine; 2 mi. E of Pipestone; Rocky Lake; Winnipeg. *Saskatchewan*. Ketepwa; McLean; Montmartre; Saskatoon; Sinaluta; Skull Creek, 6 mi. E of Piapot; Waseca. *Alberta*. Athabaska River at Rocky River; 5 mi. W of Banff; Canmore; Edmonton; Fawcett; Fort McLeod; *Fort McMurray; Jasper Park; Medicine Hat; Morley; 15 mi. E of Robb; Seba; Sturgeon River, 15 mi. N of Edmonton; 9 mi. NW of Whitecourt. *British Columbia*. Comox; Crows Nest Lake; 20 mi. W of Golden; 7 mi. NE of Greenwood; *Lake Aleza; Lillooet; Penticton; Pine Pass; Port Alberni; Summerland; Terrace; Vernon; Yoho National Park.

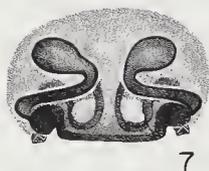
UNITED STATES. *Maine*. Cumberland; Franklin; Hancock; Knox; Lincoln; Mount Desert Island; Oxford; Piscataquis; York; Washington. *New Hampshire*. Carroll; Cheshire; Coos; Grafton; Hillsborough; Stratford. *Vermont*. Bennington; Lamoille; Rutland; Windham; Windsor. *Massachusetts*. Barnstable; Berkshire; Essex; Franklin; Hampshire; Middlesex; Nantucket; Norfolk; Plymouth. *Rhode Island*. Providence. *Connecticut*. Fairfield; Hartford; Litchfield; New Haven; Tolland. *New York*. Bronx; Cattaraugus; Cayuga; Chautauqua; Clinton; Columbia; Essex; Greene; Hamilton; Monroe; Niagara; Onondaga; Orange; Steuben; Suffolk; Tompkins; Ulster; Warren; Wayne; Wyoming. *New Jersey*. Bergen; Hunterdon. *Pennsylvania*. Carbon; Northampton; Pike. *Ohio*. Erie; Franklin;

Figs. 7-9. *Trochosa parthenus* (Chamberlin). 7-8. Female from Alachua Co., Florida, 8 Feb. 1934. 7. Spermathecae. 8. Epigynum. 9. Epigynum of female holotype from Bartow, Polk Co., Florida.

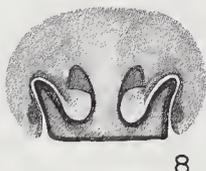
Figs. 10-16. *Trochosa terricola* Thorell. 10-12. Females from Fruitland, Payette Co., Idaho, 10-25 Sept. 1943. 10. Epigynum. 11-12. Spermathecae. 13. Epigynum of holotype of *Lycosa orophila* Chamberlin and Gertsch (= *Trochosa terricola* Thorell) from Montpelier, Bear Lake Co., Idaho, 4 July 1928. 14. Epigynum of syntype of *Lycosa pratensis* Emerton (= *Trochosa terricola* Thorell) from Salem, Essex Co., Massachusetts, May 1878. 15-16. Female from Ridgefield, Fairfield Co., Connecticut. 15. Spermathecae. 16. Epigynum.

Figs. 17-18. *Trochosa shenandoa* Chamberlin and Ivie, female from Cove Creek, Washington Co., Arkansas, Feb. 1956. 17. Spermathecae. 18. Epigynum. *lp*, longitudinal piece of median septum.

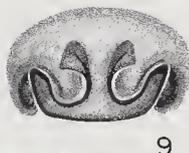
*Not on Map 1.



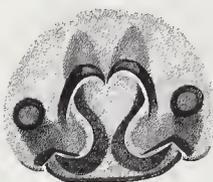
7



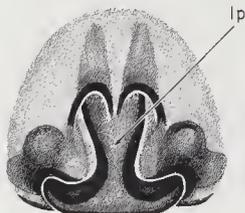
8



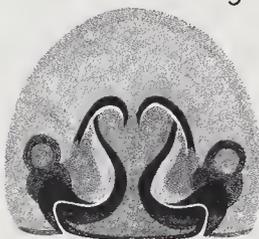
9



10



13



14



11



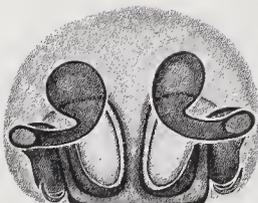
15



16



12



17



18

Knox; Trumbull. *Michigan*. Berry; Calhoun; Cheboygan; Chippewa; Clare; Clinton; Crawford; Emmet; Grateot; Ingham; Iron; Keweenaw; Livingston; Mackinac; Macomb; Marquette; Menominee; Midland; Osceola; Oscoda; Otsego; Roscommon; Saginaw; Washtenaw. *Indiana*. Lawrence Co.: Mitchell, ♀♀ (N. Banks); Starke Co.: Bass Lake, ♀ (N. Banks). *Wisconsin*. Adams; Ashland; Buffalo; Chippewa; Dane; Douglas; Eau Claire; Grant; Iron; Juneau; Manitowoc; Sauk; Vernon. *Illinois*. Cook; DuPage; Lake. *Minnesota*. Anoka; Crow Wing; Goodhue; Hennepin; Itasca; Ramsey; Todd. *Iowa*. Boone; Clayton; Clinton; Story; Winnebago; Winnesnick. *North Dakota*. Divide; Pembina. *South Dakota*. Brookings; Custer; Lawrence. *Nebraska*. Dawes Co.: Shadron St. Pk., 10 Aug. 1960, ♂ (H. S. Fitch); Hall Co.: 10 mi. W of Grand Island, 6 June 1933, ♀♀ (W. Ivie); Grand Island, 20 June 1910, ♀ (R. V. Chamberlin). *Texas*. Travis Co.: Austin, ♀ (R. V. Chamberlin). *Montana*. Flathead; Gallatin; Lewis and Clark; Powell. *Idaho*. Bannock; Bear Lake; Bonneville; Canyon; Idaho; Lewis; Madison; Nez Pearce; Payette; Twin Falls; Valley. *Wyoming*. Sublette; Teton; Yellowstone Nat. Pk. *Colorado*. Archuleta; Boulder; Gunnison; Hinsdale; Larimer; Rio Grande; Routt; Teller. *Utah*. Box Elder; Daggett; Rich; Salt Lake; Sevier; Summit; Utah. *New Mexico*. Otero Co.: Camp Mary White, 9-12 Aug. 1935, ♂♀♂♂ (S. Mulaik); Taos Co.: Beulah, ♀ (R. V. Chamberlin). *Arizona*. Apache Co.; McNary, 8 July 1940, ♀♂ (W. J. Gertsch); Coconino Co.: Flagstaff, May 1940, ♀ (Peterson). *Washington*. Benton; Klickitat; Okanogan; Stevens. *Oregon*. Baker; Benton; Klamath; Lake; Lane; Multnomah; Wallowa. *California*. Modoc Co.: Goose Lake, ♂♀ (Holleman); Siskiyou Co.: Bray, 9 Aug. 1935, ♂:6♀♀ (R. V. Chamberlin, W. Ivie); Weed, 8 Sept. 1935, ♂♀♀ (R. V. Chamberlin, W. Ivie).

Trochosa avara Keyserling

Figures 3, 19-21, 36-40. Map 2.

Trochosa avara Keyserling, 1877: 661, pl. 8, figs. 38-39, ♂♀. Syntypes (♂♀) from "North America," L. Koch collection, deposited in the British Museum (Natural History), examined. Marx 1890: 564. Fox 1892: 269. Montgomery 1904: 304, pl. 20, fig. 42, ♀.

Lycosa rufiventris Banks, 1892: 65, pl. 3, fig. 35, ♀. Three female syntypes from Fall Creek, Cayuga Lake, Tompkins Co., New York, in the Museum of Comparative Zoology, examined. Britcher 1903: 128. Scheffer 1906: 126. First synonymized by Banks 1910: 55.

- Lycosa avara*: Banks 1892: 66; 1907: 743; 1910: 55; 1916b: 81. Chamberlin 1908: 279, pl. 20, figs. 1-3, ♂♀. Bryant 1908: 80. Emerton 1909: 202, pl. 7, figs. 2-2a, ♀. Petrunkevitch 1911: 556. Comstock 1912: 640, fig. 720a, ♀; 1940: 650, fig. 720a, ♀. Barrows 1918: 313. Bishop and Crosby 1926: 410. Crosby and Bishop 1928: 1066. Worley and Pickwell 1931: 91. Elliott 1932: 422. Chickering 1935: 584. Kaston 1938: 183; 1948: 329, pls. 56, 57, figs. 1091, 1114-1116, ♀♂. Bonnet 1957: 2603.
- Trochosa (Varacosa) avara*: Chamberlin and Ivie 1942: 37; 1944: 155.
- Varacosa avara*: Roewer 1954: 306.

Discussion. Keyserling (1877) apparently recognized the resemblance in the color pattern and anatomy of *T. avara* to European species of *Trochosa*. Although most American authors have maintained *avara* in *Lycosa*, it is generally agreed that this species together with the closely related *gosiuta*, *shenandoa*, and *parthenus* are close taxonomically to *Trochosa terricola*.

Chamberlin and Ivie (1942) placed *avara* in *Trochosa* and made it the type species of their new subgenus *Varacosa*. Roewer (1954) raised *Varacosa* to genetic status. *Trochosa avara* resembles *terricola* in bodily dimensions, coloration, and habitat preference, and I see no good reason for separating it as a genus or subgenus at this stage.

Color. Females. Face pale brownish yellow, lighter along lower edge of clypeus. Chelicerae darker, orange to orange-brown. Eye nacelles black.

Carapace brownish yellow to yellow-brown with broad, lighter yellowish median stripe as in Figure 3; with only faint indications of short, darker stripes within median light stripe; with indistinct lighter yellowish submarginal stripes.

Dorsum of abdomen brownish yellow to pale brown, mottled with darker gray to black spots forming an indistinct pattern as in Figure 3. Cardiac area more evenly colored yellow-brown or tan. Venter of abdomen pale yellow to cream with a few scattered darker spots, mostly along edges.

Legs yellow to pale brownish yellow without darker markings.

Labium and endites brownish yellow, with light ivory colored distal ends. Sternum pale yellow.

Color. Males. Face pale orange-brown. Chelicerae orange-brown. Cymbium of palpus orange-brown, distal tip yellowish.

Carapace orange-brown with broad median yellowish stripe. Faint dusky dashes within median stripe. Narrow, irregular yellowish submarginal stripes.

Dorsum of abdomen with yellow ground color, suffused with brown and spotted with black. Cardiac area solid brown.

Legs pale yellow to light brown, darker above.

Labium and endites yellow with distal ends cream. Sternum yellow.

Measurements. Ten females and ten males from Ramsey, Bergen Co., New Jersey.

Females:	Mean	Range		Mean	Range
Ant. Eye Row	.809	.76- .84	Femur I	2.90	2.8- 3.0
PME	.932	.88- .98	Pat.-Tibia I	3.59	3.4- 3.9
PLE	1.234	1.16- 1.32	Meta. I	1.98	1.9- 2.1
POQ	.840	.79- .88	Tarsus I	1.30	1.2- 1.4
			Total I	9.77	9.3-10.4
Carapace					
Width	3.22	3.0 - 3.4	Femur IV	3.46	3.2- 3.7
Carapace					
Length	4.43	4.1 - 4.8	Pat.-Tibia IV	4.00	3.8- 4.2
Body Length	9.22	8.6 - 9.8	Meta. IV	3.59	3.4- 4.8
Pat.-Tibia II	3.26	3.0 - 3.4	Tarsus IV	1.59	1.5- 1.7
Pat.-Tibia III	2.86	2.8 - 3.0	Total IV	12.64	12.0-13.4
<hr/>					
Males:	Mean	Range		Mean	Range
Ant. Eye Row	.742	.70- .80	Femur I	3.06	2.8- 3.3
PME	.888	.82- .92	Pat.-Tibia I	3.88	3.6- 4.2
PLE	1.168	1.05- 1.24	Meta. I	2.46	2.2- 2.6
POQ	.812	.74- .88	Tarsus I	1.40	1.2- 1.5
			Total I	10.82	10.0-11.5
Carapace					
Width	3.24	2.8 - 3.5	Femur IV	3.60	3.4- 3.9
Carapace					
Length	4.35	3.9 - 4.6	Pat.-Tibia IV	4.20	3.9- 4.4
Body Length	8.44	7.8 - 9.0	Meta. IV	4.02	3.6- 4.4
Pat.-Tibia II	3.44	3.2 - 3.6	Tarsus IV	1.78	1.6- 1.9
Pat.-Tibia III	3.03	2.8 - 3.3	Total IV	13.60	12.8-14.6

Diagnosis. *Trochosa avara* is closest to *gosiuta* in size and coloration. It also resembles that species in the structure of the epigynum. *Trochosa avara* is usually darker than *gosiuta* and the two short dark stripes enclosed within the broad median light stripe are usu-

ally discernible in *avara*, but not in *gosiuta* (compare Fig. 3 with Fig. 4). The median apophysis of the male palpus in *avara* is far more robust than in *gosiuta* (compare Figs. 39, 40 with Figs. 45, 46). Females of *avara* usually have a blunt process at the posterior end of the longitudinal piece of the median septum and the lateral ends of the transverse arms of the median septum of *avara* are not directed as far anteriorly as in *gosiuta* (compare Figs. 20, 21 with Fig. 27).

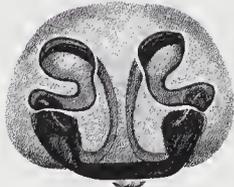
The male palpal organ of *avara* is closest to that of *shenandoa* (compare Figs. 36, 37 with Figs. 34, 35). The males of these two species are best distinguished by the robust ventral macrosetae on tibia I in *shenandoa*, which are much longer than in *avara* (compare Fig. 41 with Fig. 38).

Natural History. Kaston (1948) reports collecting this species from beneath stones and along the edges of wooded areas. In New England mature females were taken from mid-March to mid-November, males from September to mid-November. The species apparently overwinters in the adult and penultimate stages. Females with egg sacs were found in June by Kaston. One egg sac measured 4mm in diameter, another 4.5mm. The first egg case contained 32 eggs, the second 78 eggs. Eggs from the second case ranged from 1.12–1.28mm in size.

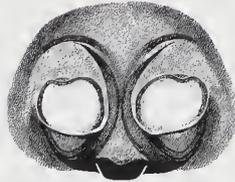
Distribution. From southern Quebec and Maine in the northeast to eastern Nebraska, Kansas, and Texas in the southwest (Map 2).

Records. CANADA. *Quebec.* Lanoraie, 16 June 1915, ♂ (J. I. Beaulne). *Ontario.* Essex Co.: Windsor, 28 April 1976, ♀ (C. D. Dondale, J. H. Redner). Pelee Island, Lake Erie, 4–16 June 1950, ♀ (W. Ivie, T. B. Kurata).

UNITED STATES. *Maine.* Cumberland Co.: Long Island, 11 Sept. 1904, ♀ (E. B. Bryant). *New Hampshire.* Belknap Co.: Gilmanton, June 1925, ♀ (J. H. Emerton). *Massachusetts.* Middlesex; Norfolk. *Rhode Island.* Providence. *Connecticut.* Fairfield; New Haven; Tolland. *New York.* Nassau; Orange; Oswego; Richmond; Rockland; Suffolk; Tompkins; Westchester. *New Jersey.* Bergen; Burlington; Cape May; Hunterdon; Mercer; Ocean; Passaic. *Pennsylvania.* Bucks; Erie; Washington. *Ohio.* Athens; Champaign; Cuyahoga; Hocking; Trumbull. *District of Columbia.* Washington. *West Virginia.* Monogahela; Pocahontas. *Virginia.* Fairfax; Falls Church (Indep. City); Nansemond; Virginia Beach (Indep. City). *Tennessee.* Hamilton; Lake; Obion; Sevier. *North Carolina.* Alamance; Durham; New Hanover; Orange; Polk. *South Carolina.* Aiken; Cal-



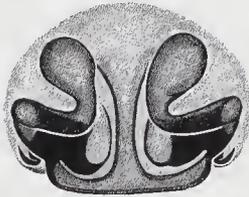
19



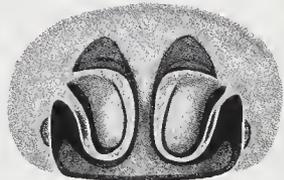
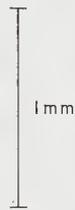
20



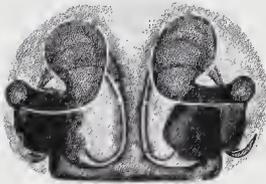
21



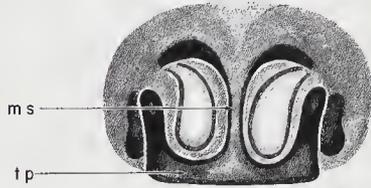
22



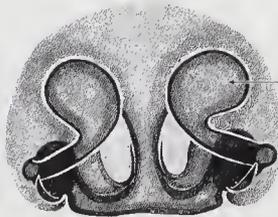
23



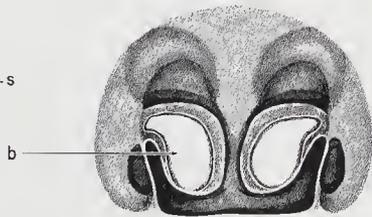
24



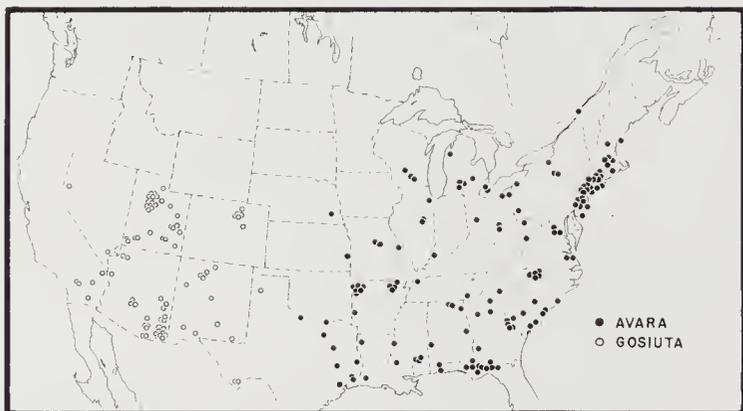
25



26



27



Map 2. Collection localities for *Trochosa avara* and *T. gosiuta*.

houn; Charleston; Darlington; Horry. *Georgia*. Clarke; Fulton; Holsersham; Rabun; Randolph; Screven; Thomas. *Florida*. Calhoun; Gadsden; Jackson; Jefferson; Leon; Liberty; Madison; Washington. *Alabama*. Baldwin; Choctaw; DeKalb; Lee; Madison. *Mississippi*. Amite; Forest; Wilkinson. *Louisiana*. Caddo. *Wisconsin*. Madison; Sauk. *Illinois*. Champaign; Cook. *Missouri*. Boone; St. Louis. *Arkansas*. Lawrence; Polk; Washington. *Nebraska*. Lancaster Co.: Lincoln, 1941, ♂ (M. J. Harbough). *Kansas*. Bourbon Co.: Redfield, 9 Oct. 1965, ♀ (J. W. Ivie). *Texas*. Anderson Co.: 19 Oct. 1951, 12 ♂♂:19 ♀♀ (K. Strawn). Dallas Co.: Dallas, 10 June 1935, ♂. Grayson Co.: Sherman, Dec. 1964, 4 ♀♀ (K. W. Haller). Hardin Co.: John Kirby St. Forest, 22 Nov. 1958, ♀♀ (A. R. Brady), Saratoga, 5 Dec. 1959, ♂ (J. C. Bequaert). Harris Co.: Seabrook, 1 Nov.

Figs. 19–21. *Trochosa avara* Keyserling. 19–20. Female from Ramsey, Bergen Co., New Jersey, 24 Sept. 1934. 19. Spermathecae. 20. Epigynum. 21. Epigynum of syntype of *Trochosa avara* Keyserling, North America.

Figs. 22–25. *Trochosa shenandoa* Chamberlin and Ivie. 22–23. Holotype from Shenandoah National Park, Virginia, 5 July 1933. 22. Spermathecae. 23. Epigynum. 24–25. Female from Beaufort, Carteret Co., North Carolina, 25 Jan. 1952. 24. Spermathecae. 25. Epigynum.

Figs. 26–27. *Trochosa gosiuta* Chamberlin, female from Timpanogos Park, American Fork Canyon, Salt Lake Co., Utah, 13 June 1941. 26. Spermathecae. 27. Epigynum. *b*, bulb of spermathecae; *ms*, median septum; *s*, spermathecae; *tp*, transverse piece.

1959, ♂ (J. C. Bequaert). Jasper Co.: Jasper, 5 Feb. 1962, ♀ (Science Club). Walker Co.: Huntsville, 2 Oct. 1950, ♂oo (W. J. Gertsch). Wichita Co.: Burkburnett, 12 Oct. 1964, 3♂♂:♀♀:o (K. W. Haller).

Trochosa gosiuta (Chamberlin)

Figures 4, 26, 27, 44-46. Map 2.

Lycosa avara var. *gosiuta* Chamberlin, 1908: 281, pl. 20, fig. 4, ♀. Female syntypes from Utah, lost. Petrunkevitch 1911: 556.

Lycosa gosiuta: Banks 1910: 56. Chamberlin and Gertsch 1928: 186. Chamberlin and Woodbury 1929: 140. Banks and Newport 1932: 31. Gertsch 1935: 20. Bonnet 1957: 2609.

Trochosa (Varacosa) gosiuta: Chamberlin and Ivie: 1942: 37.

Varacosa avara: Roewer 1954: 306.

Discussion. *Trochosa gosiuta* was first described by Chamberlin (1908) as a variety of *avara*. He indicated that females from Utah of this variety differed from *avara* in the shape of the epigynum. No type specimen was designated and the specimens from Utah upon which Chamberlin based the name *gosiuta* have apparently been lost.

Color. Females. Face orange-brown, yellowish along lower edge of clypeus. Eye nacelles black. Chelicerae brown to dark reddish brown.

Carapace orange-brown with broad median pale brownish yellow (golden) stripe, with dusky lines radiating from thoracic groove, and with brownish yellow submarginal stripes as in Figure 4.

Dorsum of abdomen pale brown ground color, freckled with numerous yellow and black spots, without distinct pattern as in Figure 4. Cardiac area light reddish brown. Venter pale brownish yellow with black spots laterally.

Legs pale yellow to brownish yellow, lighter ventrally.

Labium yellow, lighter yellow to cream distally. Endites brown with yellow distal ends. Sternum yellow.

Color. Males. Face pale yellow to orange-yellow. Lighter along lower edge of clypeus. Chelicerae pale yellow to golden. Eye nacelles black. Cymbium of palpus yellow.

Dorsum of abdomen pale brownish yellow with irregular spots of gray-brown or black without distinct pattern; venter pale yellow to cream with a few scattered gray to black spots laterally.

Legs light brownish yellow to pale yellow with ventral surface a lighter shade.

Labium and endites yellow with distal ends lighter yellow to cream. Sternum pale yellow to cream.

Measurements. Ten females and ten males from Utah.

Females:	Mean	Range		Mean	Range
Ant. Eye Row	.862	.78- .91	Femur I	3.32	2.8- 3.7
PME	1.031	.90- 1.10	Pat.-Tibia I	4.28	3.6- 4.8
PLE	1.346	1.21- 1.49	Meta. I	2.36	2.0- 2.7
POQ	.938	.85- .98	Tarsus I	1.50	1.4- 1.6
			Total I	11.45	9.9-12.9
Carapace					
Width	3.80	3.2 - 4.3	Femur IV	4.08	3.5- 4.5
Carapace					
Length	5.26	4.4 - 5.8	Pat.-Tibia IV	4.82	4.2- 5.4
Body Length	11.70	10.0 -13.0	Meta. IV	4.33	3.8- 4.8
Pat.-Tibia II	3.92	3.6 - 4.4	Tarsus IV	1.81	1.6- 2.0
Pat.-Tibia III	3.48	3.0 - 3.9	Total IV	15.04	13.2-16.4
Males:	Mean	Range		Mean	Range
Ant. Eye Row	.721	.70- .75	Femur I	2.72	2.5- 2.8
PME	.879	.84- .92	Pat.-Tibia I	3.58	3.4- 3.9
PLE	1.110	1.04- 1.16	Meta. I	2.18	2.0- 2.4
POQ	.808	.76- .89	Tarsus I	1.40	1.3- 1.5
			Total I	9.88	9.2-10.5
Carapace					
Width	3.02	2.8 - 3.2	Femur IV	3.42	3.2- 3.6
Carapace					
Length	4.20	3.9 - 4.5	Pat.-Tibia IV	4.19	3.8- 4.4
Body Length	8.50	7.4 - 9.4	Meta. IV	3.84	3.6- 4.0
Pat.-Tibia II	3.25	3.1 - 3.4	Tarsus IV	1.65	1.5- 1.8
Pat.-Tibia III	2.92	2.7 - 3.0	Total IV	13.09	12.2-13.7

Diagnosis. *Trochosa gosiuta* is similar to *avara* and *shenandoa* in size and coloration. Unlike the latter two species *gosiuta* specimens do not have the two dark dashes within the broad median stripe (compare Figs. 3 and 5 with Fig. 4). *Trochosa gosiuta* is most like *shenandoa* in the structure of the epigynum and the male palpal organ. The anteriorly directed ends of the transverse arms of the epigynum in *gosiuta* are narrower and less heavily sclerotized than in *shenandoa* (compare Fig. 27 with Figs. 18, 23, 25). The males of *gosiuta* can be most easily distinguished from *shenandoa* by the size and length of the ventral macrosetae on tibia I. These macrosetae



28



29



32



33



30



34



36



31



35



37

are less well developed in *gosiuta* (compare Fig. 41 with Fig. 44). Also the distal paleal process (*p*) and the median apophysis (*ma*) of *gosiuta* (Figs. 45, 46) are less well developed than in *shenandoa* (Figs. 42, 43).

Natural History. *Trochosa gosiuta* occurs in relatively dry, desert regions in the western states. Nothing concerning its life style beyond this has been reported.

Distribution. From western Texas across New Mexico, Arizona, and southern California to northern Colorado, Utah, and Nevada (Map 2).

Records: *Texas.* Brewster Co.: Big Bend Nat. Pk., Chisos Basin, 6,000 ft., 25 Aug. 1967, ♂♀ (W. J. Gertsch); Chisos Mtns., 14 Dec. 1954, ♂ (K. W. Haller). *Colorado.* Boulder Co.: Boulder, Bluebell Canyon, 23 Oct. 1944, ♀ (R. E. Gregg); Green Canyon, 10 Oct. 1935, ♀ (M. Calvert); Gregory Canyon, 7–28 Oct., 1938, ♂♂:6♀♀ (V. Lanham), 20 Apr. 1965, ♀ (B., C. Durden); El Paso Co.: Colorado Springs, 3 June 1945, ♂♀ (R. E. Gregg); Larimer Co.: Fort Collins, 6,400 ft., 15 Sept. 1946, ♂♀ (C. C. Hoff). *Utah.* Carbon; Duchesne; Emery; Grand; Salt Lake; San Juan; Sevier; Tooele; Utah; Wasatch; Washington; Wayne. *New Mexico.* Bernalillo; Dona Ana; Eddy; Grant; Lincoln; Rio Arriba; Torrance; Valencia. *Nevada.* Clark Co.: Las Vegas, Bouldorado Ranch, 15 Oct. 1944, ♀ (D. J. Zinn). Churchill Co.: Churchill Crossing, 17 Oct. 1941, ♀. *Arizona.* Cochise; Coconino; Graham; Maricopa; Mohave; Navajo; Pima; Pinal; Santa Cruz. *California.* Imperial Co.: Salton Sea, Fish Springs, 12 Mar. 1941, ♀♀ (A., W. Ivie), Riverside Co.: Riverside, 25 June 1941, San Bernardino Co.: Mohave Desert, 1 Oct. 1938, ♀ (J. A. Anderson), Twenty-Nine Palms, 1–15 July 1945, ♀ (J. H. Branch).

Figs. 28–31. *Trochosa terricola* Thorell. 28–29. Male from Fruitland, Payette Co., Idaho, 10–25 Sept. 1941. 28. Left palpus, ventral view. 29. Left palpus, retrolateral view. 30–31. Male from South Meriden, New Haven Co., Connecticut, Jan.–May 1939. 30. Ventral view. 31. Retrolateral view.

Figs. 32–33. *Trochosa parthenus* Chamberlin, male from Alachua Co., Florida, 9 Nov. 1928. 32. Left palpus, retrolateral view. 33. Ventral view.

Figs. 34–35. *Trochosa shenandoa* Chamberlin and Ivie, male from Beaufort, Carteret Co., North Carolina, 25 Jan. 1952. 34. Ventral view. 35. Retrolateral view.

Figs. 36–37. *Trochosa avara* Keyserling, male from Ramsey, Bergen Co., New Jersey, 24 Sept. 1934. 36. Ventral view. 37. Retrolateral view. *e*, embolus.

Trochosa shenandoa Chamberlin and Ivie
Figures 5, 17, 18, 22-25, 34, 35, 41-43. Map 3.

Trochosa (Varacosa) shenandoa Chamberlin and Ivie, 1942: 37, fig. 78. Holotype female from Shenandoah National Park, Virginia (W78°:N38°40'), 5 July 1933, (W. Ivie) in American Museum of Natural History, examined. Vogel 1967: 109. *Varacosa shenandoa*: Roewer 1954: 307.

Discussion. This species was described from a single female collected in Shenandoah National Park. The nearest locality to that of the holotype where males have been collected is Beaufort, North Carolina. There is enough agreement between the holotype female (Figs. 22, 23) and those from North Carolina (Figs. 24, 25) to consider them conspecific. Males from North Carolina (Figs. 34, 35) when compared with males from Arkansas (Figs. 42, 43) appear identical. Arkansas females (Fig. 18) are certainly more different from the holotype (Fig. 23) than the Carolina specimens. It is possible that specimens described as *shenandoa* here represent a closely related group of species, but because of the similarities in internal genitalia (Figs. 17, 22, 24) and likenesses in the aforementioned males (compare Figs. 34, 35 with Figs. 42, 43) these specimens are regarded as a single species. Male specimens from Shenandoah National park should help to clarify the matter.

Color. Female. Face yellow-brown to orange-brown, lighter yellowish along lower edge of clypeus. Chelicerae orange-brown to dark reddish brown.

Carapace orange-brown to brown with wide pale yellow to yellow-orange median stripe; with median stripe enclosing two short, dark dashes anteriorly as in Figure 5, and with lighter irregular submarginal stripes.

Dorsum of abdomen pale yellow to light brown in ground color with dark brown or gray spots as in Figure 5. Cardiac area solid brown. Faint pattern of chevrons posteriorly in some specimens. Venter cream to pale yellow with a few scattered darker spots.

Legs yellow to yellow-orange, with ventral surface lighter.

Labium and endites orange to orange-brown with distal ends yellow. Sternum yellow.

Color. Male. Face yellow-orange to brownish orange, paler yellow along lower edge of clypeus. Chelicerae yellow-orange to brownish orange. Cymbium of palpus yellow-orange with dark sclerites showing through integument.

Carapace light medium brown with broad median stripe of pale yellow-orange. Dashes within median stripe only faintly visible. Submarginal stripes paler.

Dorsum of abdomen pale yellow to light orange in ground color, heavily mottled with gray-brown. Cardiac area solid brown outlined in gray. Venter cream colored with a few scattered spots.

Legs pale yellow-orange to orange.

Labium and endites yellow-orange with distal ends yellow to cream. Sternum yellow.

Measurements. Ten females and ten males from North Carolina.

Females:	Mean	Range		Mean	Range
Ant. Eye Row	.770	.65- .85	Femur I	2.81	2.2- 3.2
PME	.936	.79- 1.02	Pat.-Tibia I	3.05	2.8- 3.9
PLE	1.186	.99- 1.29	Meta. I	2.03	1.6- 2.3
POQ	.851	.68- .89	Tarsus I	1.37	1.0- 1.5
			Total I	9.76	7.6-10.9
Carapace					
Width	3.11	2.4 - 3.4	Femur IV	3.37	2.6- 3.8
Carapace					
Length	4.44	3.4 - 5.0	Pat.-Tibia IV	4.02	3.1- 4.4
Body Length	10.46	7.8 -11.6	Meta. IV	3.70	3.0- 4.1
Pat.-Tibia II	3.20	2.5 - 3.5	Tarsus IV	1.66	1.2- 1.9
Pat.-Tibia III	2.90	2.4 - 3.2	Total IV	12.76	10.0-14.3
Males:	Mean	Range		Mean	Range
Ant. Eye Row	.714	.65- .75	Femur I	2.85	2.6- 2.9
PME	.876	.84- .90	Pat.-Tibia I	3.78	3.5- 3.9
PLE	1.120	1.00- 1.24	Meta. I	2.56	2.4- 2.6
POQ	.799	.76- .88	Tarsus I	1.44	1.4- 1.5
			Total I	10.62	10.0-11.6
Carapace					
Width	2.96	2.8 - 3.1	Femur IV	3.36	3.2- 3.5
Carapace					
Length	4.21	3.9 - 4.7	Pat.-Tibia IV	4.10	3.9- 4.2
Body Length	8.10	7.5 - 8.4	Meta. IV	3.94	3.8- 4.0
Pat.-Tibia II	3.32	3.0 - 3.4	Tarsus IV	1.78	1.5- 1.9
Pat.-Tibia III	2.94	2.8 - 3.0	Total IV	13.19	12.3-13.6

Diagnosis. *Trochosa shenandoa* is closest to *T. gosiuta* in epigynal structure. The anteriorly directed arms of the transverse piece (*tp*) of the median septum (*ms*) in *shenandoa* are longer and more

heavily sclerotized (compare Figs. 18, 23, 25 with Fig. 27). Internally the ducts of the spermathecae run nearly horizontally or straight across as they leave the bulb (*b*) in *shenandoa* (figs., 17, 22, 24), while in *gosiuta* the ducts slope diagonally posteriad as they leave the bulb (Fig. 26). The male palpus of *shenandoa* is most similar to that of *avara*. However, the median apophysis (*ma*) in *avara* is much larger than in *shenandoa* (compare Figs. 36, 37, 39, 40 with Figs. 34, 35, 42, 43). *Trochosa shenandoa* males may be easily distinguished from *avara* and *gosiuta* by the very robust pair of retroventral macrosetae on tibia I (compare Fig. 41 with Figs. 38, 44).

Distribution. Eastern coast of the United States southward along the Gulf Coast and inland in the central states. Single records from Quebec and Illinois (Map 3).

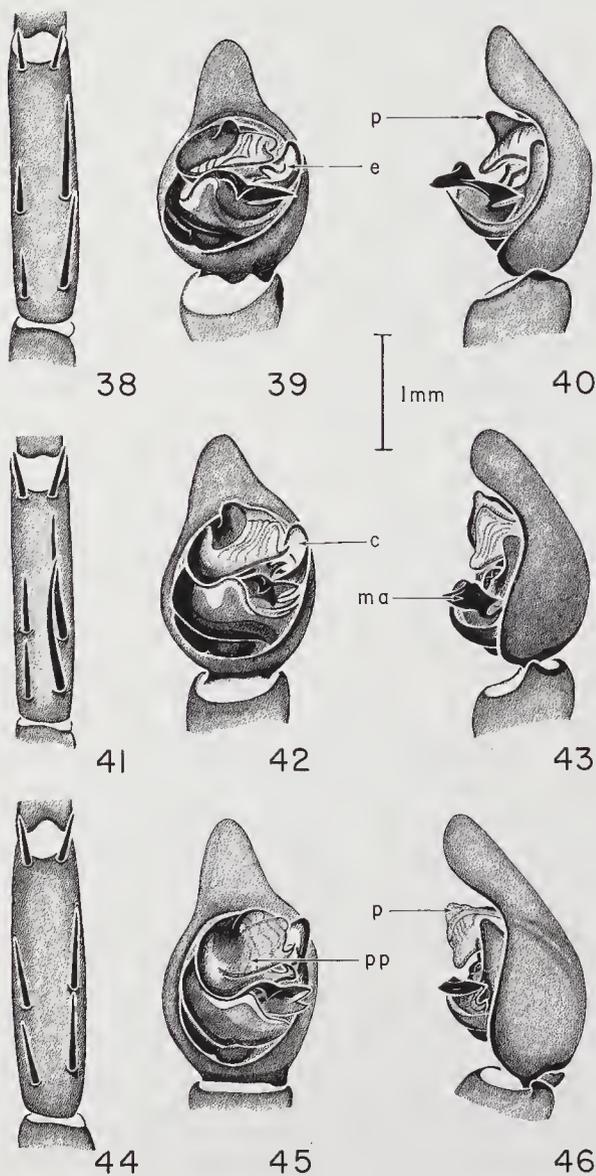
Records. CANADA. Quebec. Lanoraie, 5 July 1915, ♀ (J. I. Baeulne).

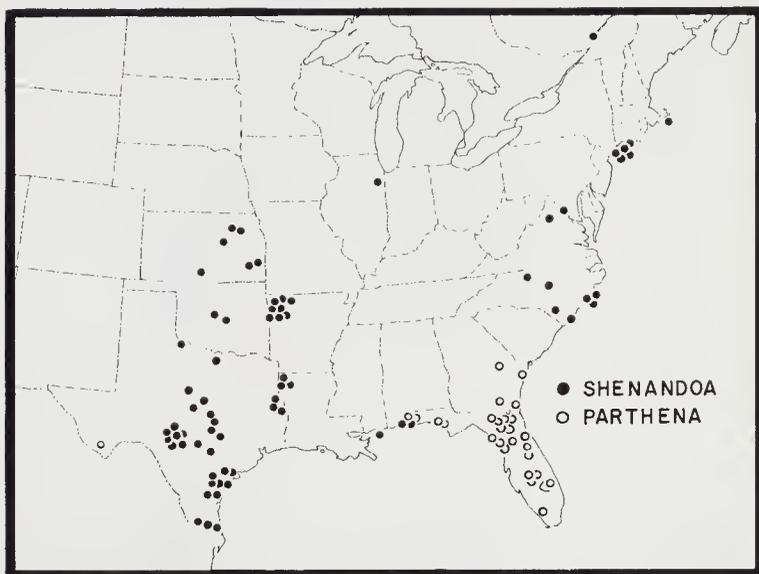
UNITED STATES. *Massachusetts.* Nantucket Co.: Nantucket, 20 Sept. 1892, ♂ (S. Henshaw). *New York.* Nassau; Suffolk. *Virginia.* Falls Church (Indep. City), ♀♀ (N. Banks); Shenandoah National Park, 5 July 1933, ♀ (W. Ivie). *North Carolina.* Bladen; Carteret; Guilford; New Hanover; Wake. *Florida.* Escambia Co.: Pensacola, 31 Jan. 1935, ♀. *Alabama.* Baldwin Co.: Gasque, 1950, ♀ (A. F. Archer). *Mississippi.* Harrison Co.: Ship Island, 16 Mar. 1936, ♀♀. *Louisiana.* Caddo Par.: Shreveport, 1-2 Nov. 1936, ♂♂ (H. K. Wallace). *Illinois.* Kankakee Co.: Pembroke, 19 May 1934, ♀ (D. C. Lowrie). *Arkansas.* Carroll; Washington. *Kansas.* Bourbon; Dickinson; Kingman; Riley; Woodson. *Oklahoma.* Canadian; Cleveland. *Texas.* Aransas; Bandera; Bastrop; Bell; Cameron; Comanche; Coryell; Denton; Hidalgo; Jasper; Jim Wells; Kendall; Kerr; Kleberg; Refugio; San Patricio; San Saba; Shelby; Travis; Victoria; Wilbarger.

Figs. 38-40. *Trochosa avara* Keyserling. 38. Male from Cove Creek, Washington Co., Arkansas, 30 Dec. 1956, ventral view of left tibia I. 39-40. Syntype from North America. 39. Left palpus, ventral view. 40. Left palpus, retrolateral view.

Figs. 41-43. *Trochosa shenandoa* Chamberlin and Ivie, male from Cove Creek, Washington Co., Arkansas, Feb. 1957. 41. Ventral view of left tibia I. 42. Ventral view. 43. Retrolateral view.

Figs. 44-46. *Trochosa gosiuta* Chamberlin, male from Salt Lake City, Salt Lake Co., Utah, July-Sept. 1931. 44. Ventral view of left tibia I. 45. Ventral view. 46. Retrolateral view. *c*, conductor; *e*, embolus; *ma*, median apophysis; *p*, palea; *pp*, pars pendula.





Map 3. Collection localities for *Trochosa shenandoa* and *T. parthena*.

Trochosa parthenus (Chamberlin)

Figures 6-9, 32, 33. Map 3.

Lycosa parthenus Chamberlin, 1925: 228. Holotype female from Bartow, Polk Co., Florida (R. V. Chamberlin) in the Museum of Comparative Zoology, examined.

Gertsch and Wallace 1935: 12, figs. 28, 29, ♀♂. Wallace 1947: 37.

Trochosa (Varacosa) parthenus: Chamberlin and Ivie 1942: 37.

Varacosa parthenus: Roewer 1954: 306.

Lycosa parthena: Bonnet, 1957: 2657.

Discussion. According to H. Don Cameron (personal communication) the specific name *parthenus* is a Latinization of the Greek noun "parthenos" meaning virgin. As such *parthenus* is a noun in apposition to *Trochosa* and is the correct form of the species name.

Color. Female. Face yellow-orange to orange-brown, lighter along lower edge of clypeus. Chelicerae yellow-orange to dark reddish brown.

Carapace light brown to dark reddish brown with a light yellow to pale orange median stripe, with two dark oblong spots within the median stripe anteriorly as in Figure 6, and with light submarginal stripes.

Dorsum of abdomen with yellowish ground color heavily pigmented with dark brown or gray producing a pattern as in Figure 6. Venter cream to pale yellow with scattered dark spots, heaviest along sides.

Legs pale yellow to yellow-orange with dusky markings, which are more prominent dorsally.

Labium and endites yellow to light brown with distal ends cream. Sternum cream to yellow.

Color. Male. Face light orange-brown, yellowish along lower edge of clypeus. Chelicerae yellow-orange to light orange-brown. Cymbium of palpus yellow-orange with dark sclerites visible through integument.

Carapace orange-brown to brown with wide median yellow stripe, with two dark spots within median stripe anteriorly as in female, and with lighter irregular submarginal stripes not as distinct as in female.

Dorsum of abdomen medium brown produced by yellowish ground color speckled with dark brown or gray spots. Cardiac area solid yellowish brown to brown. Venter cream to pale yellow with a few to many scattered dark spots.

Legs yellow to light brownish yellow with dusky markings above.

Labium and endites yellow, lighter distally. Sternum yellow.

Measurements. Ten females and ten males from Florida.

Females:	Mean	Range		Mean	Range
Ant. Eye Row	.728	.66- .82	Femur I	2.46	2.2- 2.8
PME	.876	.80- 1.00	Pat.-Tibia I	3.16	2.8- 3.6
PLE	1.100	1.01- 1.24	Meta. I	1.74	1.4- 2.0
POQ	.799	.72- .94	Tarsus I	1.16	1.0- 1.4
			Total I	8.48	7.1- 9.8
Carapace					
Width	2.82	2.5 - 3.4	Femur IV	3.00	2.5- 3.4
Carapace					
Length	3.92	3.5 - 4.7	Pat.-Tibia IV	3.70	3.2- 4.2
Body Length	8.64	7.6 - 9.4	Meta. IV	3.38	3.0- 3.8
Pat.-Tibia II	2.92	2.5 - 3.4	Tarsus IV	1.50	1.4- 1.6
Pat.-Tibia III	2.65	2.2 - 3.0	Total IV	11.58	10.0-13.0

Males:	Mean	Range		Mean	Range
Ant. Eye Row	.631	.60- .66	Femur I	2.38	2.2- 2.7
PME	.790	.74- .94	Pat.-Tibia I	3.18	2.8- 3.6
PLE	.984	.91- 1.09	Meta. I	2.03	1.8- 2.4
POQ	.701	.66- .76	Tarsus I	1.20	1.1- 1.4
			Total I	8.82	8.0-10.0
Carapace					
Width	2.60	2.4 - 3.0	Femur IV	2.84	2.5- 3.2
Carapace					
Length	3.56	3.2 - 4.0	Pat.-Tibia IV	3.56	3.2- 4.0
Body Length	6.67	5.8 - 7.6	Meta. IV	3.44	3.0- 3.8
Pat.-Tibia II	2.86	2.5 - 3.2	Tarsus IV	1.53	1.4- 1.8
Pat.-Tibia III	2.61	2.4 - 3.0	Total IV	11.37	10.0-12.9

Diagnosis. *Trochosa parthenus* resembles *shenandoa* and *gosiuta* in epigynal structure, but it can be easily distinguished from these two species (compare Figs. 8, 9 with Figs. 18, 23, 25, 27). The male palpal organ of *parthenus* (Figs. 32, 33) is most similar to that of *shenandoa* (Figs. 34, 35, 42, 43), but again can be readily distinguished. *Trochosa parthenus* is the smallest member of the *avara* species group, averaging considerably smaller in size than *avara*, *gosiuta*, or *shenandoa* (see *Measurements*). This species is also the only member of *Trochosa* occurring in peninsular Florida. Even though there is a single male specimen recorded from near Alpine, Texas, *parthenus* seems to be largely restricted to the southeastern United States.

Natural History. Wallace (1947) reported on the natural history of this species in Florida:

"*Lycosa parthenus* matures and mates during January and February in the Gainesville region; however, I have two records of males from October. Females with egg sacs have been taken only during January and February. During the spring adults gradually decrease in numbers until, by the middle of the summer, they are rare. By June the young have left the mother and are common in the leaf mould of appropriate situations.

This species is apparently confined to dry leaf mould. In such xeric situations as turkey oak or old fields it is found among the leaves under trees but is missing on open sandy stretches. Whenever dry leaf mould occurs, including all situations drier than mesophytic hammock, this species is likely to be present."

Distribution. Southeastern United States. One male from western Texas.

Records. Georgia. Chatham Co.: Savannah Beach, 5 Dec. 1962, 3♂♂:3♀♀ (W. Ivie); Emmanuel Co.: N of Swainsboro, 23 Dec. 1962, ♂ (W. Ivie); Ware Co.: 15 mi. W of Waycross, 22 Dec. 1962, ♀ (W. Ivie). *Florida.* Alachua; Bay; Citrus; Clay; Collier; Escambia; Highlands; Lake; Levy; Martin; Nassau; Orange; Pinellas; Putnam; Seminole; Volusia. *Texas.* Brewster Co.: 10 mi. W of Alpine, 28 Nov. 1946, ♂ (H. K. Wallace).

LITERATURE CITED

- ABBOT, J. T.
1792. Spiders of Georgia. Manuscript, 116 pp.
- BANKS, N.
1892. The spider fauna of the Upper Cayuga Lake Basin. *Proc. Acad. Sci. Philad.*, 1892: 11-81.
1895. A list of spiders of Long Island, with description of new species. *Journ. N. Y. Ent. Soc.*, 3: 76-93.
1897. Descriptions of new spiders. *Canad. Ent.*, 29: 193-197.
1900. Arachnida of the Expedition, in papers from the Harriman Alaska Expedition. XI. Entomological results; 5, Arachnida, *Proc. Wash. Acad. Sci.*, 2: 477-486.
1905. Synopses of North American Invertebrates. XX. Families and Genera of Araneida. *Amer. Nat.*, 39: 293-323.
1907. A preliminary list of the Arachnida of Indiana, with keys to families and genera of spiders. *Rep. Indiana Geol. Surv.*, 31: 715-747.
1910. Catalogue of Nearctic spiders. *Bull. U. S. Nat. Mus.*, 72: 1-80.
1916a. Report on Arachnida collected by Messrs. Currie, Caudell, and Dyar in British Columbia. *Proc. U. S. Nat. Mus.*, 51: 67-72.
1916b. Revision of Cayuga Lake spiders. *Proc. Acad. Nat. Sci. Philad.*, 1916: 68-84.
- BANKS, N. AND N. M. NEWPORT.
1932. Oklahoma spiders. *Publ. Univ. Oklahoma, Biol. Sur.*, 4(1): 7-49.
- BARNES, R. D.
1953a. The ecological distribution of spiders in non-forest maritime communities at Beaufort, North Carolina. *Ecol. Mono.*, 23: 315-337.
1953b. Report of a collection of spiders from the coast of North Carolina. *Amer. Mus. Novit.*, 1632: 1-21.
- BARNES, B. M. AND R. D. BARNES.
1954. The ecology of the spiders of maritime drift lines. *Ecology*, 35: 25-35.
- BARROWS, W. M.
1918. A list of Ohio spiders. *Ohio Journ. Sci.*, 18(8): 297-318.
- BERLAND, L.
1925. Spiders of the Chatham Islands. *Rec. Cant. Mus.*, 2: 295-300.
- BISHOP, S. C. AND C. R. CROSBY.
1926. Notes on the spiders of the southeastern United States with descriptions of new species. *Journ. El. Mitch. Sci. Soc.*, 41(3-4): 163-212.

- BLACKWALL, J.
1842. On new British Spiders. *Ann. Mag. Nat. Hist.*, **10**: 407-408.
- BONNET, P.
1957. Bibliographia Araneorum. Tome 2, partie 3, Les Frères Douladoure, *Toulouse*, pp. 1927-3026.
1959. Bibliographia Araneorum. Tome 2, partie 6, Les Frères Douladoure, *Toulouse*, pp. 4229-5058.
- BRITCHER, H. W.
1903. The spiders of Onondaga County. *Proc. Onondaga Acad. Sci.*, **1**: 123-130.
- BRYANT, E. B.
1908. List of the Araneina in Fauna of New England, 9. *Occ. Pap. Boston Soc. Nat. Hist.*, **7**: 1-105.
- CHAMBERLIN, R. V.
1908. Revision of North American spiders of the family Lycosidae. *Proc. Acad. Nat. Sci. Philad.*, **1908**: 158-318.
1909. Some synonyms in North American Lycosidae. *Canad. Ent.*, **41**: 376.
1925. Diagnoses of new American Arachnida. *Bull. Mus. Comp. Zool.*, **67**: 211-248.
- CHAMBERLIN, R. V. AND W. J. GERTSCH.
1928. Notes on spiders from southeastern Utah. *Proc. Biol. Soc. Wash.*, **41**: 178-188.
1929. New spiders from Utah and California. *Journ. Ent. Zool. Claremont*, **21**: 101-112.
- CHAMBERLIN, R. V. AND W. IVIE.
1933. Spiders of the Raft River Mountains of Utah. *Bull. Univ. Utah*, **23**(4): 1-53.
1942. A hundred new species of American spiders. *Bull. Univ. Utah*, **32**(13): 1-117.
1947. The spiders of Alaska. *Bull. Univ. Utah*, **37**(10): 1-103.
- CHAMBERLIN, R. V. AND A. M. WOODBURY.
1929. Notes on the spiders of Washington County, Utah. *Proc. Biol. Soc. Wash.*, **42**: 131-142.
- CHICKERING, A. M.
1933. Notes and studies on Arachnida. IV. Araneae from the Douglas Lake region, Michigan. II. *Pap. Mich. Acad. Sci.*, **17**: 515-520.
1935. Further additions to the list of Araneae from Michigan. *Pap. Mich. Acad. Sci.*, **20**: 583-587.
- COLLETT, R.
1875. Oversigt af Norges, Araneider. I. Saltigradae, Citigradae. *Forch. Vid. Selsk. Christian.*, **1875**: 225-259.
- COMSTOCK, J. H.
1912. The Evolution of the webs of spiders. *Ann. Ent. Soc. Amer.*, **5**: 1-10.
1913. The spider book. Doubleday & Page, *Garden-City, New York*, 721 pp.
1940. The spider book. Rev. and ed. by W. J. Gertsch. Comstock, *Ithaca.*, 729 pp.

CROSBY, C. R. AND S. C. BISHOP.

1928. Araneae in a list of the insects of New York. *Cornell Univ. Agr. Exper. Sta. Mem.*, **101**: 1034-1074.

CROSBY, C. R. AND H. M. ZORSCH.

1935. Spiders from the Lac St. Jean region of Quebec. *Canad. Ent.*, **67**: 38-42.

DEGEER, C.

1778. Memoires pour servir a l'histoire des insectes. *Stockholm.* 7(3-4): 176-324.

DENIS, J.

1937. Araignées recueillies dans le département du Var (Quatriéme note). *Ann. Soc. Hist. Nat. Toulon*, **21**: 166-169.

DONDALE, C. D.

1971. Spiders of Heasman's field, a mown meadow near Belleville, Ontario. *Proc. Ent. Soc. Ont.*, **101**(1970): 62-69.

ELLIOTT, F. R.

1932. Revision of and additions to the list of Araneae (spiders) of Indiana. *Proc. Indiana Acad. Sci.*, **41**: 419-430.

EMERTON, J. H.

1885. New England Lycosidae. *Trans. Conn. Acad. Arts Sci.*, **6**: 481-505.
1894. Canadian spiders. *Trans. Conn. Acad. Arts Sci.*, **9**: 400-429.
1902. The common spiders of the United States. Ginn & Co., Boston, 1902, 225 pp.
1909. Supplement to the New England Spiders. *Trans. Conn. Acad. Arts Sci.*, **14**: 171-236.
1913. The spiders of Three Mile Island. *Appalachia*, **12**: 154-156.
1914. New spiders from the neighbourhood of Ithaca. *Journ. N. Y. Ent. Soc.*, **22**: 262-264.
1920. Catalogue of the spiders of Canada known to the year 1919. *Trans. Roy. Canad. Inst.*, **12**: 309-338.
1921. The spiders of Canada. *Canad. Field Nat.*, **34**(6): 106-108.
1924. Recent collections of Canadian spiders. *Ent. News.*, **36**: 122-124.
1928. Spiders from the Lake Abitibi Region. *Univ. Toronto Stud. Biol.*, **32**: 45-46.
1930. Spiders of Nantucket. *Natuck. M. Mitchell Assoc. Publ.* 3(2): 161-174.

ENGELHARDT, W.

1964. Die mitteleuropäischen Arten der Gattung *Trochosa* C. L. Koch, 1848 (Araneae, Lycosidae). *Z. Morph. Ökol. Tiere*, **54**: 219-392.

FOX, C. J. S. AND C. D. DONDALE.

1972. Annotated list of spiders (Araneae) from hayfields and their margins in Nova Scotia. *Canad. Ent.*, **104**: 1911-1915.

FOX, W. H.

1892. A list of the spiders from Indiana. *Proc. Ent. Soc. Wash.*, **2**: 267-269.

FUHN, I. E. AND F. BURLACU.

1971. Fauna Republicii Socialiste România Arachnida, Vol. 5, part 3, Family Lycosidae. Academiei Republicii Socialiste România, *Bucuresti*, 256 pp.

- GERTSCH, W. J.
1934. Further notes on American spiders. *Amer. Mus. Nov.*, **726**: 1-26.
1935. Spiders from the southwestern United States, with descriptions of new species. *Amer. Mus. Novit.*, **792**: 1-31.
- GERTSCH, W. J. AND H. K. WALLACE.
1935. Further notes on American Lycosidae. *Amer. Mus. Novit.*, **794**: 1-22.
- GUY, Y.
1966. Contribution à l'étude des araignées de la famille des Lycosidae et de la sous-famille des Lycosinae avec étude spéciale des espèces du Maroc. *Trav. Inst. scient. chérif.* (Ser. zool.) **33**, 174 pp.
- HACKMAN, W.
1954. The spiders of Newfoundland. *Acta Zool. Fenn.* **79**: 1-99.
- HARRINGTON, W. H.
1897. Ottawa spiders and mites. *Ottawa Nat.*, **10**: 190-191.
- HOLMQUIST, A. M.
1926. Studies in arthropod hibernation. I. Ecological survey of hibernating species from forest environments of the Chicago region. *Ann. Ent. Soc. Amer.*, **19**: 395-426.
- KARSCH, F.
1878. Exotischeraraneologisches. *Zeits. gesam. Naturw.*, **51**: 323-333, 771-826.
- KASTON, B. J.
1938. Checklist of the spiders of Connecticut. *Bull. Conn. Geol. Nat. Hist. Surv.*, **60**: 175-201.
1948. Spiders of Connecticut. *Bull. Conn. Geol. Nat. Hist. Surv.*, **70**: 1-874.
1972. How to know the spiders. 2nd ed. Wm. C. Brown, *Dubuque*, 290 pp.
1978. How to know the spiders. 3rd ed. Wm. C. Brown, *Dubuque*, 272 pp.
- KEYSERLING, E.
1877. Ueber amerikanische Spinnenarten der Unterordnung Citigradae. *Verh. zool.-bot. Ges. Wien.* **26**: 609-708.
- KOCH, C. L.
1836. Arachniden. in Panzer, Faunae Insectorum Germaniae itinita. Heft 134, 137, 139. *Regensburg*, 1836, [Spinnen, **134**: 1-24; **137**: 3-6; **138**: 3-6; **139**: 3-6].
1840. Crustacea, Myriapoda et Arachnides. in Furnrohr (A. E.), Naturhistorische Topographie von Regensburg, 3, die Fauna von Regensburg enthaltend, pp. 387-458. [Araneae, pp. 398-416.]
1847. System der Myriapoden mit Verzeichnissen und Berichtungen zu Deutschlands Crustaceen, Myriapoden und Arachniden. *Regensburg*, 1847, pp. 1-270. [Spinnen, pp. 226-232.]
1848. Die Arachniden. Vol. 14. *Nürnberg*, 1848, 210 pp.
1851. Uebersicht des Arachnidensystems. *Nürnberg*, 1851, 104 pp.
1875. Aegyptische und Abyssinische Arachniden gesammelt von Herrn C. Jickeli. *Nürnberg*, 1875, 1-96 pp.
- LINDROTH, C. H.
1957. The faunal connections between Europe and North America. Almqvist & Wiksell, *Stockholm* and John Wiley & Sons, Inc., *New York*, 344 pp.

LOCKET, G. H. AND A. F. MILLIDGE.

1951. British spiders I. Ray Society, London, 310 pp.

MCCOOK, H. C.

1894. American spiders and their spinningwork. Vol. 3, Philadelphia, 1894, 98 pp.

MCKAY, R. J.

1979. The wolf spiders of Australia (Araneae:Lycosidae): 13. The genus *Trochosa*. *Mem. Qd. Mus.*, 19(3): 277-298.

MARX, G.

1890. Catalogue of the described Araneae of temperate North America. *Proc. U. S. Nat. Mus.*, 12: 497-594.

MONTGOMERY, T. H.

1903. Supplementary notes on spiders on the genera *Lycosa*, *Pardosa*, *Pirata* and *Dolomedes* from the northeastern United States. *Proc. Acad. Nat. Sci. Philad.*, 1903: 645-655.

1904. Descriptions of North American Araneae of the Families Lycosidae and Pisauridae. *Proc. Acad. Nat. Sci. Philad.*, 1904: 261-323.

NOSEK, A.

1904. Pavoukovití clenovci Cerné Hory. Arachnoidea montgenigrina. *Sitzber. Böhm. Ges. Wiss.*, 1903(46): 1-4.

PETRUNKEVITCH, A.

1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. *Bull. Amer. Mus. Nat. Hist.*, 29: 1-791.

1928. Systema Araneorum. *Trans. Conn. Acad. Arts Sci.*, 29: 1-270.

PICKARD-CAMBRIDGE, O.

1874. Systematic list of the spiders at present known to inhabit Great Britain and Ireland. *Trans. Linn. Soc. Lond.*, 30: 319-334.

PROCTOR, W.

1933. Biological survey of the Mount Desert Region. Part V. A report of the organization, laboratory equipment . . . to which are added a list of Arachnida and other non-marine forms. Philadelphia, 1933, 402 pp. [Araneae, pp. 270-279.]

REIMOSER, E.

1919. Katalog der echten spinnen (Araneae) des Paläarktischen Gebietes. *Abh. Zool. bot. Ges. Wien*, 10(2): 1-280.

ROEWER, C. F.

1954. Katalog der Araneae. Band 2. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, 2: 1-923.

RUTHVEN, A. G.

1906. Spiders and insects from the Porcupine Mountains and Isle Royale, Michigan. *Rep. Geol. Surv. Michigan*, 1905: 101-106.

SCHEFFER, T. H.

1905. A preliminary list of Kansas spiders. *Trans. Kansas Acad. Sci.*, 19: 182-193.

1906. Additions to the list of Kansas Arachnida. *Trans. Kansas Acad. Sci.*, 20(1): 121-130.

- SCUDDER, S. H.
1882. Nomenclator zoologicus. An alphabetical list of all generic names that have been employed by naturalists for recent and fossil animals from the earliest times to the close of the year 1879. *Washington*, 1882. + *Bull. U. S. Nat. Mus.*, **19**: 1-376.
- SIMON, E.
1864. Histoire naturelle des Arignées (Aranéides). *Paris*, 1864, 540 pp.
1885. Etude sur les Arachnides recueillis en Tunisie en 1883 et 1884 par M. M. A. Letourneux, M. Sédillot et Valéry Mayet, membres de la Mission de l'Exploration scientifique de la Tunisie. in *Exploration scientifique de la Tunisie*, *Paris*, **1885**, 55 pp.
- SLOSSON, A. T.
1898. List of the Araneae taken in Franconia, New Hampshire. *Journ. N. Y. Ent. Soc.*, **6**: 247-249.
- STRAND, E.
1906. Die arktischen Araneae, Opiliones und Chernetes. in *Fauna Arctica*, **4**: 431-478.
- THORELL, T.
1856. Recensio critica Araneorum Suecicarum, quas descripserunt Clerckius, Linnaeus, de Geerus. *Nat. Act. Reg. Soc. Sci. Upsala*, (3)**2**(1): 61-176.
- WALCKENAER, C. A.
1837. Histoire naturelle des Insectes. Aptères, Tome 1. *Paris*, 1837, 682 pp.
- WALLACE, H. K.
1947. A new wolf spider from Florida, with notes on other species. *Florida Ent.*, **30**(3): 33-38.
- WESTRING, N.
1861. Araneae svecicae. *Göteborg. Kongl. Vet. Handl.*, **7**: 1-615 + *Gothoburgi*, 1861, 615 pp.
- WORLEY, L. G.
1932. The spiders of Washington, with special reference to those of the San Juan Islands. *Univ. Wash. Publ. Biol.*, **1**(1): 1-63.
1931. The spiders of Nebraska. *Univ. Stud. Nebraska*, **27**(1-4): 1-129.

SELECTIVE MATE CHOICE BY FEMALES OF
HARPOBITTACUS AUSTRALIS
(MECOPTERA: BITTACIDAE)*

BY JOHN ALCOCK
Department of Zoology
Arizona State University, Tempe, AZ 85281

The use of nuptial gifts in courtship is a relatively rare phenomenon among insects but it is well developed in the Bittacidae where it has been studied in detail by Thornhill (1976, 1977, 1979). In an investigation of *Hylobittacus apicalis* Thornhill (1976) demonstrated that females exercise choice in the selection of mates, preferring those that offer superior gifts; males that gave their mates large nutritious prey were permitted to copulate longer and transfer more sperm than males that offered small or unpalatable food presents. This paper outlines limited evidence that the duration of feeding and copulation by females of Australian mecopteran, *Harpobittacus australis* Klug, is also linked to the quality of the nuptial gifts provided by the male.

METHODS

The species was studied in Warrumbungle National Park in northern New South Wales between 18-23 December 1978, a period of dry, warm weather when insects were active. Males and females appeared in the late morning and afternoon and perched on flowers, grasses and shrubs on a hillside by a small brook. I searched for males that were carrying a prey present, and upon finding one remained with it until the prey was discarded or until the insect moved and was lost to sight. As soon as a male was detected, I estimated the length of the prey in mm, recorded the manner in which it was carried and made notes on any social interactions that occurred.

RESULTS

My observations of the sexual behavior of *H. australis* are in general agreement with those of Bornemissza (1966). Males carry nuptial gifts impaled on the beak or gripped with the hind tarsi

*Manuscript received by the editor November 2, 1979.

while they hang from a perch with their front legs. Prey carried by the hindlegs had a mean estimated length of 8.8 mm ($N = 9$) and included three bulky moths and one large lepidopterous larva. Prey pierced by the beak averaged 3.8 mm in length ($N = 11$) and consisted entirely of delicate mirids and various soft-winged beetles.

Males with prey release a sex pheromone from glands in the posterior abdomen, an attractant that draws both males and females to them. In 19.5 hr of observation, I recorded 10 male-male encounters and 31 male-female interactions. Male visitors uniformly attempted to steal the prey from the calling male and succeeded on two occasions. Prey piracy by males is common among bittacids (Thornhill 1979). Some females may also visit calling males solely to secure a food gift. One male-female interaction ended when the female removed the prey from the male and flew away. In another case, the female probed the male's prey for about 3 min after coming to his perch; the male attempted without success to effect a copulation and eventually a tussle for control of the prey ensued leading the pair to tumble off the perch and onto the ground. The female left; the male returned to his perch and probed the prey briefly before discarding it, apparently because the female had drained it of its contents.

In more typical interactions between males and females, the arriving female alighted causing the male to transfer the prey to his mouthparts. In my observations, unlike those of Bornemissza (1966) the female usually probed nuptial gift briefly with her beak ($N = 26$); on only three occasions a female refrained from "testing" the prey and all three involved unusually large nuptial gifts whose potential value might have been assessed visually. As the female probed the gift, the male attempted to couple with her. In fifteen cases, the female refused to permit mating to occur, withdrawing from the male after the initial probe of his present.

In cases in which copulation occurred the male usually succeeded in pulling the prey from the female with his hindlegs shortly after insertion of his genitalia. The female, which had been facing the male in this initial phase of the interaction, would then drop down so that the bodies of the copulating pair formed an "L". (The average time from the start of an encounter to assumption of the "L" position was 3.1 min.)

While the female hung below the male she employed her hindlegs to pull vigorously at the male's hindlegs which were holding the prey

away from the female's mouthparts. Males appeared reluctant to extend their legs and so permit the female to feed. The time required for the female to draw the nuptial gift to her averaged 0.95 min with a maximum of 4.6 min ($N = 11$). When the male's legs were fully extended the female could reach the prey with her mouthparts; she fed upon it for as little as 1 min to as much as 17.25 min. Immediately upon cessation of feeding the female disengaged from her partner and flew off.

Selective Mate Choice by Females

It seems likely that the probing of the prey by the female at the start of an encounter between the sexes permits the female to assess the nutritional/caloric value of the male's present. Females offered small prey or insects that had been consumed by an earlier partner of the male frequently rejected the male outright, leaving before copulation could begin. If we consider the first *observed* reaction of a female to a prey offered by a male, copulation occurred only once in ten cases in which the prey was a tiny 3–4 mm mirid or beetle. In contrast, if the prey were estimated to be 6 mm or larger, mating occurred in 8 of 10 cases ($\chi^2 = 7.3$, $P < .05$).

Five of twenty prey were offered to more than one (2–4) females in sequence. All five prey were 6 mm or larger. In one case, the prey was discarded by the male immediately after the second of two lengthy copulations. In the remaining four cases, the male dropped his gift only after it had been probed and rejected by a female, presumably because she found it an empty husk whose contents had been removed by earlier females.

Thus the quality of the nuptial gift must be of a certain minimum standard if the female is to permit the male to copulate with her at all. In addition, Bornemissza (1966) felt that the size of the prey was related to the duration of copulation in *H. australis*. Table 1 shows that there is indeed a correlation between the estimated size of a prey and (1) the duration of the feeding phase of copulation and (2) the overall length of the copulation. Large food items evidently contain within them sufficient materials to keep the female occupied for some time, during which period the male presumably transfers sperm to her.

Still more support for the hypothesis that the food value of the gift determines how long a female will feed on the prey and therefore how long she will copulate comes from comparisons of the response

of several females offered the same prey. In the three cases in which a male presented the same food item to three different females, copulation lengths were (a) 10.2, 7.8, and 0 min, (b) 15.7, 17.2, and 0 min, and (c) 12.3, 3.8 and 0 min and the feeding phase lasted (a) 10.2, 4.8, and 0 min, (b) 15.3, 14.8, and 0 min, and (c) 12.3, 3.8 and 0 min.

Table 1. The relation between the estimated length of the prey offered a female as a nuptial gift and the time that she fed upon the prey and the duration of copulation.¹

Size of gift	N	Mean time of feeding	Range	Mean time of copulation	Range
3-4 mm	10	0.2 min	0- 1.8	1.1 min	0- 8.0
6-8 mm	6	3.6	0-17.3	6.2	0-19.3
10-14 mm	4	12.3	10.2-15.3	13.7	10.2-16.8

Correlation between size of prey and feeding time, $r = 0.70$, $p < .01$

Correlation between size of prey and copulation time, $r = 0.62$, $p < .01$

¹Data collected from the first observed interaction between a male carrying a nuptial present and a female.

DISCUSSION

The species of bittacids studied to date exhibit reasonably similar sexual behavior including the use of pheromones, nuptial gift giving, female sampling of the present before copulation, and copulations of variable length but with means of about 10-20 min (Thornhill, 1977). An unusual feature of the mating behavior of *Harpobittacus* is the removal of the prey from the female by the male for a short period after the onset of copulation. In some other bittacids females feed continuously on the nuptial gift. The apparent struggle between copulating partners of *H. australis* for possession of the prey demonstrates the male and female interests are not identical. Perhaps the risk of prey thievery by females favors males that are cautious about relinquishing their valuable presents; perhaps they refuse to let potential mates feed until sperm have begun to be accepted by their partners.

Sperm transfer in *Hylobittacus apicalis* is proportional to the duration of copulation (up to about 20 min) and it would not be surprising if this were also true for *H. australis*, whose females feed

in copulo for from 1–17 min. Certainly females discriminate among males on the basis of edible volume of the nuptial gift, refusing to couple at all with males offering very small presents or prey that have been drained by previous mates. This mecopteran, therefore, probably provides another example of a species whose females exercise mate choice, accepting sperm preferentially from individuals that make a large parental investment in the form of a food gift that may promote egg development or female survival.

ACKNOWLEDGEMENTS

This study was conducted while the author was a visiting lecturer at Monash University. I thank the members of the Zoology Department at Monash for their help, my sons Joey and Nicky for their assistance with field work, and Randy Thornhill for reading the manuscript.

REFERENCES

BORNEMISSZA, G. F.

1966. Observations on the hunting and mating behaviour of two species of scorpion flies (Bittacidae: Mecoptera). *Aust. J. Zool.* **14**: 371–382.

THORNHILL, R.

1976. Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *Amer. Nat.* **110**: 529–548.
1977. The comparative predatory and sexual behavior of hanging flies (Mecoptera: Bittacidae). *Occ. Papers Mus. Zool., Univ. Mich.* **677**: 1–43.
1979. Adaptive female-mimicking behavior in a scorpionfly. *Science* **205**: 412–414.

NEOTROPICAL BUTTERFLIES OF THE GENUS *ANARTIA*:
SYSTEMATICS, LIFE HISTORIES AND GENERAL
BIOLOGY (LEPIDOPTERA: NYMPHALIDAE)

BY ROBERT E. SILBERGLIED¹
ANNETTE AIELLO¹
AND
GERARDO LAMAS²

INTRODUCTION

Butterflies of the genus *Anartia* Hübner are among the most common and conspicuous diurnal Lepidoptera encountered in the New World tropics. While their abundance and ease of capture have made them popular subjects for research in various aspects of lepidopteran biology, the genus has never been thoroughly reviewed or revised. Two of the authors, (R.E.S. and A.A.) have been conducting genetic, behavioral and ecological experiments on members of this genus for four years, and we feel it is both an opportunity and a necessity to condense the scattered published information with some of our own observations and results. Our experimental findings will be published separately.

As treated here, *Anartia* consists of five species (Figure 1) in three well-defined groups (Godman and Salvin, 1882).

SYSTEMATICS

Genus *Anartia* Hübner

Anartia Hübner, [1819]: 33.

Type species, *Papilio jatrophae* Linnaeus (Scudder, 1875: 111).

Celaena Doubleday, [1849]: 214.

Type species, *Papilio fatima* Fabricius (Hemming, 1941: 425). Invalid and unavailable; published in synonymy (ICZN, Art. 11d).

Celoena Boisduval, 1870: 38.

Type species, *Papilio fatima* Godart (mon.). Junior subjective synonym.

Anartia subgenus *Anartiella* Fruhstorfer, 1907: 112.

Type species, *Vanessa lytrea* Godart (mon.). Junior subjective synonym.

¹Smithsonian Tropical Research Institute, Box 2072, Balboa, Republica de Panamá.
Present address: Museum of Comparative Zoology, Harvard University, Cambridge,
Mass. 02138

²Museo de Historia Natural "Javier Prado," Universidad Nacional Mayor de San
Marcos, Av. Arenales 1256, Apto. 1109, Lima, Perú.

Manuscript received by the editor February 26, 1980.

Medium-sized, lightly built butterflies. *Head* small; *eyes* hemispherical, prominent; *labial palpi* elongate, curved upwards and densely scaled, with first and third segments about 1/4 to 1/3 the length of the second (Reuter, 1896, fully describes the palpi); *antennae* slender, slightly shorter than the body in length, with slightly flattened, pointed, nine-segmented club; *thorax* strong, thinly scaled; *forewing* slightly angled apically, anterior margin curved at base, apex slightly truncate, outer margin sinuate, inner margin straight, Sc-R system variable among the species (Figure 2; Doubleday, 1849; Schatz, [1887]; Godman and Salvin, 1882), costal cell open; *hindwing* somewhat quadrate, longer than wide, produced distally into a slight tail at vein M3, veins Rs, M1 and M2 diverging nearly from the same point, costal cell open; *prothoracic legs of male* thin, tibia longer than the femur, a single tarsomere half the length of the tibia, clothed in fine white setae; *prothoracic legs of female* thicker than those of the male, tibia shorter than the femur, five tarsomeres, together nearly equalling the tibia in length, each tarsomere bearing stout spines, especially the apical one; *meso- and metathoracic legs* long, femora shorter than tibiae, tibiae and four basal tarsomeres spiny, claws moderately curved; *abdomen* equal in length to head and thorax combined; *male genitalia* (Figure 3) with a bifid, curved uncus and simple valves. *Chromosome number*, $n=31$ (*A. amathea*, *A. fatima* and *A. jatrophae*; Maeki and Remington, 1961; Wesley and Emmel, 1975).

Scudder (1893) suggests that the generic name is derived from the Greek for "incongruous; in allusion to its great difference in marking from its fellows." Glaser (1887) states that *Anartia* is a "prince of the caste of the children of the sun" (Indian mythology). The only common name used for the genus as a whole is "the American Peacocks" (Brown and Heineman, 1972).

Anartia amathea and *A. fatima*

Anartia amathea (Linnaeus)

amathea (Linnaeus), 1758: 478 (*Papilio*).

Type locality: ["Indiis."]

[*amalthæa* (Clerck), 1764: pl. 40, fig. 3. Emendation; see below.]

amalthæa (Cramer), 1780: 29, 173, pl. 209, fig. A, B.

Unjustified emendation; see below.

roeselia (Eschscholtz), 1821: 207, pl. 5, fig. 9 (*Cynthia*).

Type locality: "Brasil."

silvae Burmeister, 1861: 168.

New synonymy.

Type locality: Argentina, Tucumán, Manantial de Marlopa.

amathea subspecies *sticheli* Fruhstorfer, 1907: 101.

Type locality: Bolivia, "5 days north of Cochabamba."

amathea subspecies *thyamis* Fruhstorfer, 1907: 102.

Type locality: Brasil, São Paulo; Santa Catarina; Rio Grande [do Sul]; "Paraguay."

[*amathea* subspecies *roeselia* aberration "conjuncta" Zikan, 1937: 387.

Type locality: Brasil, Minas Gerais, Passa Quatro, 900 m.]

Linnaeus may have committed a 'lapsus calami,' or mistransliterated *amathea* from Greek to Latin. The etymologically correct spelling is *amalthea*, for the goat that nursed Jupiter. (The reddish, innermost satellite of the planet Jupiter is also named Amalthea.) Clerck's emendation was followed by Cramer, and used by many others since then, but *A. amathea* must stand as the *nomenclaturally* correct name, since there is no "clear evidence of an inadvertent error" by Linnaeus (ICZN, 32 (a) (ii)), and no "demonstrably intentional change in the original spelling" by Clerck (ICZN, 33 (a)). Clerck's names have no standing in nomenclature, as he did not use the binomial system. The etymology of *amathea* is discussed in greater detail by Fruhstorfer (1907).

Anartia fatima (Godart)

fatima (Godart), [1824]: 375 (*Nymphalis*).

Type locality: "des Indes." Suggested replacement for *fatima* Fabricius. See below.

fatima Fabricius, 1793: 81 (*Papilio*).

Type locality: "Indiis." Junior homonym of *Papilio fatima* Cramer, 1780.

Application for suppression of this name has been forwarded to the ICZN. See below.

fatima subspecies *venusta* Fruhstorfer, 1907: 111.

Type locality: "México," "Guatemala."

moreno Kruck, 1931: 234, fig. 1.

Type locality: México, Oaxaca. Aberration.

fatima form *albifasciata* Hoffman, 1940: 281.

Type locality: "México".

[*fatima* aberration "albifusa" Hoffmann, 1940: 281, fig. 6, 7.

Type locality: México, Veracruz, Tierra Blanca.]

[*fatima* subspecies *venusta* form "colimensis" Hoffmann, 1940: 283, fig. 5b.

Type locality: México, Colima; [Michoacán], Río Balsas.]

[*fatima* aberration "oscurata" [sic] Maža, 1976: 103, fig. 1.

Type locality: México, Veracruz, Cerro El Vigía.]

[*fatima mirus* Martin, 1923: 54.

Type locality: Paraguay. Nomen nudum.]

If we were to follow strictly the rules of zoological nomenclature, *A. fatima* (Fabricius), as a junior primary homonym of the riodinid *Emesis fatima* (Cramer), would be invalid, since they were both described in the genus *Papilio*. However, considering the large amount of biological information published on this species, it would be in the best interest of a stable nomenclature if the specific epithet could be conserved. Accordingly, we have applied to the International

Commission on Zoological Nomenclature, for conservation of the name *fatima*, by recommending that the use of the name *fatima* Fabricius be suppressed until 1824, when Godart transferred the species to the genus *Nymphalis*. This would not affect the nomenclature of the riodinid, and would have the advantage of keeping the name *fatima* in use for what is certainly the most familiar Central American butterfly. The synonymy presented here reflects this recommendation.

The name *fatima* was first used in *Anartia* in 1837, by Geyer, in Hübner [1824-]1825[-1837] (see Hemming, 1937, p. 479).

Anartia amathea and *A. fatima* (Figure 1) are a pair of very closely-related species, restricted to the tropical and subtropical mainland of Latin America, including Trinidad and offshore islets. The ranges of these species abut in eastern Panamá (Darién); hybrids between them have been collected in the field at the juncture of their distributions on several occasions (e.g., Brown, 1975). Intensive study of the mortality and development of F1 hybrids (Figure 4) and their offspring reveals strong hybrid breakdown, and behavioral research on courtship and mating preferences reveals a complex picture of assortative mating. These results and their evolutionary consequences will be reported elsewhere; we here want to emphasize that we interpret *amathea* and *fatima* as biologically separate species.

The wing venation, male genitalia and larvae of *amathea* and *fatima* are, so far as we have been able to tell, identical. The wing venation (Figure 2) differs from that of other members of the genus by the two small veins that leave the Sc-R complex and branch towards the costa in the forewings. The valvae of the male genitalia (Figure 3) lack the basal swellings and sharp ventro-medial spines characteristic of *chrysopelea* and *lytrea*, and are similar to, but more lanceolate than, those of *jatrophae*.

A. amathea is easily distinguished from all other members of the genus by the extent of its vivid red coloration. On the dorsal surface, the red coloration extends into two spaces between the four postbasal/submedian lines of the anterior forewing, fills the median area of the posterior forewing, the submedian and median area of the hindwing (except for a dark line running through it from anterior to posterior), and the hind submarginal area of the hindwing. There are usually three to four subapical, five postmedial and four submarginal white spots on the forewing, and from one to four small submarginal white spots on the hindwing. The basal and postbasal regions of the wings are brown; all other markings are dark brown to black.

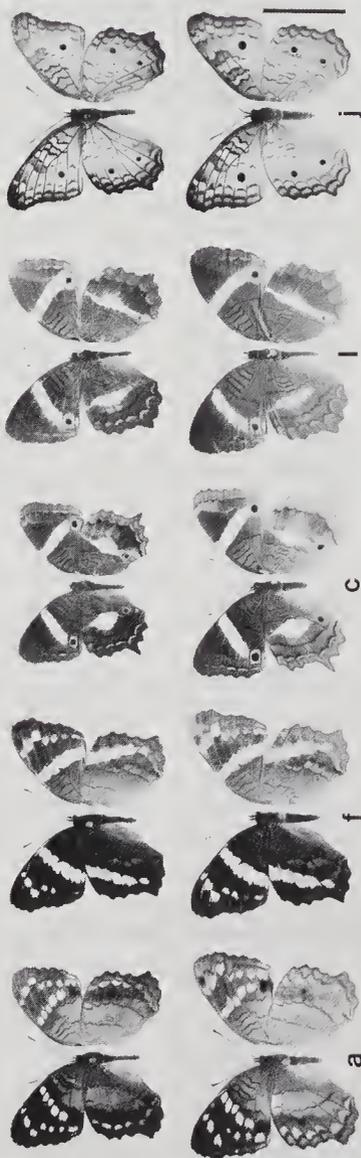


Figure 1. Adult butterflies of the genus *Anartia* (male above, female below). a = *A. amathea* [male: stock from Panamá, Darién Prov., Río Sambú, ex ovum, lot no. 107, ind. no. A-436, 1976, reared on *Blechnum brownnei*, R. E. S. & A. A.; female: same as male, except lot. no. 99, ind. no. A-434]; f = *A. fatima* [male: Panamá, Zona del Canal, Barro Colorado Is., ex ovum, ind. no. 78-52-14, 1978, reared on *Blechnum brownnei*, A. A. & R. E. S.; female: same as male, except ind. no. 78-52-17]; c = *A. chrysopetea* [male: Cuba, Sierra Maestra, 1,000 ft., 23 Nov 1929, O. Querci; female: same as male, except 21 Sep 1930]; l = *A. lytrea* [male: Hispaniola, Haiti, coll. F. E. Church [AMNH]; female: Hispaniola, Rep. Dom., Santo Domingo, ex coll. J. Doll, Ac. no. 24352 [AMNH]]; j = *A. jatrophae* [male: Panamá, Zona del Canal, Barro Colorado Is., ex ovum, ind. no. 79-133-H, 1979, reared on *Lindernia diffusa*, A. A. & R. E. S.; female: same as male except ind. no. 79-133-E]. Scale = 2 cm.

The pattern is similar but much paler on the ventral surface. Most of the markings that are black dorsally are brown ventrally. There are, in addition, two dark postmedian spots, an elongate one in forewing cell Cu2 and a small, round one in hindwing cell M1. The saturation of the red color, and the overall contrast of the pattern, is more pronounced among males than among females, especially on the dorsal wing surfaces. The red color is noticeably faded on older individuals and on old museum specimens.

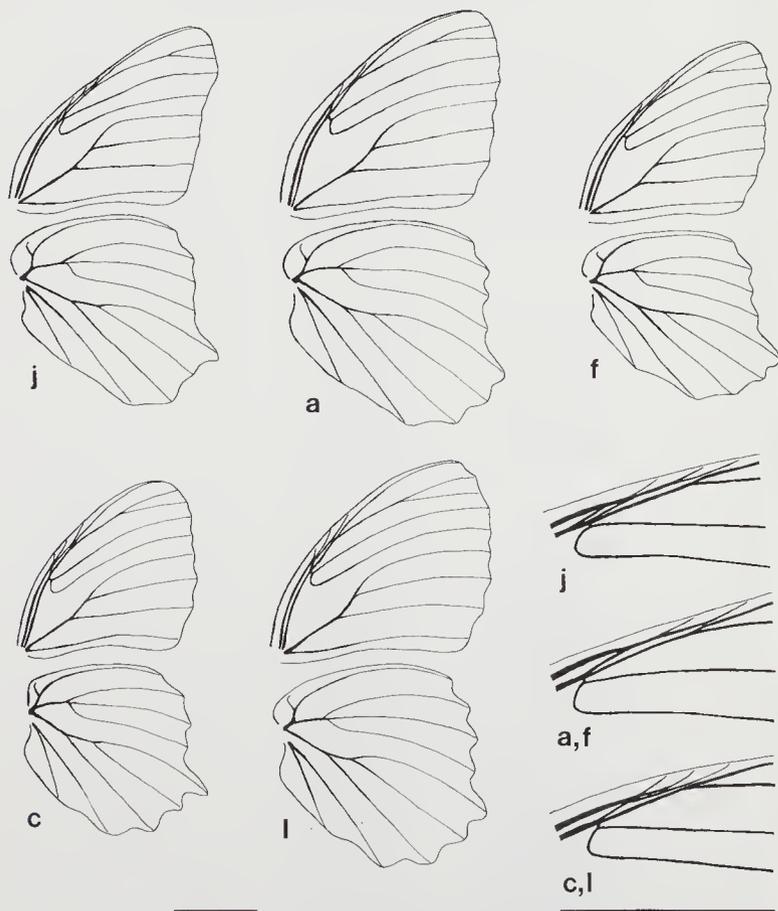


Figure 2. Wing venation of the five species of *Anartia*. a = *A. amathea*, f = *A. fatima*, c = *A. chrysopelea*, l = *A. lytrea*, j = *A. jatrophae*. Scales = 1 cm. See text.

Specimens of *A. amathea* from the southeastern part of its range are characterized by fusion of the five postmedian forewing spots into a broad, white band. Examination of large numbers of specimens reveals that this spot fusion exhibits much variation both within and between populations, and forms a cline running from northwest to southeast (Figure 5). Accordingly, we recognize Eschscholz' "roeselia" simply as that end of the cline showing the most distinctive forewing banding, not as a subspecies. Burmeister's "silvae," and Fruhstorfer's "thyamis" and "sticheli," are poorly-characterized variants that fall well within the ordinary range of variation.

Several common names have been coined for *amathea*, including the "Coolie" (Barcant, 1971), the "Tomato" (Kaye, 1921), and the "Red *Anartia*" (Riley, 1975).

The wing pattern of *A. fatima* is built around elements similar to those of *A. amathea*, but modified and colored in such a manner as to produce quite a different appearance. The wings are dominated by the distinctive bands, composed in the forewings of seven, and in the hindwings of five, enlarged postmedian spots, fused with one another. When *A. fatima* is at rest, the forewing and hindwing bands are joined in a continuous line. *A. fatima* also has three to four subapical and one to four submarginal spots on the forewing, of the same color as the band. The red coloration is restricted to a narrow median band on the hindwing (composed of four spots, distal to the position of the dark median line of *A. amathea*), and along the hind margin in some specimens. The remainder of the wings is largely dark brown to black, including the spaces between the four black postbasal/submedian lines on the anterior forewing. The ventral surface is similar in pattern to, but much lighter than, that of the dorsum; the bands are occasionally infuscated with darker scales beneath, and there is usually a well-developed, black, postmedian c-shaped mark in hindwing cell M1 just basal to the band. Males and females have similar patterns, but that of the male is generally more saturated and of higher contrast than that of the female.

The color, nature and function of the distinctive bands of *A. fatima* have been subjects of much research. In all populations, individuals can be found with yellow bands, white bands, or any shade from yellow to white. Fruhstorfer (1907) considered the white-banded form to be a distinct subspecies, *venusta*. Emmel

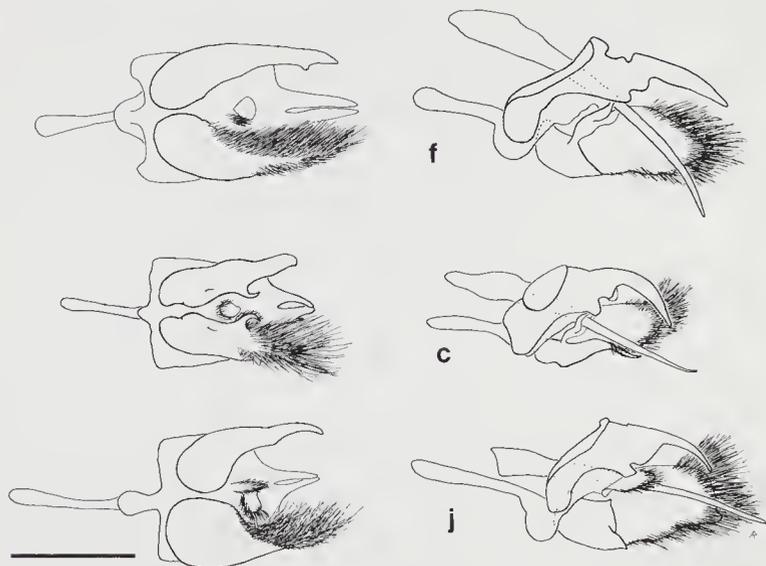


Figure 3. Male genitalia of the three species-groups of *Anartia*. Left: ventral view; Right: lateral view with left valve removed. Scale = 1 mm. [Specimen data: *A. fatima*: Panamá, Zona del Canal, Barro Colorado Island; *A. chrysopelea*: "Cuba"; *A. jatrophae*: Colombia, Cali.]

(1972, 1973), assuming that the band color differences had a genetic basis, reported "phenotype" frequencies, as well as behavioral experiments designed to learn more about the maintenance of such a polymorphism. Taylor (1973) disputed Emmel's assumptions, demonstrating that the band color was age- and sex-related, and correlated with physical and physiological measures of age. Young and Stein (1976) showed that the band colors, of marked individuals in a population, fade with time; they also reported some equivocal data on the colors of individuals at eclosion.

Our own (R.E.S. and A.A., in prep.) studies, which include rearings of over a thousand individuals, and the following of over a thousand marked individuals in a natural population, will be reported in detail elsewhere. But our clear-cut results are relevant to a consideration of the nature of Fruhstorfer's *venusta* and can be summarized as follows: Males *always* eclose with clear yellow wing-bands (N=1119). The color of the female wing-bands at the time of eclosion is variable, and may be anywhere in the continuum from

yellow to white; it appears to be independent of the length of the period of larval and pupal development. The bands of males, and of females that are not already white, always fade to white over a period of approximately two weeks under natural conditions. Fading appears to be related to light exposure; it can be induced in dead specimens exposed to sunlight (Taylor, 1973), but does not occur in museum specimens protected from light.

A. fatima shows marked variation in the extent of red coloration on the hindwings, with an increasing expression of red on the hind margin of the hindwing, in the northwestern part of its range. Hoffmann's "colimensis" (Figure 5) represents the extreme expression of red in *A. fatima*. There is an intriguing resemblance between this variant of *A. fatima*, and the banded "roeselia" of *A. amathea*, at the northern and southern extremes of their respective ranges.



Figure 4. F1 hybrids of *A. amathea* and *A. fatima*, male above, female below. Reared on *Blechnum brownei* at Barro Colorado Is., Panamá. Left: *A. amathea* female x *A. fatima* male: male AF-17, 1977, female AF-160, 1976. Right: *A. fatima* female x *A. amathea* male: male FA-151, 1976, female FA-274, 1976.

Several other variants of *A. fatima* have also been reported or described, most of which are well within the normal phenotypic range. The more unusual forms include Kruck's "moreno" (a melanic lacking the characteristic band), and Hoffmann's striking "albifusa" (with the forewing band extending toward and fusing with the subapical white spots). Aiello and Silberglie (1978) reported, but did not describe taxonomically, an aberration with orange instead of red hindwing markings³, apparently due to the homozygous condition of a recessive allele at a single locus. A similar, probably homologous aberration apparently exists in *amathea* (A. Shapiro, pers. comm.).

The only common name we know for *A. fatima* is simply "Fatima" (Klots, 1951).

F1 hybrids between *amathea* and *fatima* are illustrated in Figure 4. These reared specimens closely resemble those captured by G. B. Small, K. S. Brown (1975), and ourselves at several localities in eastern Panamá where the two distributions are contiguous. The two reciprocal hybrids are intermediate between the parental species, and similar to one another, in color and pattern, and there is relatively little variation among the offspring of either cross. A paper illustrating and describing the F1, backcross and F2 generations, and discussing the interspecific genetics of pattern characters, is in preparation.

Anartia chrysopelea and *A. lytrea*

Anartia chrysopelea Hübner

chrysopelea Hübner, [1831]: 34, pl. [95], fig. 547, 548.

Type locality: Cuba, La Habana.

[*litraea*, Herrich-Schäffer, 1864: 163.

Misspelling.]

lytrea subspecies *eurytis* Fruhstorfer, 1907: 112 (*Anartia* (*Anartiella*)).

Type locality: "Haiti (?), Puerto Rico (?)."

Anartia lytrea (Godart)

lytrea (Godart), 1819: 299 (*Vanessa*).

Type locality: unknown; "de l'expédition du capitaine Baudin."

dominica Skinner, 1889: 86.

Type locality: Haiti, [Artibonite], Samana Bay.

³We have since found that the red color of normal *fatima* (and *amathea*) can be changed to orange, identical to that of this aberration, by immersing the wings in dilute hydrochloric acid.

These two species, endemic to the largest islands of the West Indies, are very similar to one another and evidently closely related. They are identical in wing venation and genitalic structure, and differ only slightly in size, wing shape and wing pattern. Seitz (1924) and Bates (1935) considered them to be subspecies ('chromorphs' of Bates). However, since there is little variation within each of these entities, since the differences between them are very consistent, and since they are well-isolated geographically, they are evidently *biologically* separate species and are so treated here.

The venational features that distinguish these species are the combination of a single vein crossing from R to Sc, and three veins



Figure 5. Above, variation among specimens of *A. amathea* in the expression of postmedial forewing banding. Specimen data, from left: Colombia, Villavicencio, Dept. Meta, 588 m, 28 Sep 1942, M. Bates; Peru, La Merced; Brasil, Rio del Janeiro, Brasil, Pelotas, C. Biezanko ["roeselia"]. Below: A western Mexican specimen of *A. fatima* illustrating extreme expression of dorsal hindwing red coloration, and ventral infuscation of the band. Specimen data: México, Colima, Jacob Doll coll. ["colimensis"].

branching from Sc toward the costa in the forewing (Figure 2). The male genitalia (Figure 3) are very distinctive, with a pronounced basal swelling and ventro-medial spine on each valve.

A. chrysopelea is the smallest member of the genus, and has the most strongly developed "tail" at hindwing vein M3. The dorsal ground color of the wings is very dark brown, the males being darker than the females. A 2-3 mm wide, white postmedian band crosses the forewing, similar to that of *A. fatima* but composed of only five fused postmedian spots, and extending only to Cu2. Each hindwing bears an oval to rhomboid median white macula. A round 'ocellus' (eye-spot), consisting of black ringed with dull orange, is located in the anal angle of both fore- and hindwing, that of the forewing being slightly larger than that of the hindwing. The fine, dark, postbasal and submedian lines are present but obscured. Both wings have a series of dull orange submarginal lunules.

The ventral ground color is lighter; the hindwing macula is infuscated and crossed basally by a narrow stripe that extends from the costal margin to, and nearly surrounding, the 'ocellus.' The ventral forewing 'ocelli' are of the same relative size as they are dorsally. Occasional specimens have a suffusion of lavender scales postmedially in the ventral hindwing.

A. lytrea is somewhat larger than *A. chrysopelea*, with lighter brown ground color and less distinct markings. Dorsally, the white bands are slightly infuscated, with less sharply defined edges. Those of the hindwings are more elongate, and not as wide in the middle. The orange ring surrounding the 'ocellus' in the anal angle of the forewing is much wider in *A. lytrea*, and the hindwing 'ocelli' are far smaller than the forewing 'ocelli.' As in *A. chrysopelea*, there is a narrow row of submarginal orange lunules, more strongly curved in *A. lytrea*. The underside pattern is modified in a way similar to that of *A. chrysopelea*, but in the hindwing the orange ring does not quite surround the 'ocellus.' The "tail" at hindwing vein M3 is not as pronounced in *A. lytrea* as in *A. chrysopelea*.

A. chrysopelea and *A. lytrea* have been called "Huebner's Anartia" and "Godart's Anartia," respectively (Riley, 1975).

Anartia jatrophae

Anartia jatrophae (Linnaeus)

jatrophae ([Linnaeus] in Johansson), 1763: 25 (*Papilio*).

Type locality: "America"; Surinam (Munroe, 1942: 2).

corona Gosse, 1880: 199, pl. 8, fig. 1.

Type locality: Paraguay, "near Asunción." Aberration.

saturata Staudinger, [1885]: pl. 39, fig. [6] [as species]; [1866]: 104 [as variety].

Type locality: Haiti, Port-au-Prince; "Puerto Rico."

jatrophae variety *jamaicensis* Möschler, 1888: 27.

Type locality: "Jamaica."

[*jatrophae* aberration "margarita" Oberthür, 1896: 30, pl. 9, fig. 18.

Type locality: Brasil, Bahia.]

jatrophae subspecies *luteipicta* Fruhstorfer, 1907: 112.

Type locality: "Honduras."

jatrophae variety *pallida* Köhler, 1923: 24, pl. 2, fig. 12.

Type locality: Argentina, Misiones.

jatrophae subspecies *luteopicta* Munroe, 1942: 2.

Type locality: Honduras. Incorrect spelling, not available.

jatrophae subspecies *guantanamo* Munroe, 1942: 2.

Type locality: Cuba, Oriente, Guantánamo, San Carlos Estate.

jatrophae subspecies *semifusca* Munroe, 1942: 3.

Type locality: Puerto Rico, San Juan.

jatrophae subspecies *intermedia* Munroe, 1942: 4.

Type locality: "St. Croix."

The name *Jatrophae* (which may be a misnomer based on Merian's [1705] erroneous larval foodplant association) has been attributed to Johansson, but we agree with Hodges (1971, p. 29-30) that authorship should properly be ascribed to Linnaeus.

A. jatrophae has the widest geographic range of any species in the genus. Morphologically, it is distinctive in the combination of two veins crossing separately from R to Sc, and three veins branching from there to the costa (Figure 2). The male genitalia (Figure 3) are most similar to those of *A. amathea* and *A. fatima*, but have blunter and slightly asymmetrical valves.

A. jatrophae has a distinctive appearance that sets it apart from the other species. The ground color of most of the wings is dirty white or light gray, with marginal and submarginal dull, rusty orange in some populations. The wings often have a pearly lustre, especially beneath. The pattern is quite complex and highly variable in the tone of pigmentation, distal ground color and expression of certain details. Besides the intricate series of dark lines, chevrons and lunules in the lighter field (better studied in the photographs than described), there are three characteristic postmedian dark spots: a large one in forewing cell Cul and others in hindwing cells M1 and Cul.

The ventral surface is much lighter in ground color, and even more variable than the dorsum. There are often red-orange submar-

ginal lunules, and edgings of the same color on the lines in the ventral hindwing. The center of the dark spot in hindwing cell M1 is often suffused with blue scales.

Geographic and seasonal pattern variation in *A. jatrophae* have been the subjects of several papers (e.g., Munroe, 1942; Gillham, 1957; see also Longstaff, 1912). Consideration of large numbers of specimens from many localities and dates reveals an unusually large amount of phenotypic plasticity in pattern detail, both geographic and seasonal. The "several recognizable but not easily defined subspecies" (Riley, 1975) were the subject of a careful quantitative investigation by Gillham (1957), who concluded that they resulted from discordant variation in several characters. Although several modern authors (Brown and Heinemann, Howe, Klots, Riley, etc.) continue to recognize subspecies in *jatrophae* (especially for the West Indian populations), we see no reason to do so. They are better referred to as "*jatrophae* from . . ." than by taxonomic epithets that substitute for knowledge of the factors underlying their variation.

Common names used for *A. jatrophae* include the "White Peacock" (e.g., Holland, 1898; Klots, 1951; Riley, 1975; Rawson, 1976) and the "Biscuit" (Barcant, 1971).

BIOLOGY

ADULT BEHAVIOR AND ECOLOGY

Habitats, seasonality and population structure

Species of *Anartia* are found wherever their larval foodplants occur. Feeding as they do on herbaceous tropical weeds (Table 1), they are restricted to well-watered, disturbed habitats. Under natural conditions, these would include flood plains, landslide areas, treefall gaps, and similar sites, to 2,000 m or more, depending on latitude.

Human activities benefit *Anartia*. Their foodplants grow well along irrigation and drainage ditches, and large populations are found along roadsides, and in agricultural situations, throughout most of Latin America (see Young and Muysshondt, 1973; Young and Stein, 1976). *Anartia* are frequently found flying in the company of *Junonia* spp., with whom they have several larval foodplants in common. *A. jatrophae* appears to succeed in drier sites, and those with lower vegetation (e.g., Leck, 1974), where foodplants not utilized by the other species grow. In seasonally dry areas, populations usually diminish in size during the months of little rainfall

Table 1. Larval foodplants reported for *Anartia* species.

FOODPLANT SPECIES	FAMILY	USED BY	LOCALITY	REFERENCE
<i>Blechnum brownnei</i>	Acanthaceae	A	Brasil	Müller (1886)
<i>Blechnum brownnei</i>	Acanthaceae	A	Colombia	A.A. & R.E.S.
<i>Blechnum brownnei</i>	Acanthaceae	A, F, J	Panamá	A.A. & R.E.S.
<i>Blechnum pyramidatum</i>	Acanthaceae	F	Costa Rica	Young & Stein (1976)
<i>Blechnum pyramidatum</i>	Acanthaceae	F	Costa Rica	Young & Muyshondt (1973)
<i>Blechnum costaricense</i>	Acanthaceae	F	Costa Rica	Young & Stein (1976)
<i>Blechnum costaricense</i>	Acanthaceae	A, F	Panamá	A.A. & R.E.S.
<i>Justicia candalerianae</i>	Acanthaceae	F	Costa Rica	Young (1972)
<i>Dicliptera unguiculata</i>	Acanthaceae	F	Costa Rica	Young & Stein (1976)
<i>Jacobinia magnifica</i>	Acanthaceae	A	Costa Rica	cited in Lima (1967-1968)
<i>Ruellia occidentalis</i>	Acanthaceae	J	Brasil	cited in Howe (1975)
<i>Ruellia tweediana</i>	Acanthaceae	A	?	
<i>Ruellia tweediana</i>	Acanthaceae	A	Brasil	cited in Lima (1967-1968)
<i>Melissa officinalis</i>	Labiatae	A	Brasil	cited in Lima (1967-1968)
<i>Melissa officinalis</i>	Labiatae	J	Brasil	cited in Lima (1967-1968)
<i>Mentha piperita</i>	Labiatae	J	Brasil	cited in Lima (1967-1968)
<i>Mentha pulegium</i>	Labiatae	J	Brasil	cited in Lima (1967-1968)
<i>Lippia citriodora</i>	Verbenaceae	J	Brasil	cited in Lima (1967-1968)
<i>Lippia</i> sp. ¹	Verbenaceae	J	Florida	cited in Lima (1967-1968)
<i>Lippia</i> sp.	Verbenaceae	J	Florida	Scudder (1892)
<i>Lippia</i> sp.	Verbenaceae	J	Florida	A.A. & R.E.S.
<i>Lippia</i> sp.	Verbenaceae	J	Cuba	Gundlach (1891)
<i>Lippia</i> sp.	Verbenaceae	J	Cuba	Dethier (1941)
<i>Lippia</i> sp.	Verbenaceae	C	Cuba	Dethier (1941)
<i>Bacopa monniera</i>	Scrophulariaceae	J	Florida	Rawson (1976)
<i>Bacopa monniera</i>	Scrophulariaceae	J	Puerto Rico	Wolcott (1951)
<i>Lindernia diffusa</i>	Scrophulariaceae	J	Panamá	A.A. & R.E.S.
<i>Jatropha manihot</i> ²	Euphorbiaceae	J	Surinam	Merian, Sepp. . . .

¹ Riley (1975) disputed *Lippia* as a larval foodplant.² Undoubtedly a mistake, traceable to Merian (1705), who figured *A. jatrophae* on this species of plant; see text.A = *A. amathea*, C = *A. chrysopelea*, F = *A. fatima*, J = *A. jatrophae*.

(cf. Emmel and Leck, 1970). Local extinctions are frequent. *A. jatrophae* usually persists for awhile after its local congener has disappeared. During these dry times, populations are restricted to moist refugia, and search for these otherwise common species may be frustrating (e.g., Hall, 1925). Although some individuals enter a nonreproductive physiological state during the dry season (O. R. Taylor, Jr., in ms.), there is no evidence for prolonged physiological diapause in *Anartia*. Among other things, their short adult longevity would seem to preclude survival through a long dry season. Groups of adults may seek shelter in the same location (Young, 1979), but they do not form structured aggregations characteristic of many other tropical butterflies.

Adults are also influenced by the availability of nectar sources, and may leave an otherwise suitable area if no flowers are in bloom. They take nectar from many species, especially *Lantana camara* (but *not* from *L. trifolia*; Shemske, 1976; Barrows, 1976; they feed only at the yellow flowers of *L. camara*), *Hyptis mutabilis* and *Sida* sp. (Fosdick, 1973). The seasonal fluctuation in quality, of larval and adult habitats, affects the biogeography (*q.v.*) of *Anartia*.

Based on study of collecting localities and dates, we believe that much of the phenotypic variation seen in *A. fatima* and *A. jatrophae* is due in part to environmental conditions experienced during development.

The population biology of *A. fatima* has been studied in Costa Rica by Young (1972) and Young and Stein (1976), and in Panamá by Silberglied, Aiello and Windsor (in prep.). *A. amathea* has been studied in Ecuador by Fosdick (1973; but cf. Sheppard and Bishop, 1973!). Population sizes differed considerably between the species and studies; in Panamá, dramatic differences in population size were noted from one year to the next. During one year, striking cycles of recruitment from the immature stages occurred on a monthly basis (R. E. S., A. A. and D. M. Windsor, in prep.).

In spite of a sex ratio of 1:1 at eclosion in *A. amathea* ($\delta:\text{♀} = 1.04$, $N=1,957$) and *A. fatima*, ($\delta:\text{♀} = 0.96$, $N=2,281$), samples from *Anartia* populations may be strongly skewed toward one sex or the other. The population of *A. fatima* on Barro Colorado Island, for example, always had a significant preponderance of males, due in part to greater emigration by females in search of oviposition sites (R. E. S., A. A. and D. M. Windsor, in prep.; Organization for Tropical Studies report, cited in Young and Stein, 1976). On the

other hand, Fosdick's population of *A. amathea* in Ecuador was skewed toward females; it is likely that his site contained an abundant supply of larval foodplant on which females oviposited.

Survivorship was low in all populations studied, and it appears that under natural conditions, adult life is short—averaging from one to two weeks (maximum 9 weeks) in the field (R. E. S. and A. A., unpubl.). Young (1972) reported a longevity of 45 days in the laboratory. Adults are subject to heavy predation during their adult lives (see below). There are no field studies of the immature stages of any species.

Palatability and natural enemies

Due to their wide geographic ranges and local abundance, the three mainland species of *Anartia* have frequently been used in experiments on butterfly palatability, mimicry and predator learning. All three species were completely acceptable to the numerous insectivorous vertebrate and invertebrate predators to which they were offered (Table 2). Human subjects report that *A. fatima* have "no taste" or a "walnut flavor" (Emmel, et al., 1968). The predators of adult *Anartia* are those generalist insectivores common in disturbed habitats, especially spiders and insectivorous birds. Larvae probably suffer greatly from predation by social and solitary wasps. We have reared one (unidentified) tachinid parasitoid from a wild *Anartia* larva, but have never encountered viral or bacterial disease during the rearing of over 5,000 individuals.

In spite of their palatability, *Anartia* are often the most common species in the habitats where they occur. The tremendous losses of adults, and probably greater losses of larvae, are more than compensated for by the great fecundity in this genus (see below).

Function of coloration

Various functions have been suggested for the color patterns of *Anartia* species. *Anartia* orient to the sun and bask (Longstaff, 1912; Fosdick, 1973). There is no distal circulation in their wings, so only the colors of the body and wing bases play a role in thermoregulation (see Wasserthal, 1975; Douglas, 1979).

Brower, et al. (1971) present convincing experimental evidence to support the idea that *A. amathea* is an "incipient" Batesian mimic of *Heliconius erato*. Caged predators that tasted, and learned to avoid, *H. erato*, also refused the similar-colored *A. amathea*, even though

Table 2. Palatability tests using *Anartia* species: all three species tested were found to be palatable to all predators.

PREDATOR	PREY	CONDITIONS	LOCALITY	REFERENCE
ARANEAE (Araneidae)				
<i>Argiope argentata</i>	A	field obs.	Panamá (Darién)	R.E.S. & A.A.
<i>Argiope argentata</i>	F	field obs.	Panamá	R.E.S. & A.A.
ORTHOPTERA				
(Mantodea)	F	field obs.	Panamá	R.E.S. & A.A.
(Mantodea)	F	feeding exp.	Costa Rica	Emmel (1972)
HEMIPTERA (Reduviidae)				
<i>Apiomerus</i> sp.	F	field obs.	Panamá	R.E.S. & A.A.
HYMENOPTERA (Vespidae)				
<i>Polistes canadensis</i>	F, larva	field obs.	Panamá	R.E.S. & A.A.
REPTILIA				
<i>Ameiva ameiva</i> (Teiidae)	F	field exp.	Panamá	Boyden (1976)
"several lizard species"	F	field exp.	Costa Rica	Emmel (1972)
AVES				
(Corvidae)				
<i>Cyanocitta cristata</i>	A	lab exp.	Trinidad	Brower & Brower (1964)
<i>Cyanocitta cristata</i>	A	lab exp.	Trinidad	Coppinger (1970)
<i>Cyanocitta cristata</i>	J	lab exp.	Trinidad	Coppinger (1970)

Table 2. continued

(Icteridae)					
<i>Agelaius phoeniceus</i>	A	lab exp.	Trinidad	Coppinger (1970)	
<i>Agelaius phoeniceus</i>	J	lab exp.	Trinidad	Coppinger (1970)	
<i>Quiscalus quiscula</i>	A	lab exp.	Trinidad	Coppinger (1970)	
<i>Quiscalus quiscula</i>	J	lab exp.	Trinidad	Coppinger (1970)	
(Thraupidae)					
<i>Ramphocelus carbo</i>	A	lab exp.	Trinidad	Coppinger (1969)	
<i>Ramphocelus carbo</i>	A	lab exp.	Trinidad	Brower, et al. (1971)	
<i>Ramphocelus carbo</i>	J	lab exp.	Trinidad	Coppinger (1969)	
<i>Ramphocelus carbo</i>	J	lab exp.	Trinidad	Brower, et al. (1971)	
(Tyrannidae)					
<i>Muscivora tyrannus</i>	A	lab exp.	Trinidad	Alcock (1969)	
<i>Muscivora tyrannus</i>	A	lab exp.	Trinidad	Coppinger (1969)	
<i>Muscivora tyrannus</i>	A	lab exp.	Trinidad	Brower, et al. (1971)	
<i>Muscivora tyrannus</i>	J	lab exp.	Trinidad	Coppinger (1969)	
<i>Muscivora tyrannus</i>	J	lab exp.	Trinidad	Brower, et al. (1971)	
MAMMALIA (Hominidae)					
<i>Homo sapiens</i>	F	taste test	Costa Rica	Emmel, et al. (1968)	

A = *A. amathea*, F = *A. faima*, J = *A. jatrophae*.

the patterns in which the colors are arranged are very different in the two species. Less convincing is Emmel's (1972) suggestion that *A. fatima* mimics other, striped, *Heliconius* species. *A. fatima* resembles far more closely various *Adelpha*, *Doxocopa*, and other presumably palatable nymphalines.

The wing-bands of *A. fatima* are visible from both above and below, like those of a great many other banded butterflies (e.g., *Graphium kirbyi*, *Cyrestis acilia*, *Limenitis arthemis*, etc.). Such "disruptive" patterns presumably protect their bearers from predators (Platt and Brower, 1968), but the only evidence available to date does not support this hypothesis (Silberglied, et al., 1980). The wings of *Anartia* are brittle and easily fractured; mutilated individuals bearing evidence of unsuccessful attacks by predators, are common (e.g., Longstaff, 1912; see Silberglied et al., 1980).

The wing color patterns of *Anartia* spp. also play important intra- and interspecific communicatory roles between butterflies. These are discussed below under "courtship and mating."

Flight and daily activity

A. amathea and *A. fatima* have a jaunty, somewhat erratic flight that enables them to move about beneath the foliage of low herbaceous vegetation when seeking eclosing females (males) or oviposition sites (females). However, much of their time is spent in more open spaces as they feed at flowers, bask, chase other butterflies, etc. *A. jatrophae* has a strikingly different flight, in which long glides are interrupted by abrupt, mid-air pauses ("... spasmodic . . . alternate 'start' and 'glide,'" Walker in Brown and Heineman, 1972). Since less time is spent beating the wings, this type of flight requires less energy per unit distance travelled, than that of *A. amathea* and *A. fatima*; it may enable individuals to fly considerably greater distances. When alarmed, *A. jatrophae* seems to use an ascending escape maneuver more often than *A. amathea* or *A. fatima*.

Anartia species are active under sunny conditions, and during light rain. They avoid the dark interior of the forest, and rarely fly in strong winds (Young, 1979). Emmel (1972) plotted morning courtship activity curves for yellow- (young) and white-banded (older) male *A. fatima*, and Young (1972) reported daily oviposition activity of *A. fatima* to be between 10:00 and 13:00 hours.

Courtship and mating

Male *A. fatima* use both 'waiting' and 'seeking' behaviors (Magnus, 1963) to locate females. 'Waiting' males are found sitting on vegetation, often with wings slightly spread, from which they fly to inspect nearly any butterfly that passes. These chases may be quite prolonged, even when chasing other species or conspecific males. While such behavior has often been called 'aggressive' (e.g., Walker, in Brown and Heineman, 1972), we know of no way to differentiate it from simple inspection flights in which the responses of the pursued individual provides information to the pursuer (see Silberglied, 1977). Under crowded conditions in flight cages, groups of males sometimes form 'strings,' each male courting the one ahead. Males often return to the same waiting site after an unsuccessful chase. *A. jatrophae* males seem to prefer lower waiting sites than males of *A. amathea* and *A. fatima*.

When chasing, the male of *A. fatima* attempts to get above and slightly behind the female. If she does not avoid him, the male executes a 'bobbing' flight, during which he may be sending chemical and/or visual signals. Such 'bobbing' pairs persist for up to several minutes, the female descending lower and lower until she alights upon vegetation. The male alights next to the female, and attempts to couple with her by bending his abdomen laterally as he walks forward (Emmel, 1972), but she may still refuse his advances by flying off, or by spreading her wings. A side-to-side motion of the sitting female has been reported as denial behavior in *A. amathea* (Fosdick, 1973).

'Seeking' males fly low into vegetation, where they are often successful in locating and mating with teneral females (Emmel, 1972). Females usually mate during their first two days of adult life, but males generally do not mate until the third day after eclosion (R. E. S. and A. A., in prep.). Males do not mate more than once per day, but may mate on several days in succession. We have known individual males to mate up to nine times and still be capable of producing a spermatophore.

Color and pattern appear to be important stimuli to males seeking females. Preference tests with dummies of *A. fatima* show that males prefer normally-colored females, and that obliteration of either the light bands or red markings reduces the number of approaches (Emmel, 1972; Taylor, 1973). Female *A. fatima* with

yellow wing-bands are less attractive to males than those with white bands. The white band color reflects ultraviolet light more strongly (25% reflection) than does the yellow (14%)⁴; whether this component is important behaviorally remains to be determined. Males of *A. amathea* mate far less frequently with living females whose red color has been obliterated (R. E. S. and A. A., in prep.), than with red control females. Since *A. amathea* and *A. fatima*, like some other butterflies but unlike most other insects, see red (Bernard, 1979), it is not surprising that this color may be an important social signal. It has also been suggested that the black spots of *A. jatrophae* may be important as a visual signal (Atsatt, 1968).

Female mating behavior has been studied in *A. amathea* and *A. fatima* (R. E. S. and A. A., in prep.). Virgin females, isolated in flight cages from males, frequently approached other females in what may be "solicitation" behavior, but of course this rarely would happen in nature.

The outcome of most courtships of non-teneral females is probably determined primarily by female acceptance/rejection behavior (Taylor, 1972; R. E. S. and A. A., in prep.). Females of *A. amathea* mate assortatively, preferring conspecific males, but females of *A. fatima* do not discriminate between their own males and those of *A. amathea*. In *A. amathea*, females do not discriminate between conspecific males that had the red color obliterated, and normally-colored control males. The asymmetry of assortative mating, that results from these differences in female behavior of *A. amathea* and *A. fatima*, has evolutionary and ecological consequences at the juncture of the two species' ranges in eastern Panamá.

Copulation generally lasts from thirty minutes to one hour, but may be prolonged to as much as twelve hours. Young and Stein (1976) suggest that female *A. fatima* mate but once, Ehrlich and Ehrlich (1978) report a mean of 0.92 spermatophores per female in *A. amathea* (N=12, with no more than one per female) and Andersen (196?) reported a small number of female *A. fatima* with two spermatophores. Ehrlich and Ehrlich (1978) also suggest that *Anartia* might be a species capable of absorbing spermatophores:

⁴ Reflectance was measured densitometrically (Silberglied, 1976); on extreme yellow and white individuals. Emmel's (1972) description is misleading because, among other things, the television camera he used adjusts contrast automatically. Reflectance comparisons made with such a camera setup (Eisner, et al., 1969) are qualitative at best.

THE LIFE CYCLE

Oviposition and Larval Foodplants

Females in search of oviposition sites fly within a few centimeters of low vegetation, and land frequently and briefly upon a variety of plants. Eggs are laid singly, usually, but not always, on the larval foodplant (Table 1). *A. chrysopelea* has been seen ovipositing on *Tradescantia* sp. (Dethier, 1941), *A. jatrophae* on *Cyperus diffusa*, *Oldenlandia corymbosa* and *Polygala verticillata*, and *A. fatima* on "dead twigs, moss, rocks, walls, dry leaves, logs" (Young and Stein, 1976), "grasses, especially *Oplysminus* spp." (Young, 1972), *Croton hirtus*, *Chaptalia nutans*, garden hoses and cement walkways — none of which are acceptable larval foods. In the laboratory, *A. fatima* deposited more eggs on cage walls than on the *Blechnum brownei* leaves provided. Apparently the only requirement for an oviposition site is that it be near the correct foodplant, but the stimuli important in eliciting oviposition behavior remain unknown (cf. Young and Stein, 1976). We have never seen any species of *Anartia* oviposit in an area that did not contain a real larval foodplant.

Anartia species have unusually high fecundity. A single female may lay several hundred eggs over the course of a few days (Young, 1972; Silberglied and Aiello, in prep.). Ehrlich and Ehrlich (1978) report that female *A. amatheia* have approximately 100 eggs per ovariole, or a potential 800 eggs per female. Considering the sort of mortality for which such fecundity must compensate, the larva that survives to adulthood must be rare indeed.

The larval foodplants of *Anartia* are listed in Table 1. While *A. fatima* and *A. amatheia* accept *Blechnum brownei* and *B. costaricense* as foodplants in Panamá, in their natural habitat they would be less likely to encounter *B. costaricense*, a forest species. Neither *A. amatheia* nor *A. fatima* will feed on *Nelsonia brunellodes*, another member of the same family, that often grows with *B. brownei* in Panamá.

A. jatrophae has been reared upon numerous and diverse foodplants (see Table 1). Assuming that this pattern is real and not an artifact of limited data, we find it interesting that *A. jatrophae*, the most widespread of the three species, also has the broadest range of foodplants. This flexibility may enable it to coexist side by side with its congeners, with less direct competition for food. Furthermore, *A.*

jatrophae's range extends to higher latitudes in both hemispheres than any other congener; its more polyphagous nature may be compared with the similar patterns found for temperate papilionids by Scriber (1973).

Immature stages

The first reliable account of the immature stages of *Anartia* was that of Müller (1886), who described five larval instars and the pupa of *A. amathea*, and correctly identified the foodplant family as Acanthaceae. Earlier authors (Merian, 1705, copied by Sepp, 1852-1855 — see Müller, 1886; Seitz, 1914) erroneously reported the foodplant for *A. jatrophae* as "Manihot," and figured adult butterflies together with a pubescent moth-like larva lacking scoli, and a pupal exuvium of dubious affinity. Later accounts of the immature stages are given for *A. jatrophae* by Scudder (1893), Dethier (1941), Klots (1951), Riley (1975) and Rawson (1976); for *A. amathea* by Riley (1975); for *A. chrysopelea* by Dethier (1941); and for *A. fatima* by Young and Stein (1976). Nothing is known concerning the immature stages of *A. lytrea*.

Eggs

The eggs (Figure 6) of *A. amathea* and *A. fatima* are yellowish green, 0.65 to 0.70 mm in diameter, slightly taller than wide, and have eleven to thirteen longitudinal wax-crested ribs which extend to within 15 degrees of the upper pole, which is centered on the micropyle. The ventral surface is flat. The ribs are perpendicular to and rest upon 40-50 low ridges with which the egg is banded. The number of vertical ribs is variable within species and even among the eggs of a single female (Dethier, 1941). The eggs of *A. jatrophae* are similar (Dethier, 1941; Rawson, 1976), but those of *chrysopelea* are wider than they are high (Dethier, 1941). We were unable to distinguish the eggs of *A. amathea* and *A. fatima* from one another.

Larvae

While *Anartia* larvae have been described by several authors, only Dethier (1941) used morphological terminology⁵ precise enough for

⁵In their accounts of larval armature, some authors refer to setae as "hairs" or "spines," and to scoli beset with numerous setae as "branched spines." Many other inaccuracies are found in several published larval descriptions. Our terminology follows that of Peterson (1962); bilaterally arranged thoracic and abdominal armature units (e.g., scoli, verrucae, chalazae, setae) are described in the singular.

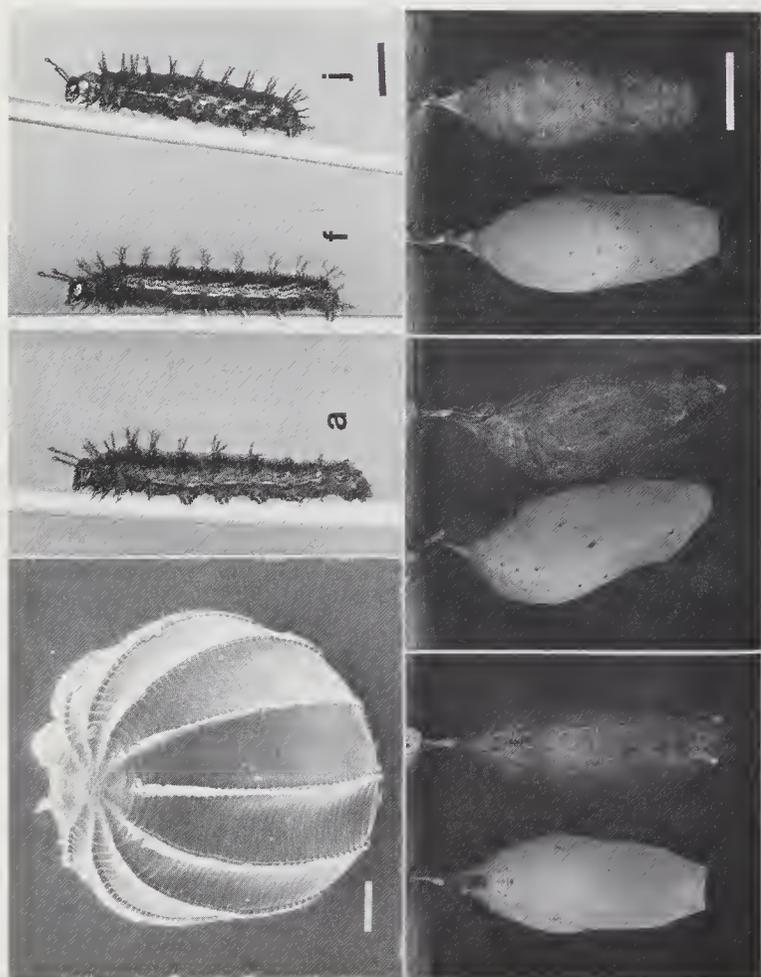


Figure 6. Developmental stages of *Anartia* spp. Upper left: egg of *A. fatima*, scale = 0.1 mm; scanning electron micrograph by E. Selig. Upper right, lateral view of three larvae: a = *A. anathaea* (several abdominal scoli missing), f = *A. fatima* (both last instars), j = *A. jatrophae* (penultimate instar), scale = 5 mm. Below: *A. fatima*, pupae, showing color variation, ventral lateral and dorsal views, scale = 5 mm.

comparative work. Since the known larvae differ little between species, the following account may be considered generic except as noted.

FIRST INSTAR (based primarily on *A. fatima*: *Head* (Figure 7): well-sclerotized, scoli lacking; *labrum* emarginate, bearing six pairs of setae; *frons* triangular, bearing three pairs of setae, ventral margin concave; two pairs of *adfrontal setae*, upper pair shorter than lower; *epicranium* rounded, each side bearing five long setae; three setae associated with the *stemma* ("ocelli") and one with the *antennae*, as figured. *Thorax*: ventral *eversible prothoracic gland* between the legs and head; *cervical shield* with four pairs of setae, three dark pairs directed forwards, and one pale, thinner pair, directed backwards; *subdorsal chalaza* on meso- and metathorax; *supraspiracular chalaza* on pro-, meso- and metathorax, that of prothorax bearing two setae; *subspiracular chalaza* on meso- and metathorax, situated slightly above plane of spiracles; *prespiracular chalaza* on prothorax, bearing two setae; a chalaza located between subspiracular and subventral chalazae on meso- and metathorax may be serially homologous with the prothoracic prespiracular chalaza; *subventral chalaza* on pro-, meso- and metathorax, that of prothorax bearing two setae. *Abdomen*: first segment darker than the others; *subdorsal chalaza* on segments 1-9, a small chalaza between, and posterior to, the subdorsal and subspiracular chalaza on segments 1-8 (situated posterior to subdorsal chalaza on segment 8); *supraspiracular chalaza* on segments 1-9; *subspiracular chalaza* on segments 1-9, that of segment 9 bearing two setae; *subventral chalaza* on segments 1-10 (segment 10 with two, located posteriorly); *suranal plate* rounded; *prolegs* on segments 3-6 and 10, well developed; *crochets* uniserial, uniordinal, arranged in a circle; *setae* (one per chalaza except as noted) microscopically serrate, and curved anteriorly.

SECOND INSTAR (based on *A. amathea*, *A. fatima* and *A. jatrophae*): *Head* (Figure 7): as in first instar except for addition of a pair of epicranial scoli, and secondary setae in epicranial, frontal, anterior, and ocellar areas. *Thorax*: ventral *eversible prothoracic gland* between legs and head; *cervical shield* with four pairs of setae, two dark pairs and two pale pairs; *subdorsal scolus* on meso- and metathorax; *supraspiracular verruca* on pro-, meso- and metathorax; *subspiracular scolus* on pro-, meso- and metathorax; *prespiracular verruca* on prothorax; a verruca located between subspiracular and

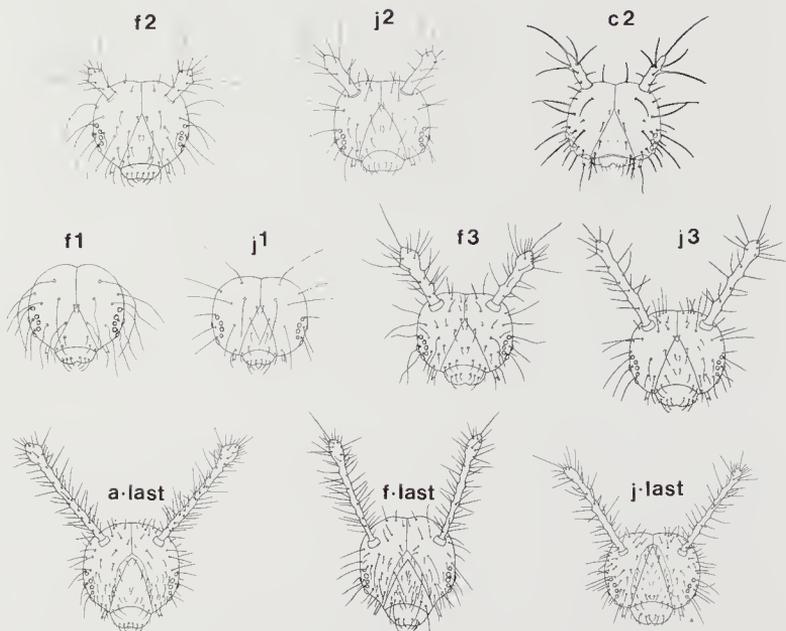


Figure 7. Head capsules of *Anartia* spp. a = *A. amathea*, c = *A. chrysopelea*, f = *A. fatima*, j = *A. jatrophae*. Numbers on figure indicate instar number; numbers in brackets are head capsule widths in mm. f2 [width of head capsule = 0.6 mm], j2 [0.5], c2 [0.575, measurement and figure from Dethier, 1941], f1 [0.4], j1 [0.4], f3 [1.0], j3 [0.9], a-final [2.5], f-final [3.0], j-final [2.7].

subventral scoli on meso- and metathorax may be serially homologous with the prothoracic prespiracular verruca; *subventral scolus* on pro-, meso- and metathorax. *Abdomen*: *mediodorsal scolus* on segments 1-8 (segment 8 with two, one anterior, one posterior); *subdorsal scolus* on segments 1-8; *supraspiracular scolus* on segments 1-10; *subspiracular scolus* on segments 1-8; *subventral scolus* (small) on segments 1, 2 and 7; pair of *subventral verrucae*, one anterior, one posterior, on segments 3-6; pair of posterior subventral verrucae, one above the other, on segment 10; *suranal plate* triangular; *prolegs* as in first instar; *crochets* uniserial, triordinal, arranged in a mesoseries; *setae* numerous on each scolus.

MORPHOLOGICAL DIFFERENCES BETWEEN FIRST AND SECOND INSTARS: In the second instar⁶, scoli and additional setae appear on the head (Figure 7); the chalazae of the first instar are replaced by scoli and verrucae; the setae are no longer serrate; the central pair of setae on the cervical shield is pale; a prothoracic subspiracular scolus appears (no prothoracic subspiracular chalaza in the first instar); mediodorsal armature appears on abdominal segments 1-8; the following armature is lost: subdorsal chalaza on segment 9, the small chalaza between and posterior to the subdorsal and supraspiracular chalazae on segments 1-8, the subspiracular chalaza on segment 9, and the subventral chalaza on segments 8 and 9; a supraspiracular scolus appears on segment 10; the subventral chalaza on segments 3-6 is now a pair of scoli; the suranal plate becomes triangular; the crochets become triordinal and are arranged in a mesoseries.

THIRD AND SUBSEQUENT INSTARS: The head scoli are clubbed (slightly more so in *A. amathea* and *A. fatima* than in *A. jatrophae*) in the third through final instars (Figure 7). The head width increases by factors of 1.5 (*A. fatima*), and 1.6 (*A. amathea* and *A. jatrophae*) (see Figure 8). The adfrontal sutures become conspicuous in the final instar, by which time the body is black, the scoli are reddish brown, and there are often coarse longitudinal stripes composed of light dots. The prothoracic eversible gland is present in all instars.

The interspecific differences in larval morphology are very subtle. A detailed, comparative larval study must await the discovery of the larva of *A. lytrea*, and the collection of new material of *A. chrysopelea*.

The number of instars is variable: *A. amathea* from Colombia had five instars (Müller, 1886; R. E. S. and A. A.); *A. fatima* from Panamá had six (A. A. and R. E. S.); from Costa Rica five (Young and Stein, 1976); *A. jatrophae*⁷ from Panamá had five (A. A. and R.

⁶Dethier's (1941) description, of a second instar *A. jatrophae* from Cuba, differs from ours in the number of scoli on abdominal segments 8-10, and in the reported absence of a subspiracular scolus on the prothorax. From his account of the first four instars of *A. chrysopelea*, the larvae of that species are very similar in setal arrangement to the three described above. However, he reports that the setae of the first instar larva "... do not arise from conspicuous sclerotized areas ..."

⁷Rawson (1976) reported three instars for *A. jatrophae* from Florida, but from his illustrations it is probable that he missed one or more instars; his "third" instar is probably a fifth or sixth. The sum of Rawson's development times is also unusually short. Further rearing in Florida should be done to corroborate his account.

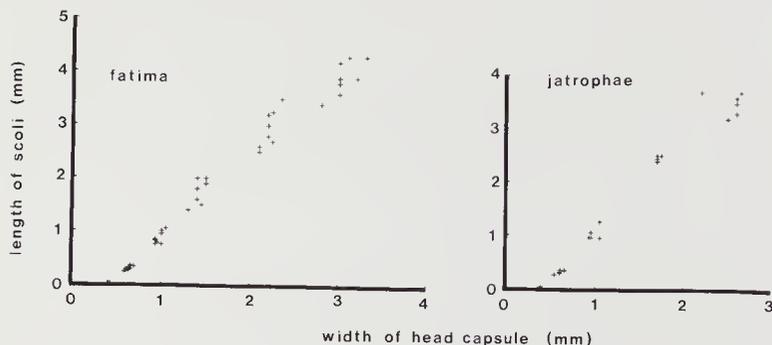


Figure 8. Dimensions of head capsules and scoli of the larvae of *A. fatima* and *A. jatrophae*, reared individually. Note that *A. jatrophae* has one less instar, but grows more per instar, than *A. fatima*. However, the final larval head capsule size of *A. jatrophae* is not quite as large as that of *A. fatima*. [Instar 1 lacks scoli.]

E. S.). Development times for *A. amathea*, *A. fatima* and *A. jatrophae*⁷ in Panamá are given in Table 3 (reared individually) and Figure 9 (reared under crowded conditions). Similar times are given for partial life cycles of *A. jatrophae* by Dethier (1941) and Rawson (1976), and for *A. chrysopelea* by Dethier (1941). Young (1972) reported 28 days, and Young and Stein (1976) reported 46–49 days, both for *A. fatima* in Costa Rica. Under identical rearing conditions, *A. jatrophae* takes less time and fewer instars to develop to adult than does *A. fatima* (Table 3).

Table 3. Development time (days) for two species of *Anartia*, reared as isolated individuals under identical conditions in Panamá. The difference between total mean development times for the two species is significant ($t = 5.599$, $df = 21$, $p < .0005$).

STAGE	<i>A. jatrophae</i> (N=7)		<i>A. fatima</i> (N=16)	
	mean	s.d.	mean	s.d.
egg	3.86	0.38	5.06	0.25
instar 1	4.00	0.00	3.25	0.45
instar 2	3.14	0.38	3.06	0.25
instar 3	2.43	0.53	2.81	0.40
instar 4	3.29	0.49	3.13	0.50
instar 5	7.14	0.38	3.31	0.60
instar 6	—	—	6.88	0.84
pupa	7.86	0.38	6.88	0.50
TOTAL	31.72	0.76	34.38	1.54

Pupae

A larva nearing pupation wanders for about one day, then prepares a silk pupation platform several centimeters above the ground on the underside of a leaf or twig. Platform making usually begins in the late afternoon or early evening, and is quickly followed by spinning of the silk stalk from which the pupa will be suspended. During platform making and stalk spinning, larvae evert the whitish gland located ventrally on the prothorax between the legs and head. The function of this gland is not known. Once the silk stalk is completed, the larva walks forward until its tenth segment prolegs are positioned over it. These prolegs are then used to pull and shape the stalk before they finally clamp onto it, and support the larva during its final molt. By midnight most larvae have let go with all but the tenth segment prolegs, and now hang in a "J" position until 8 or 9 AM, when ecdysis takes place.

In the laboratory, larvae hang from the cage cover to pupate. Under crowded conditions, freshly-formed pupae may be cannibalized by hungry final instar larvae.

Pupae of *A. amathea* (Müller, 1886), *A. fatima* (Young and Stein, 1976), and *A. jatrophae* (Scudder, 1893; Wolcott, 1951; Rawson, 1976) are 15–22 mm long, smooth, spindle-shaped and without protuberances. They are usually translucent jade green in color, with dark spots (Figure 6; see also Young and Stein, 1976) in the same positions occupied by scoli in the final larval instar, plus a few additional dark marks on the wings. Occasional individuals of all three species are black (Scudder, 1893; A. A. and R. E. S.).

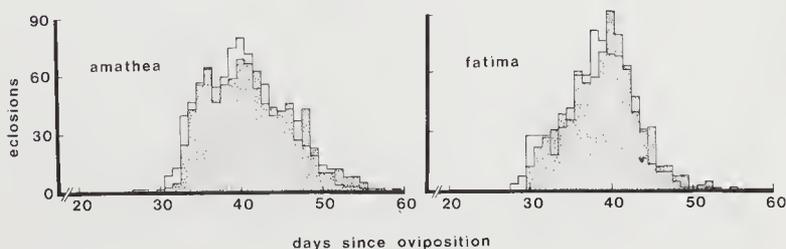


Figure 9. Development times of male and female (stippled) *A. amathea* (N=1,764) and *A. fatima* (N=1,579), reared under crowded conditions (up to 20 larvae per container).

The pupal period usually lasts six to eight days in the three species we have studied (see also Rawson, 1976; Young, 1972; Young and Stein, 1976). A day or two before eclosion, color changes can be seen through the pupal skin. The eyes turn yellow and finally brown, and the wings become pale brown (in *A. jatrophae*) or black (*A. amathea* and *A. fatima*). In *A. fatima* the wing-bands show clearly by the morning of eclosion. Adults emerge during the morning and are ready to fly within one to two hours.

BIOGEOGRAPHY

The three distinctive evolutionary lines of the genus *Anartia* have well-defined and interesting geographic distributions (Figure 10). *A. lytrea* and *A. chrysopelea* are West Indian endemics on Hispaniola and Cuba, respectively. (*A. chrysopelea* is also known from the Isle of Pines, Swan Island, and southern Florida.) *A. fatima* and *A. amathea* are widely distributed in tropical Central and South America, respectively. *A. jatrophae* is ubiquitous throughout all the warm regions of the Western Hemisphere, including the southern United States, the Bahamas and West Indies, all of Central and most of South America, to about 30 degrees north and south latitude. It has been difficult to determine the limits in some areas because of the tendency of collectors not to collect common species once a series has been obtained. Since all species can be collected around human habitations, many collectors do not bother with them soon after arrival in the tropics. Another problem has been the profusion of mislabelled specimens and erroneous reports, such as *A. fatima* from "Brasil," and *A. amathea* from "Mexico" (da Silva, 1907) and "Havane" (Lucas, 1857). The southernmost limits of *A. jatrophae* and *A. amathea* are poorly documented; neither species occurs in Chile.

Within these broad distributions, *Anartia* spp. are restricted to moist, or at least not very dry, disturbed habitats where their larval foodplants grow. Distributions may change markedly during the year in areas having pronounced dry seasons. Local extinctions of many populations occur through the dry season, with recolonization following the start of the rains. For example, during 1977, *A. fatima* went extinct throughout most of central and southern Panamá, with occasional individuals remaining at isolated refugia (including dripping air conditioners and lawn sprinklers), but with a



Figure 10. Geographical distributions of *Anartia* species. See "Biogeography."

substantial population remaining active on the moister Caribbean side of the isthmus. Within two months after the rains began, the species had reestablished itself in most of its former habitats.

All species of *Anartia* are highly vagile. Based on our study of the Barro Colorado Island population, it appears that females of *A. fatima* emigrate more than males do. The ecological adaptations of *A. fatima* as a colonizing species have been summarized by Young (1972) and Young and Stein (1976). *A. jatrophae*, with its gliding flight similar to that of many migratory species, appears to be the most vagile, for it usually recolonizes former habitats long before *A. fatima* arrives. It also has a wider geographic range, and its populations, while variable, are not strongly differentiated from one another, suggesting considerable gene flow. Vagrants of all species fly considerable distances, and occasionally establish local, temporary populations beyond the normal range. For example, *A. fatima* reaches Kansas (Howe, 1975), *A. jatrophae* reaches Kansas and southern New England (Ehrlich and Ehrlich, 1961), *A. chrysopelea* has turned up in southern Florida on at least two occasions (Anderson, 1974; Bennett and Knudson, 1976) and possibly once on Antigua (Fruhstorfer, 1907), Godman and Salvin's (1882) record of *A. lytrea* on Jamaica, while unconfirmed (Brown and Heineman, 1972), is certainly within the realm of possibility, and *A. amathea* ". . . occurs sporadically . . . on Antigua, Grenada and Barbados . . . no doubt a vagrant . . . sometimes established for short periods (Godman and Salvin, 1896; Riley, 1975).

The distributions of all *Anartia* species, except *A. jatrophae*, are strictly allopatric of one another. *A. jatrophae* coexists with all; it is a better colonizer, utilizes a wider array of larval foodplants (Table 1), takes less time to develop (Table 3), and withstands drier conditions. Such correlation of ecological distinctness with coexistence illustrates well the concept of limiting similarity of sympatric congeners, and their comparative ecology would be worth a more detailed study (see also Young and Stein, 1976).

EVOLUTION

Relationships to other genera

Young and Stein (1976) reported the "outstanding discovery" that the immature stages of *A. fatima* are similar to those of *Siproeta*, and suggested a close relationship between the two genera. This similarity, which involves the larval foodplants, egg and larval mor-

phology, and open discal cell in both fore- and hindwing, had been discovered and published ninety years earlier by Müller (1886; see also Brown and Heineman, 1972). While we agree with such an assessment, we want to take this opportunity to point out that this section of the subfamily is replete with genera of uncertain affinity, and we feel it is unwise to speculate further on phylogenetic positions until a broad, modern generic revision of the Nymphalinae, employing larval and biological as well as adult characters, is undertaken.

Evolution within the genus

Anartia clearly contains three distinct phylogenetic lines:

- (1) *A. amathea* and *A. fatima* probably represent a pair of sister-species, derived from a widespread neotropical ancestor. We envision a scenario in which the populations of this ancestor were isolated from one another during the Tertiary subsidences of the Panamanian isthmus, after which time the distinctive colors and patterns of the two species evolved. The secondary contact and occasional hybridization between *A. amathea* and *A. fatima* in the Darien represents a recent event in geologic time, the consequences of which are of considerable interest.
- (2) *A. chrysopelea* and *A. lytrea* probably represent another pair of sister-species, derived from a common ancestor (Bates, 1935). Their physical isolation on separate islands probably fostered their differentiation.
- (3) *A. jatrophae* is a widely-distributed species of great geographic variation. Tendencies toward the formation of distinct, geographically isolated populations are thwarted by the high vagility of individuals.

These three species-groups differ from one another in only a few morphological characters. It is not possible at present to decide which character states are plesiomorphic, and which derived, for these features. For this reason we do not feel it would serve a useful purpose to present speculations on the branching sequence within the genus.

DEPOSITION OF SPECIMENS

Voucher specimens of the immature stages of *A. amathea*, *A. fatima* and *A. jatrophae* have been deposited in the Museum of Comparative Zoology (MCZ). All adult specimens illustrated,

except for *A. lytrea* (American Museum of Natural History [AMNH]), are in the MCZ collection. F1 hybrids have also been deposited with G. B. Small, K. S. Brown, the Museo de Historia Natural "Javier Prado," the Peabody Museum (Yale University), the AMNH, and the National Museum of Natural History (Smithsonian Institution), as well as the MCZ.

ACKNOWLEDGEMENTS

We thank the numerous individuals and institutions who made specimens and data available to us. In particular, R. E. S. and A. A. thank G. B. Small for introducing them to hybridization between *A. amathea* and *A. fatima*, K. Radcliffe Dressler for help with rearing, J. M. Sigda for statistical assistance, E. Mayr for suggestions on conservation of the same *fatima*, and the Smithsonian Tropical Research Institute for financial support and the use of facilities.

REFERENCES CITED

- AIELLO, A., AND SILBERGLIED, R. E.
1978. "Orange" bands, a simple recessive in *Anartia fatima* (Nymphalidae). *J. Lepidopt. Soc.* 32: 135-137.
- ALCOCK, J.
1969. Observational learning by fork-tailed flycatchers (*Muscivora tyrannus*). *Anim. Behav.* 17: 652-657.
- ANDERSEN, A.
1967. Proportions within a polymorphic population of *Anartia fatima* butterflies. Organization for Tropical Studies report, unpublished.
- ANDERSON, R. A.
1974. Three new United States records (Lycaenidae and Nymphalidae) and other unusual captures from the lower Florida keys. *J. Lepidopt. Soc.* 28: 354-358.
- ATSATT, L.
1968. Population biology of a nymphalid butterfly — *Anartia jatrophae*. Organization for Tropical Studies report, unpublished.
- BARCANT, M.
1971. *Butterflies of Trinidad and Tobago*. Collins. London.
- BARROWS, E. M.
1976. Nectar robbing and pollination of *Lantana camara* (Verbenaceae). *Biotropica* 8: 132-135.
- BATES, D. M.
1924. Notes on Florida Lepidoptera. *Florida Entomol.* 7: 42-43.
1935. The butterflies of Cuba. *Bull. Mus. Comp. Zool.* 78: 63-258.
- BENNETT, R., AND KNUDSON, E. C.
1976. Additional new butterfly records from Florida. *J. Lepidopt. Soc.* 30: 234-235.

- BERNARD, G. D.
1979. Red-absorbing visual pigment of butterflies. *Science* 203: 1125-1127.
- BOISDUVAL, J. B. A. D. DE
1870. *Considerations sur des Lépidoptères envoyés du Guatemala à M. de l'Orza*. Oberthür et Fils, Rennes, [ii] + 100 p.
- BOYDEN, T. C.
1976. Butterfly palatability and mimicry: experiments with *Ameiva* lizards. *Evolution* 30: 73-81.
- BROWER, L. P., ALCOCK, J., AND BROWER, J. V. Z.
1971. Avian feeding behaviour and the selective advantage of incipient mimicry. Chapter 12 (pp. 261-274). In *Ecological Genetics and Evolution, essays in honour of E. B. Ford*, R. Creed, ed. Blackwell Scientific Publications, Oxford & Edinburgh.
- BROWER, L. P., AND BROWER, J. V. Z.
1964. Birds, butterflies and plant poisons: a study in ecological chemistry. *Zoologica (New York)* 49: 137-159.
- BROWN, F. M., AND HEINEMAN, B.
1972. *Jamaica and its Butterflies*. E. W. Classey, Ltd. London.
- BROWN, K. S.
1975. Field Season Summary: zone 10, South America: Peru, Colombia and Panama [sic]. *News Lepidopt. Soc.* 15 May 1976, No. 2: [17].
- BURMEISTER, H.
1861. *Reise durch die La Plata-Staaten mit besonderer Rücksicht auf die physische Beschaffenheit und den Culturzustand der Argentinischen Republik, ausgeführt in den Jahren 1857, 1858, 1859 und 1860*. Tucumán Fauna 2: 163-173. H. W. Schmidt. Halle.
- CLERCK, C. A.
1759-
1764. *Icones insectorum rariorum cum nominibus eorum trivialibus, locisque e C. Linnaei Arch: R: et Equ: Aur: Syst: Nat: allegatis*. Holmiae. (1): [12] p., pl. 1-16 (1759); (2) : [8] + [3] p., pl. 17-55 + [7] (1764).
- COMSTOCK, J. A., AND VÁZQUEZ, L.
1960
(1961). Estudios de los ciclos biológicos en Lepidópteros Mexicanos. *An. Inst. Biol. (México)* 31: 349-488.
- COPPINGER, R. P.
1969. The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies. Part I. Reactions of wild-caught adult blue jays to novel insects. *Behaviour* 35: 45-60.
1970. The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies. II. Reactions of naive birds to novel insects. *Amer. Natur.* 104: 323-335.
- CRAMER, P.
1780. *De uitlandische Kapellen voorkomende in de drie Waereld-Deelen Asia, Africa en America . . .* S. J. Baalde, Amsteldam; B. Wild, Utrecht 3:176 pp., pl. 193-288.

- DETHIER, V. G.
1941. Metamorphoses of Cuban Nymphalidae and Lycaenidae. *Psyche* 48: 70-78.
- DOUBLEDAY, E.
1844. *List of the specimens of lepidopterous insects in the collection of the British Museum. Part I.* London.
1849. *The Genera of Diurnal Lepidoptera: . . .* In Doubleday, E., Westwood, J.O. 1846-1850. 1: 214-216. Longman, Brown, Green and Longmans. London.
- DOUGLAS, M.
1979. Hot butterflies. *Natur. Hist.* 88(9): 56-65.
- EHRlich, P. R., AND EHRlich, A. H.
1961. *How to Know the Butterflies.* Wm. C. Brown Co. Dubuque, Iowa.
1979. Reproductive strategies in butterflies: I. Mating frequency, plugging, and egg number. *J. Kansas Entomol. Soc.* 51: 666-697.
- EISNER, T., SILBERGLIED, R. E., ANESHANSLEY, D., CARREL, J. E., AND HOWLAND, H. C.
1969. Ultraviolet video-viewing: the television camera as an insect eye. *Science* 166: 1172-1174.
- EMMEL, T. C.
1972. Mate selection and balanced polymorphism in the tropical nymphalid butterfly, *Anartia fatima*. *Evolution* 26: 96-107.
1973. On the nature of the polymorphism and mate selection phenomena in *Anartia fatima* (Lepidoptera: Nymphalidae). *Evolution* 27: 164-165.
- EMMEL, T. C., AND LECK, C. F.
1969
(1970). Seasonal changes in organization of tropical rain forest butterfly populations in Panama. *J. Res. Lepidopt.* 8: 133-152.
- EMMEL, T. C., VANDERMEER, J., TOWNER, H., HAWKINS, L., KLOEK, G., MORROW, P., AND JUVIK, K.
1968. Field problem report: mimetic complexes in butterflies: experimental tests with predators. Organization for Tropical Studies report, unpublished.
- ESCHSCHOLTZ, J. F.
1821. *Beschreibung neuer ausländischer Schmetterlinge, nebst Abbildungen*, 201-219, 11 pl. In Kotzebue, O. v., *Entdeckungs-Reise in die Süd-See . . . Dritter Band.* Gebrüder Hoffmann. Weimar.
- FABRICIUS, J. C.
1793. *Entomologia systematica emendata at aucta, . . .* Christian Gottlieb Proft. Hafniae. 3(1): iv + 487 p.
- FOSDICK, M. K.
1972
(1973). A population study of the neotropical nymphalid butterfly, *Anartia amalthaea*, in Ecuador. *J. Res. Lepidopt.* 11(2): 65-80.
- FRUHSTORFER, H.
1907. Uebersicht der bekannten *Anartia* und Beschreibung neuer Formen. *Internat. Entomol. Zeit.* 1(14): 97, (15): 101-102, (16): 111-112.

- GEYER, C.
1833. (See Hübner, [1832-]1837, and Hemming, 1937.)
- GILLHAM, N. W.
1957. Subspecies versus geographic variation in Caribbean populations of *Anartia jatrophae* Johansson (Lepidoptera, Nymphalidae). Amer. Mus. Novit. No. 1845. 22 p.
- GLASER, L.
1887. *Catalogus etymologicus Coleopterorum et Lepidopterorum*. R. Friedland & Sohn. Berlin. iv + 396 p. [p. 274].
- GODART, J. B.
1819
[-1824]. In Latreille, P. A. and Godart, J. B., *Encyclopédie Methodique. Histoire Naturelle. [Zoologie] 9. Entomologie*. Veuve Agasse. Paris.
- GODMAN, F. D., AND SALVIN, O.
1882. *Anartia*. In *Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera. 1*: 221-222.
1896. On the butterflies of St. Vincent, Grenada, and the adjoining islands of the West Indies. Proc. Zool. Soc. London 1896: 513-520.
- GOSSE, P. H.
1880. The butterflies of Paraguay, and La Plata. Entomologist, 13: 193-205 + pl. 2.
- GUNDLACH, J.
1891. Suplemento segundo para la contribución del la entomología cubana. I (Lepidopteros): 445-480. La Habana.
- HALL, A.
1925. List of the butterflies of Hispaniola. Entomologist 58: 161-165, 186-190.
- HEMMING, F.
1937. *A Bibliographical and Systematic Account of the Entomological Works of Jacob Hübner*. Royal Entomol. Soc. London. 2 vol.
1941. The types of the genera established by Doubleday (E.) in the *Genera of Diurnal Lepidoptera* and by Westwood (J. O.) in the continuation thereof. J. Soc. Bibliogr. Natur. Hist. 1(11): 413-446.
1941. The dates of publication of the specific names first published in Doubleday (E.) *Genera of Diurnal Lepidoptera* and in the continuation thereof by Westwood (J. O.). J. Soc. Bibliogr. Natur. Hist. 1(11): 447-464.
- HERRICH-SCHÄFFER, G. A. W.
1864. Die Schmetterlingsfauna der Insel Cuba. Corresp.-Bl. zool.-min. Ver. Regensburg 18: 159-172.
- HODGES, R. W.
1971. *The moths of North America, including Greenland. Fascicle 21. Sphingoidae. Hawkmoths*. E. W. Classey, Ltd. London. [pp. 29-30.]
- HOFFMANN, C. C.
1940. Lepidópteros nuevos de México IV. An. Inst. Biol. Univ. Nac. Autónoma México 11: 275-284.
- HOLLAND, W. J.
1898. *The Butterfly Book. A Popular Guide to a Knowledge of the Butterflies of North America*. Doubleday and McClure Co. New York.

- HOWE, W. H.
1975. *The Butterflies of North America*. Doubleday and Co. New York.
- HÜBNER, J. [See Hemming, 1937, for dates.]
1816
[-1826]. *Verzeichniss bekannter Schmettlinge* [sic]. Augsburg.
[1824-]
1825
[-1831]. *Zuträge zur Sammlung exotischer Schmetterlinge* 3. Augsburg.
[1833-]
1837. *Zuträge zur Sammlung exotischer Schmetterlinge* 5. Augsburg.
- JOHANSSON, B.
1763. *Centuria Insectorum rariorum, . . . quam . . . praeside . . . C. von Linne . . . submittet B. Johansson*. Upsaliae. [names attributed to Linnaeus; see Hodges, 1971].
- KAYE, W.
1921. A catalogue of the Trinidad Lepidoptera Rhopalocera (butterflies). Mem. Dep. Agric. Trinidad and Tobago, 2: i-xii, 13-163, 1 pl.
- KLOTS, A. B.
1951. *A Field Guide to the Butterflies of North America, east of the Great Plains*. Houghton Mifflin Co. Boston.
- KÖHLER, P.
1923. Fauna argentina. Lepidoptera e collectione Alberto Breyer. I. Teil. Rhopalocera. Systematischer Katalog und Studien, Berichtigungen u. Neubeschreibungen. Z. wiss. Insekten-Biologie 18(12) (Sonderbeilage): 1-34, 3 pl., 6 maps.
- KRUCK, A.
1921. Neue Falterformen von Zentralamerika. Entomol. Rundschau 48: 234-236.
- LECK, C. F.
1973
(1974). Butterflies of St. Croix. J. Res. Lepidopt. 12: 161-162.
- LIMA, A. M. DA COSTA
1967-
1968. *Quarto catalogo dos insetos que vivem nas plantas do Brasil, seus parasitos e predadores. Parte 1-2*. Ministério da Agricultura. Rio de Janeiro. [4 vol.].
- LINNAEUS C.
1758. *Systema Naturae, Ed. X*. L. Salvius. Holmiae. 1.
1767. *Systema Naturae, Ed. XII*. L. Salvius. Holmiae. 1 (2).
- LONGSTAFF, G. B.
1912. *Butterfly-hunting in Many Lands, Notes of a Field Naturalist, . . .*
Longmans, Green and Co. London.
- LUCAS, P. H.
1857. Ordre des lépidoptères, p. 474-750, pl. 14-17. In *Histoire Physique, politique et naturelle de l'île de Cuba*. Sagra, Ramon de la., ed. Arthus Bertrand, ed. Paris.

- MAEKI, K., AND REMINGTON, C. L.
1960.
(1961) Studies of the chromosomes of North American Rhopalocera. 4. Nymphalinae, Charaxiinae and Libytheinae. *J. Lepidopt. Soc.* 14: 179-201.
- MAGNUS, D. B. E.
1963. Sex limited mimicry II — visual selection in the mate choice of butterflies. *Proc. XVI Internat. Congr. Zool. (Washington, D. C.)* 4: 179-183.
- MARTIN, L.
1923. *The Fruhstorfer collection of butterflies. Catalogue of types with general account and list of the more interesting forms.* J. Gastaud. Nice. 8 + 135 + ix p., 9 pl.
- MAZA, R. DE LA
1976. Nueva aberración en *Anartia fatima* Fabr. (Nymphalidae). *Rev. Soc. mexicana Lepidopt.* 2(2):103.
- MERIAN, M. S.
1705. *Metamorphosis insectorum surinamensium* G. Valck. Amsterdam.
- MÖSCHLER, H. B.
1886. Beiträge zur Schmetterlings-Fauna von Jamaica. *Abh. Senckenbergischen Naturf. Ges.* 14(3): 25-84.
- MÜLLER, W.
1886. Südamerikanische Nymphalidenraupen, versuch eines natürlichen Systems der Nymphaliden. *Zool. Jahrb., Zeit. Syst., Geogr. Biol. Tiere* 1: 417-678 + pl. 12-15.
- MUNROE, E. G.
1942. The Caribbean races of *Anartia jatrophae* Johansson (Lepidoptera: Nymphalidae). *Amer. Mus. Novit.* No. 1179. 4 p.
- OBERTHUR, C.
1896. De la variation chez les lépidoptères. *Études d'entomologie* 20: xx + 74 p., 24 pl., 5 fig.
- PETERSON, A.
1962. *Larvae of insects, an introduction to nearctic species, fourth edition. Part I. Lepidoptera and plant-infesting Hymenoptera.* Edwards Bros., Inc., Ann Arbor, Michigan. 315 p.
- PLATT, A. P., AND BROWER, L. P.
1968. Mimetic versus disruptive coloration in intergrading populations of *Limnitis arthemis* and *astyanax* butterflies. *Evolution* 22: 699-718.
- RAWSON, G. W.
1976. Notes on the biology and immature stages of the white peacock butterfly, *Anartia jatrophae guantanamo* (Nymphalidae). *J. Lepidopt. Soc.* 30: 207-210.
- REUTER, E.
1896. Über die Palpen der Rhopaloceren. *Acta Soc. Scient. Fennicae* 22: i-xvi, 577.
- RILEY, N. D.
1975. *A Field Guide to the Butterflies of the West Indies.* Quadrangle (Deme-ter) Press. New York.

SCHATZ, E.

1887. *Exotische Schmetterlinge. II. . . . Die Familien und Gattungen der Tagfalter systematisch und analytisch bearbeitet von Dr. E. Schatz. Nach dem Tode des Verfassers fortgesetzt von J. Röber.* (3): 93–136, pl. 17–26. G. Löwensohn. Fürth (Bayern).

SCHEMSKE, D. W.

1976. Pollinator specificity in *Lantana camara* and *L. trifolia* (Verbenaceae). *Biotropica* 8: 260–264.

SCRIBER, J. M.

1973. Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). *Psyche* 80: 355–373.

SCUDDER, S. H.

1875. Historical sketch of the generic names proposed for butterflies: a contribution to systematic nomenclature. *Proc. Amer. Acad. Arts Sci. (Boston)* 10: 91–293.

1893. The tropical faunal element of our southern Nymphalidae systematically treated. *Proc. Amer. Acad. Arts Sci. (Boston)* 27: 237–251.

SEITZ, A.

1914. *The Macrolepidoptera of the World. (The American Rhopalocera)* 5: 462–463 + pl. 94.

SEPP, J. AND SON

1852–

1855. *Surinaamsche vinders naar het leven geteekend/Papillons de Surinam dessinés d'après nature.* Vol. 3. J. Sepp and Son. Amsterdam.

SHEPPARD, P. M., AND BISHOP, J. A.

1973. The study of populations of Lepidoptera by capture-recapture methods. *J. Res. Lepidopt.* 12: 135–144.

SILBERGLIED, R. E.

1976. Visualization and recording of longwave ultraviolet reflection from natural objects. *Funct. Photogr.* 11(2): 20–29, 11(3): 30–33.

1977. Communication in the Lepidoptera. pp. 362–402, in *How Animals Communicate*, T. A. Sebeok, ed. Indiana Univ. Press. Bloomington.

SILBERGLIED, R. E., AIELLO, A., AND WINDSOR, D. M.

1980. "Disruptive" coloration in butterflies: lack of support in *Anartia fatima*. *Science, in press.*

SILVA, B. R. DA

1907. *Lepidopteros do Brasil, contribuição para a historia natural.* Imprensa Nacional. Rio de Janeiro.

SKINNER, H.

1889. Two new species of butterflies. *Trans. Amer. Entomol. Soc.* 16: 86–87.

STAUDINGER, O.

1886. *Exotische Schmetterlinge. I. . . . Exotische Tagfalter in systematischer Reihenfolge mit Berücksichtigung neuer Arten von Dr. O. Staudinger unter technischer Mitwirkung von Dr. H. Langhans. I. Band. Beschreibungen.* (13): 103–122. G. Löwensohn. Fürth (Bayern).

- TAYLOR, O. R., JR.
1972. Reproductive isolation in *Colias eurytheme* and *C. philodice*: random vs. non-random mating. *Evolution* 26: 344-356.
1973. A non-genetic "polymorphism" in *Anartia fatima* (Lepidoptera: Nymphalidae). *Evolution* 27: 161-164.
- WASSERTHAL, L. T.
1975. The role of butterfly wings in regulation of body temperature. *J. Insect Physiol.* 21: 1921-1930.
- WESLEY, D. J., AND EMMEL, T. C.
1975. The chromosomes of neotropical butterflies from Trinidad and Tobago. *Biotropica* 7: 24-31.
- WOLCOTT, G. N.
1948
(1951). The insects of Puerto Rico. *J. Agric., Univ. Puerto Rico* 32: 417-748.
- YOUNG, A. M.
1972. Breeding success and survivorship in some tropical butterflies. *Oikos* 23: 318-326.
1979. Aggregative behavior of *Anartia fatima* (Nymphalidae) in Guanacaste Province, Costa Rica during the dry season. *J. Lepidopt. Soc.* 33: 58-60.
- YOUNG, A. M., AND MUYSHONDT, A.
1973. Ecological studies of the butterfly *Victorina stelenes* (Lepidoptera: Nymphalidae) in Costa Rica and El Salvador. *Stud. Neotrop. Fauna* 8: 155-176.
- YOUNG, A. M., AND STEIN, D.
1976. Studies on the evolutionary biology of the neotropical butterfly *Anartia fatima* in Costa Rica. *Contr. Biol. Geol. Milwaukee Publ. Mus.* No. 8, March 29, 1976. 29 p. + col. frontispiece.
- ZIKAN, J. F.
1937. Neue Nymphaliden-Arten und -Formen aus Brasilien. *Entomol. Rundschau* 54: 385-387.

LOWER PERMIAN INSECTS FROM OKLAHOMA
PART 2. ORDERS EPHEMEROPTERA
AND PALAEODICTYOPTERA*

BY FRANK M. CARPENTER
Museum of Comparative Zoology
Harvard University, Cambridge, Mass. 02138

Nature is always on the watch for our follies and trips us up when we strut.—R. W. Emerson

The discovery and exploration of the insect-bearing deposit in the Midco member of the Wellington Formation were made by Dr. Gilbert Raasch and me about forty years ago, just before the beginning of the Second World War. Preparation and publication of my first paper on the insects were necessarily deferred until after the war (Carpenter, 1947). By that time I had become convinced of the necessity of my studying in detail as many as possible of the Palaeozoic insects already described from European and North American deposits before continuing with the new material. Having spent several months before the war with the Commeny specimens in the Laboratoire de Palaeontologie in Paris and at least as much time on type specimens in museums in the United States, I had come to realize that many of the published figures and descriptions were unreliable and that most of the fossils had never been properly prepared for study, the body structures usually remaining hidden within the rock matrix. In part because of administrative duties at Harvard University after the war and in part because of the political conditions in Europe during the 1950's, I found it impossible to resume the study of such collections, especially in Paris and Moscow, until 1961. Since then I have been able to study the greater part of the more important collections and to publish on some of them, as time and occasion have permitted.

It now seems feasible for me to continue with the series of articles on the insects in the Midco beds. The collection at the Museum of

*Partial financial support of this research is gratefully acknowledged to the National Science Foundation, Grant no. DEB-09947, F. M. Carpenter, Principal Investigator. I am also indebted to the authorities of the Peabody Museum, Yale University, for the loan of type specimens.

Manuscript received by the editor October 15, 1979

Comparative Zoology contains about 8,000 specimens from that deposit. Most of them were obtained on the 1940 expedition but others were found from 1948 to 1957. All were collected at the localities listed in Part 1 of this series of papers (Carpenter, 1947).

Several years after the publication of that part, Dr. Paul Tasch of the Department of Geology, University of Wichita, Kansas, made several collections of fossils in extensions of the Midco beds or in associated deposits, mainly for the purpose of obtaining *Conchostraca*, in which he was especially interested; and with an associate, Dr. J. R. Zimmerman, he published a brief account of some of the insects found there (Tasch & Zimmerman, 1962). I am indebted to Dr. Tasch for placing at my disposal certain of the types in his collection, as well as some unstudied specimens.

The previous part of this series of papers dealt with the palaeopterous orders Megasecoptera, Diaphanopteroidea [included as a suborder of Megasecoptera], Protodonata, and Odonata. The present paper covers the remainder of the palaeopterous orders, the Ephemeroptera and Palaeodictyoptera.

Order Ephemeroptera

Three families of mayflies are known from Permian deposits: *Protereismatidae*, *Misthodotidae* (including *Eudoteridae*) and *Palingeniopsidae*.¹

The first two of these families are well represented in the Midco beds. Adult mayflies, however, are not nearly as abundant in the Midco deposit as at Elmo, in Kansas. Over a hundred adults have been found in the Elmo beds in collections including about 8,000 specimens; only 26 adults have been found in the Midco beds in an approximately comparable collection. On the other hand, nymphs of mayflies, which are virtually absent at Elmo, are exceedingly abundant in the Midco beds.

Family *Protereismatidae* Sellards

Protereismephemeridae Sellards, 1907:345.

Protereismatidae Handlirsch, 1919:63

Protereismatidae Tillyard, 1932:237; Carpenter, 1933:489

Kukalovidae Demoulin, 1970:6 (new synonymy)

¹I consider this to be a distinct family, not synonymous with *Mesephemeridae*.

ADULTS

As now known the protereismatid adults ranged from moderate to large in size. The wings were elongate-oval, without maculations, the hind wings were similar to the fore pair in form and venation, and were only slightly shorter; the costal margin was serrate and prominent setae were present on at least some of the veins; the costal brace was very well developed in both pairs of wings; MA, almost immediately after its origin, coalesced for a short distance with the basal part of RS; RS had three complete triads, and both MP and CUA had a single triad; cross veins were very numerous. The antennae, although short, were relatively longer than in existing mayflies;

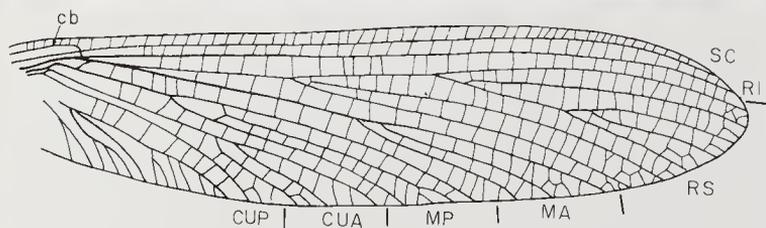
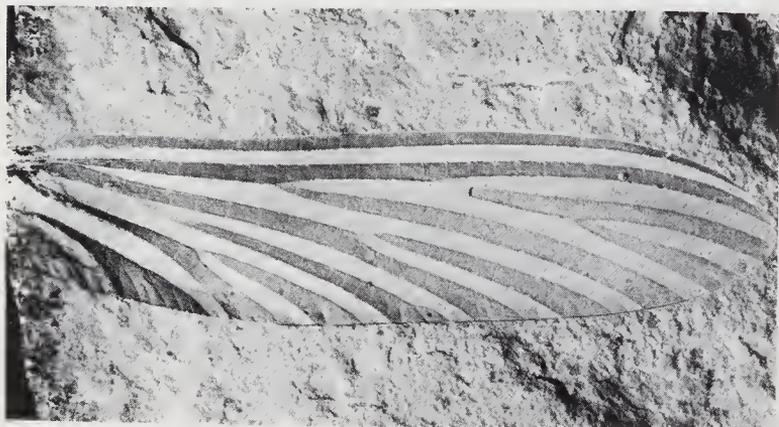


Figure 1 (above). *Protereisma directum*, n.sp. Photograph of holotype (fore wing), MCZ 5180a, Permian of Oklahoma. Length of wing, 26 mm.

Figure 2 (below). *Protereisma directum*, n.sp. Drawing of fore wing (holotype). SC, subcosta; RI, radius; RS, radial sector; MA, anterior media; MP, posterior media; CUA, anterior cubitus; CUP, posterior cubitus; cb, costal brace. The convexities and concavities of the veins are shown in figure 1.

sclerotized, dentate mandibles were present; the compound eyes were large; all legs were very long and slender, with five tarsal segments; the cerci and the median caudal filament were elongate, and the males possessed prominent claspers.

This family, known only from the Permian, was originally described from the Elmo beds. It is represented in the Midco collection by 18 specimens of adults, as well as by numerous nymphs. All of the Midco specimens belong to the genus *Prottereisma* and most of them to the large and striking species described below.

Genus *Prottereisma* Sellards

Prottereisma Sellards, 1907:347 [For generic synonymy see Tillyard, 1932, and Carpenter, 1933]

This genus, the only one at present in the family, is known by five species from Elmo. The insect described by Guthörl (1965) as *Prottereisma rossenrayensis*, from an Upper Permian deposit near Rheinberg, West Germany, is almost certainly a prottereismatid, but the published description is not sufficient for generic determination. Two other species, generally referred to as *Prottereisma uralicum* Zalesky (1946) (upper part of Lower Permian) and *P. apicale* (Martynov, 1927) (Upper Permian), both from the Soviet Union, are based on wing fragments that lack parts necessary for family determination. At the present time, therefore, the genus *Prottereisma* is definitely known only from the Lower Permian of Kansas and Oklahoma.

Prottereisma directum, n.sp.

Figures 1-4

Fore wing: length 26 mm, width, 6 mm; relatively long and narrow, the front and hind margins nearly straight; the venation, typical of *Prottereisma*, is shown in figure 2. Holotype: no. 5180ab, collected at locality 15-L, Noble County, Oklahoma, by F. M. Carpenter. This is a complete fore wing, with excellent preservation.

The two following specimens are designated as paratypes: no. 5182ab, consisting of the four wings and parts of the body. The fore wing is 31 mm long and 7 mm wide; the hind wing, 28 mm long and 6 mm wide. The body is preserved in dorso-ventral view; the head is 2 mm long and 4 mm wide across the eyes; the prothorax is 1.2 mm long and 4 mm wide; the mesothorax is 3 mm long and 4 mm wide;

the metathorax, 2.5 mm long and 4 mm wide. The abdomen (incomplete) is 25 mm long and 2 mm wide. The other paratype, no. 5181, consists of two fore wings and one hind wing; the fore wings are 28 mm long and 6.5 mm wide; the hind wing, 26 mm long and 6 mm wide.

In addition, there are 11 other specimens apparently belonging to this species, all isolated wings.

The wings of this insect differed from those of other *Protereisma* by their large size, slender form, nearly straight anterior and posterior margins and the longer costal brace. The species was only slightly larger than *P. insigne* Tillyard, from Elmo, but the latter had a much broader wing, with a strongly curved posterior margin. *P. directum* presumably had a wing spread as great as 70 mm, which is larger than that of most existing mayflies but much smaller than the Jurassic *Ephemeropsis tristalis*, which had a wing spread of about 90 mm.

Specimen no. MCZ 5182 is of special interest because of the excellent preservation of some parts of the body. The thorax, although somewhat crushed, shows the individual tergites very clearly (figure 4). Previously described specimens of *Protereisma* from Elmo have shown that the metanotum, although smaller than the mesonotum, was very much larger than it is in existing mayflies; this is shown in the accompanying photograph of *directum*. The pronotum consisted of a broad plate 1.2 mm long and 4 mm wide, about the same width as the mesonotum.

The serrations along the costal margins of the fore and hind wings of *Protereisma* were described by Tillyard in 1932. They are clearly visible on the specimens from Midco, especially those of *directum*. Tillyard was apparently not aware that the serrations were equally well developed or even more strongly developed on the hind margins of the wings of *Protereisma*. They are especially well preserved in the neotype of *Protereisma latum* Sellards, from Elmo (specimen MCZ 3419), and I take this opportunity to include two photographs (figure 5) of that specimen here, one showing the serrations along the costal margin and the other, those along the hind margin. The former also shows the setal bases on some of the veins. The serrated margins and setae on the veins are unknown in existing Ephemeroptera, but they were well developed in the extinct Palaeozoic orders Palaeodictyoptera, Megasecoptera, Diaphanopteroidea, and Pro-

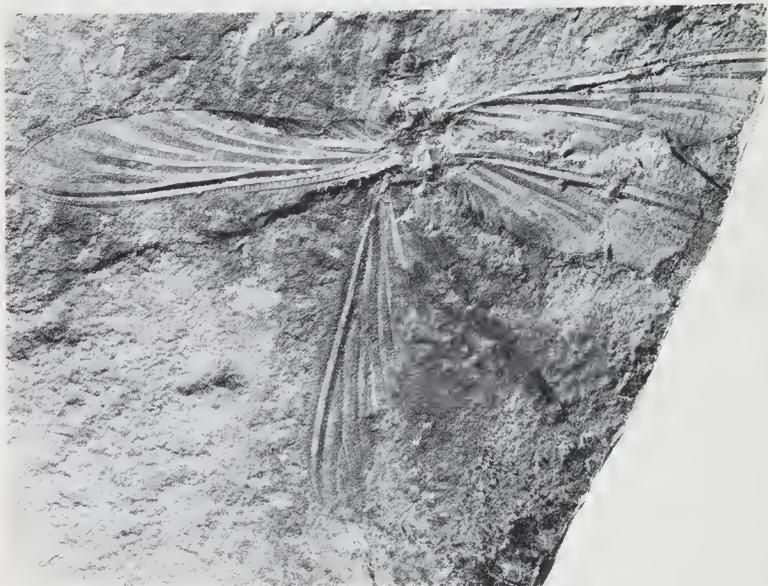


Figure 3. *Protoreisma directum*, n.sp. Photograph of paratype, MCZ 5182a, Permian of Oklahoma. Length of fore wing, 32 mm.

tondonata. Serrated anterior margins are present in the existing Odonata and occur in isolated families of some other Recent orders, but their functional significance is not understood.²

In addition to the specimens of *directum*, there are several other isolated wings belonging to *Protoreisma*. One of these (MCZ 5185ab) appears to be a large specimen of *P. arcuatum* Sellards, described from Elmo. Six other specimens are clearly *Protoreisma* but are too incomplete for specific determination. Zimmerman (Tasch and Zimmerman, 1962) has figured a specimen of a mayfly from a deposit a few feet above the Midco insect bed in which the MCZ specimens were collected. I have not seen that specimen, which he identifies as *P. latum* Sellards. It might be that species, but if the costal brace is formed as shown in his figure, the insect could not even be assigned to the Protoreismatidae.

²In some existing insects the serrate margins appear to have a function in aggressive behavior. See Owen's account of the butterfly genus *Charaxes* (1961).

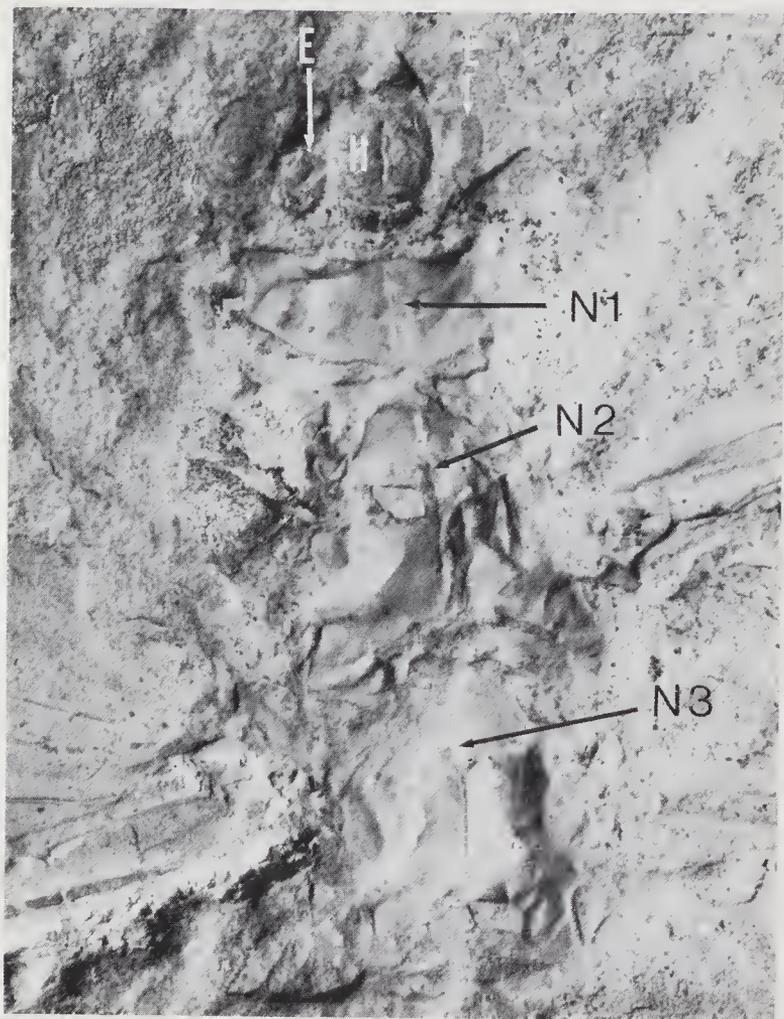


Figure 4. *Protoreisma directum*, n. sp. Photograph of head and thoracic region of paratype, MCZ 5182a, showing eyes (E), head proper (H), pronotum (N1), mesonotum (N2), and metanotum (N3). The left fore wing is preserved with its posterior margin directed anteriorly, as shown in figure 3. The dark circular object to the left of the head is a shell of a conchostracan.

Family Protereismatidae

NYMPHS

In 1968 Dr. Jarmila Kukalova, while making an extended visit to my laboratory at Harvard University, brought from Czechslovakia several fossil mayfly nymphs that she had collected in Permian beds in Moravia. Since only a very few, poorly preserved Palaeozoic mayfly nymphs were known at that time, I suggested that she might also study, along with her specimens from Moravia, some well-preserved specimens that I had collected in the Midco beds in 1940. However, since I had not yet published on or even studied carefully the mayfly adults in that deposit, I requested that the specimens be mentioned by numbers, instead of by new generic or specific names. The reason for that request, of course, was that the systematic position of the nymphs should be investigated in conjunction with similar studies of the adults in the same deposit. Accordingly, in Dr. Kukalova's published account (1969) of these nymphs, the fossils were identified as nymphs no. 1, no. 2, etc., of *Protereisma* sp., the generic assignment being probable but not certain.

However, my efforts to defer the naming of the Midco nymphs until the adult mayflies had been studied were defeated by Demoulin with his publication in 1969 of a paper entitled, "Remarques critiques sur des larves 'Ephemeromorpha' du Permien." In this publication Demoulin, without of course seeing any of the specimens, formally erected the new genus *Kukalova* and the new family *Kukalovidae* to receive the Midco species, which he named *americana* (type-species), and one of the Moravian species, *moravica*. The diagnoses were based on his interpretation of Kukalova's account. He also erected the new genus *Jarmila* for another of the Moravian nymphs, termed *elongata*, placing it in the new family *Jarmilidae*. The two new families were assigned to the extinct order *Archodonata*, and he established a new superorder, *Ephemeromorpha*, to include the *Ephemeroptera* and the *Archodonata*. Had Demoulin communicated his intentions to Dr. Kukalova or to me, we could have corrected his misconceptions of both the nymphs and the *Archodonata* and thus have prevented the publication of what certainly must be one of the most futile articles in all the literature on fossil insects. That the nymphs from the Midco beds are in fact members of the genus *Protereisma* will become obvious from the following account. Since the Moravian specimens are not available to me, I am unable to comment on them except by inference.

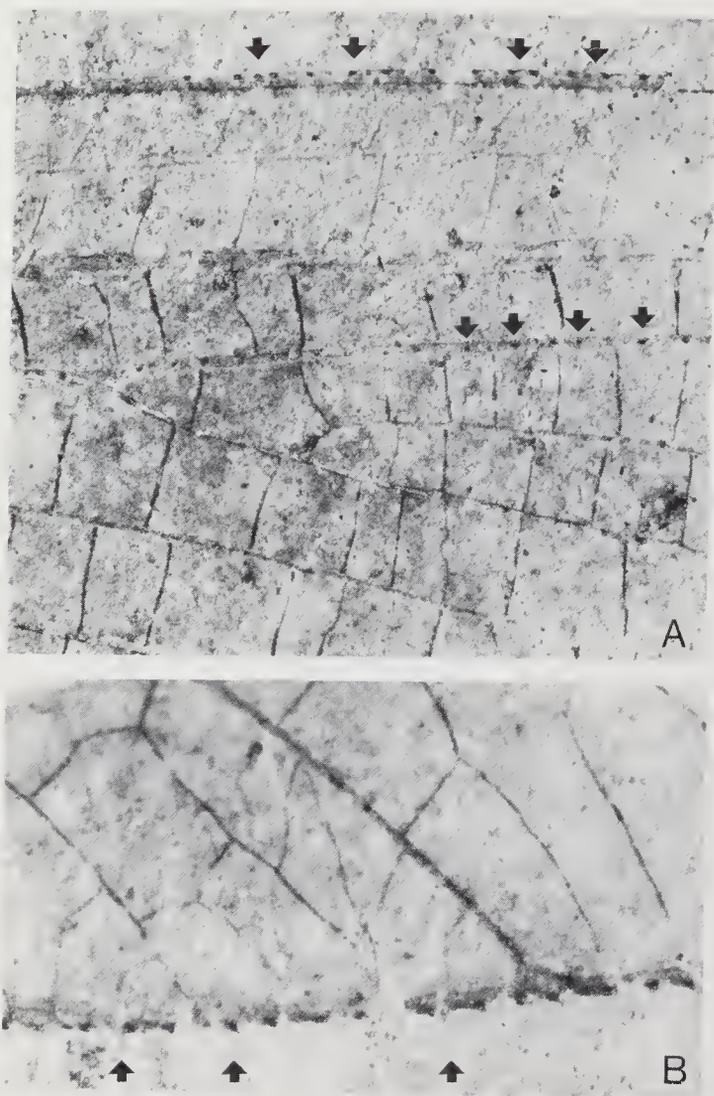


Figure 5. *Protoreisma latum* Sellards. Photographs of neotype, MCZ 3419a, from Permian of Kansas, showing A, anterior part of hind wing, the arrows pointing to setal bases along the front margin of the wing and on certain veins ($\times 24$); B, posterior part of same wing, the arrows pointing to the serrated hind margin ($\times 38$).

Specimens of the mayfly nymphs are by far the most numerous of all the insects in the Midco deposit. Several hundred were collected on my 1940 trip, when Dr. Raasch and I made the first exploration of the deposit, and as many again were collected on subsequent trips. Double that number were simply discarded in the field. Because of their number and the nature of their preservation, it is virtually certain that these fossils are the cuticular remains shed by the nymphs at molting. More than 90% of the specimens consist of isolated wing-pads from the nymphs and most of the remainder represent a single thoracic segment with two wing-pads attached. Only a very few consist of the entire nymph, with all wing-pads and many body structures, these being the specimens that I turned over to Dr. Kukalova in 1969. Since she has given a detailed account of these specimens, I will include here only the salient features, with special reference to the venation of the wing-pads.

The head of the nymphs was slightly narrower than the prothorax, and had well developed, dentate mandibles; the antennae were slender; the prothorax about half as long as the mesothorax, and the meso- and metathorax nearly equal; the legs were subequal, with five tarsal segments; abdominal segments subequal, the cerci and caudal filament well-developed; nine pairs of tracheal gills were present on the abdomen, the anterior ones somewhat larger than the others.

The wing-pads were well developed but were attached to the thorax only along the articular area (of the adult wing), and were independent of each other; the pads projected posteriorly at an oblique angle to the longitudinal axis of the body. The venation of the wing-pads was described by Kukalova, but unfortunately her figure (1969, figure 2) and her interpretation of the homologies of the veins were incorrect. The most conspicuous feature of the venational pattern of the nymphal wings is the difference in the apparent degree of development of the convex and concave veins. In the wing of an adult mayfly (figure 8), the *convex* veins include, in addition to the main veins R1, MA, and CUA, the intercalary veins of the radial sector and of the posterior media; the *concave* veins include, in addition to the main veins RS, MP, and CUP, the intercalary veins of the anterior media and the anterior cubitus. In the Midco nymphs (figure 9) all of the convex veins are very strong and distinct but all of the concave veins are weak and indistinct. Comparison of the nymphal wing with the adult wing of *Protereisma* (figure 8) shows

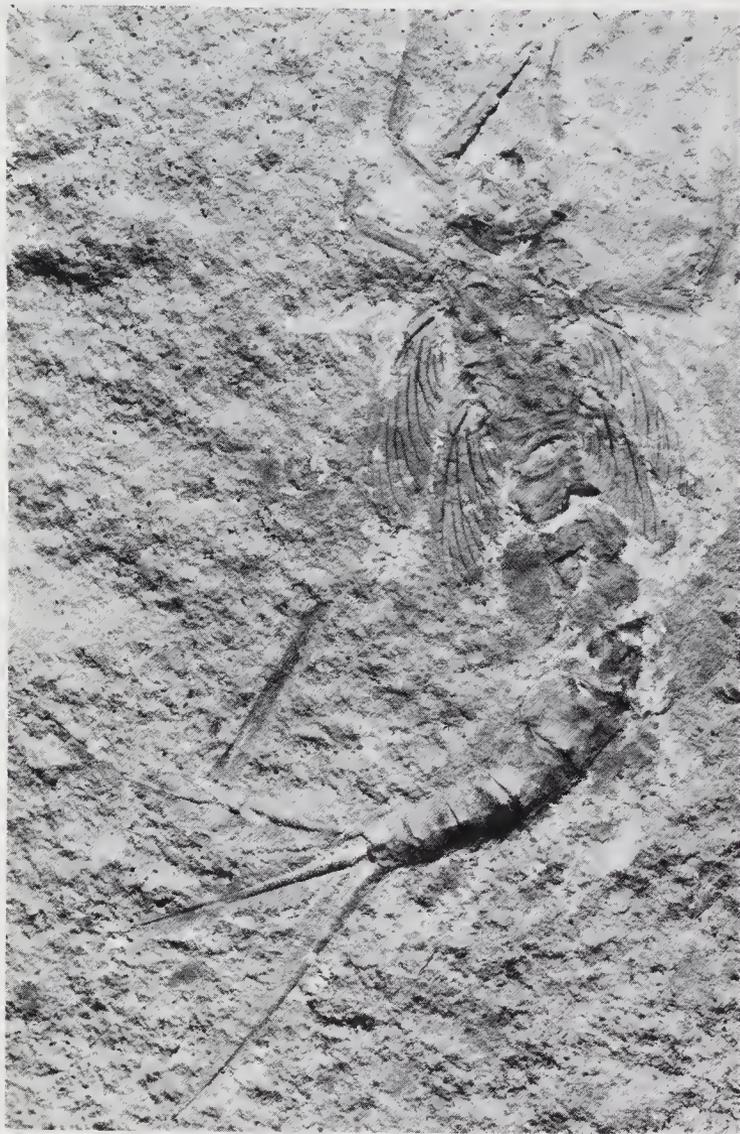


Figure 6. *Protoreisma americanum* (Demoulin), nymph. Photograph of holotype, MCZ 6311, Permian of Oklahoma. Length of body, 16 mm.



Figure 7. *Protoreisma americana* (Demoulin). Photograph of fore and hind wing-pads of holotype. The dark veins are convex, the weak ones (hardly visible) are concave. Length of fore wing-pad, 5.5 mm.

the precise correspondence of the heavy (convex) veins of the nymphal wing pad with the convex veins of the adult wing, including the intercalary veins of the radial sector and the posterior media. Kukalova, in her interpretation of the nymphal wings, apparently assumed that all of the heavy veins were the main veins and that all of the weak veins were the intercalary veins. As a result, the true MA was included in her radial sector, the true MP was termed MA, CUA was termed MP, and 1A was termed CUP, etc. In figure 9 I include a drawing of the front wing-pad of a nymph (MCZ 8637) with the correct interpretation of the venation. A photograph of the fore and hind wing-pads of the holotype of *americana* is in figure 7.

It is at once obvious from the venation that these nymphs do indeed belong to the genus *Protoreisma*. The presence of the deep fork and triad on CUA eliminates them from the Misthodotidae, for reasons shown below. Demoulin, in removing the nymphs from the Ephemeroptera, was clearly misled by Kukalova's account of their venation but his assignment of them to the order Archodonata was indefensible. The Archodonata had haustellate mouthparts, whereas the nymphs had well developed mandibles. Also, the Archodonata lacked the costal brace, as well as the system of triads and intercalary veins, so well developed in the nymphs.³

³In my opinion the Archodonata are members of the order Palaeodictyoptera.

The family name Kukalovidae Demoulin is consequently a synonym of Protereismatidae and the generic name *Kukalova* is a synonym of *Protereisma*. However, since there are adults of several species of *Protereisma* known in the Midco beds, and since there is no way of correlating the nymphs specifically with the adults, a different specific name is needed for the nymphs from the Midco beds. For this, of course, the name *americana* must be used. I can make no definite comment about the systematic position and nomenclature for the Moravian nymphs described by Kukalova and named by Demoulin. Examination of the original nymphs would be necessary to clear up the uncertainties of the venation. However, on the basis of Kukalova's figure, I think it unlikely that the nymph which Demoulin named *Kukalova moravica* is a protereismatid.

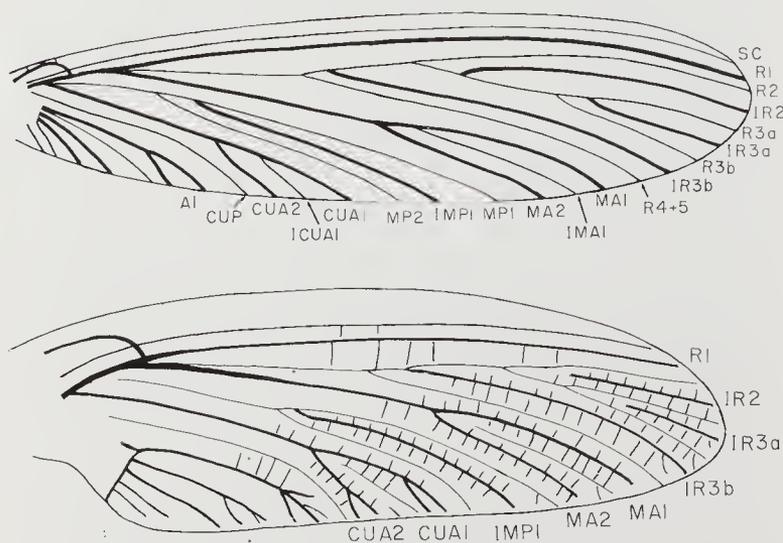


Figure 8. (above) *Protereisma permianum* Sellards. Diagram of venation of fore wing of neotype, MCZ 3405, Permian of Kansas. Convex veins are shown in heavy lines, concave veins in thin lines. Compare with figure 9. Lettering as in figure 2. A1, first anal vein; IR2, IR3, IMA, IMP, and ICUA, intercalary veins.

Figure 9. (below) *Protereisma americanum* (Demoulin). Drawing of fore wing-pad, based mainly on MCZ 8637. Length of wing-pad, 5 mm. Compare with figures 8 and 10. Lettering as in figure 8, but only convex veins labeled.

Protereisma americana (Demoulin)

Figures 6, 7, 9 and 10

Kukulova americana Demoulin, 1970:6

The holotype specimen is numbered 6311ab, Museum of Comparative Zoology; collected by F. M. Carpenter, locality 15-L, Midco insect bed, Noble County, Oklahoma, in 1940 [type designated by Demoulin by reference to plate 29 and figure 1 in Kukulova, 1969]. This specimen, undoubtedly consisting of the cast cuticle of a nymph, shows the general body structure as well as the four wing-pads. Its dimensions are as follows: fore wing-pad, 5.5 mm long, 1.5 mm wide; hind wing, 4.5 mm long, 1.3 mm wide. The body is 16 mm long, exclusive of the terminal appendages and antennae. A detailed description of this nymph is given in Dr. Kukulova's paper and a photograph of the specimen is included here for convenience of reference (figure 6). This is the best and oldest of the mayfly nymphs that have been found in any Palaeozoic deposit. In addition to the type, there are four other specimens (MCZ 8641-8644) showing the gills and other characteristic features; all are about 10 mm long, much smaller than the type, and their wing-pads are very small or absent. As noted above, isolated wing-pads are very numerous in the Midco beds. All have the basic pattern of *P. americana* but of course they may represent more than one species. The smallest (MCZ 8638) of these pads is 2.8 mm long and 1 mm wide (figure 10A); this shows the venational pattern clearly as well as the convexity and concavity of the veins. The largest pad (MCZ 8636) is 7 mm long and 2.2 mm wide; the cross veins and concave veins are more distinct than in the others (figure 10D). Most of the wing-pads are 5.5 mm long and about 1.7 mm wide (figures 10B, 10C).

There are two aspects of these wing-pads, briefly noted above, that are of unusual interest. One is the distinct fluting of the pads, even small ones, resulting from the convexity and concavity of the developing veins. The fluting seems to be much more pronounced in

Figure 10. *Protereisma americanum* (Demoulin). Photographs of wing-pads in several stages of development. A, smallest wing-pad found, 2.8 mm long, 1 mm wide, showing definite convexities and concavities; MCZ 8638, Permian of Oklahoma. Lettering as in figure 9. B, wing-pad 5 mm long, seen under oblique lighting; MCZ 8639. C, same specimen as shown in B but with flat lighting, showing the intensity of the convex veins. D, largest wing-pad found, 7 mm long, the concave veins somewhat more distinct; MCZ 8636, Permian of Oklahoma.



Figure 10

the fossil nymphs than in existing ones. It is possible that the greater amount of fluting, which presumably strengthened the wing-pad, may have been correlated with the limited attachment of the pad to the thorax. In this connection it is pertinent to note that wing-pads of the nymphs of the Palaeodictyoptera and Megasecoptera, which also had the limited attachment to the thorax, show a strong fluting.

A second feature of interest is the marked difference in the fossil nymphs between the convex and concave veins. The convex veins are preserved as dark brown, thick lines, whereas the concave veins are almost without pigment and appear as fine lines. Even the cross veins (see figure 7) are more obvious than the concave veins. If our inference is correct that these wing-pads represent the cast cuticle of the nymphs, then the dark lines seem to have been pigmented thickenings on the cuticle that was cast off in molting. I have no explanation for the difference in appearance of the convex and concave veins. The pattern of difference is the same in both obverse and reverse halves of the fossils. This eliminates the possible inference that the pattern might have been different on the dorsal as opposed to the ventral surface of the wing-pads.

Family Misthodotidae Tillyard

Misthodotidae Tillyard, 1932: 260

Eudoteridae Demoulin, 1954: 561. New synonymy.

The misthodotid adults were of moderate size and generally much smaller than the protereismatids. The wings were broadly oval, usually with maculations, and the hind wings were similar to the fore wings in form and venation, but distinctly broader and with a strongly curved posterior margin. The costal margin was serrate (at least in *Misthodotes*). The costal brace, although distinct, was weaker than in the Protereismatidae. The venation was basically like that of the protereismatids, except that CUA was unbranched and therefore lacked the triad. Cross veins were somewhat less numerous than in the protereismatids. The body structure is not well known. The antennae were like those of the protereismatids and the mandibles were similarly developed. The legs, however, were apparently much shorter and apparently heteronomous, the fore legs being shorter than the others. The tarsi included four segments (at least in *Misthodotes*), the 2nd and 3rd being the shortest. The cerci and median caudal filament were very long.⁴

This family was originally described from the Elmo beds in Kansas. Tschernova (1965) has described adults of two species of *Mis-*

thodotes (*zalesskyi* and *sharovi*) from the Permian of Chekarda in the Soviet Union.⁵ These adults appear to be typical of the family except for the tarsal structure, as noted below. Kinzebach (1970) has published an account of a supposed mayfly from the Permian of Germany and has placed it with some question in the family Misthodotidae. Since the wing venation is not preserved, there is no evidence that the specimen belongs to the Ephemeroptera. If it does, the long, slender legs would be more suggestive of the Protereismatidae than the Misthodotidae.

The nymphs of the Misthodotidae are not definitely known. Tschernova (1965) has described a fragment of a nymph from the Chekarda beds and identified it as belonging to *Misthodotes sharovi*. The nymph has nine pairs of gill plates, as in the protereismatid nymphs, but since the entire thoracic region, including the wing pads, is not preserved, there is really no evidence for associating the specimen with *Misthodotes* or even with its family.

There are several adult specimens of Misthodotidae in the MCZ collection from the Midco beds, all belonging to the genus *Misthodotes*. Study of this material and reexamination of the Elmo species have indicated that some revision of the diagnosis of the genus is necessary.

Genus *Misthodotes* Sellards

Dromeus Sellards, 1907: 351 (nec *Dromeus* Reiche) Type species, by monotypy, *D. obtusus* Sellards.

Misthodotes Sellards, 1909: 151. Tillyard, 1932: 261; Carpenter, 1939: 63.

Eudoter Tillyard, 1936: 443. New synonymy.

⁴In one Elmo specimen of *M. obtusus* (MCZ 4388ab) the cerci and the caudal filament, apparently complete, are 20 mm long, or about two and one-half times the length of the abdomen. The full length of the cerci or the caudal filament is unknown in *Protereisma*.

⁵However, Tschernova's account of these fossils is very confusing: the labeling of the veins in the drawings of the wings is different from the terminology used in the descriptions. In her discussion of the venation she states that CUA is either unbranched (i.e., simple) or possesses only a short terminal fork, as is characteristic of the genus *Misthodotes* and its family. But in the figures of both species she has shown CUA as consisting of two long branches, labeled CUA1 and CUA2. The convexities and concavities of the veins are not indicated in her figures, but in the Oklahoma and Elmo specimens of *Misthodotes* the long branch that she has labeled CUA2 is concave and is obviously CUP. The two veins that she has labeled CUP1 and CUP2 are of course anal veins.

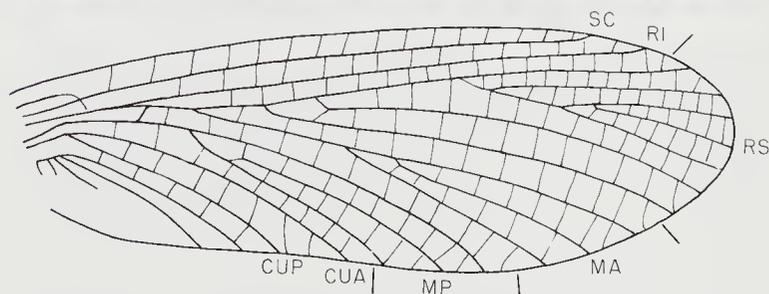
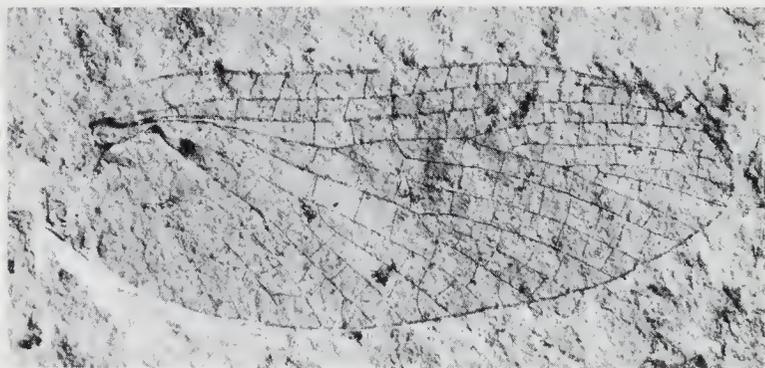


Figure 11 (above). *Misthodotes obtusus*. Sellards. Photograph of hind wing (neotype): YPM 5470, from Permian of Kansas. Length of wing, 10 mm.

Figure 12 (below). *Misthodotes obtusus* Sellards. Drawing of fore wing, based on MCZ 4386ab, from Permian of Kansas. Length of wing, 10 mm. Lettering as in figure 2.

Since the type of *obtusus* was accidentally destroyed in 1927, I subsequently designated (1933) specimen numbered YPM 5470 in the Peabody Museum at Yale University as the neotype of *obtusus*.

The differences between the fore and hind wings of *Misthodotes* and the nature of the cubital-anal area of the wings have not been definitely known. From a survey of all the Elmo specimens in both the Peabody Museum and the MCZ collections, I believe that we can now make a better diagnosis of the genus than has previously been possible and it seems advisable to summarize that before continuing with the account of the Midco specimens.

The best specimen of the fore wing of *obtusus* from Elmo is MCZ 4386, which shows the complete venation, except for the cubital-anal region (figure 12). It should be noted that the costal area near

the wing base does not gradually narrow but ends abruptly. The best specimen of the hind wing is YPM 5470 (figure 11), a drawing of which was given by Tillyard (1934). However, in his figure the costal area is shown as gradually tapering in the region of the costal brace. Although Tillyard stated in his description that the costal vein was obsolescent near the base, on examining the specimen I found that the base of the costa was only covered by a small piece of the rock matrix. On removing that I found that the costal area at the base was in fact like that of the fore wing, not gradually but abruptly narrowed. This is significant because one of the Midco species does have the costal margin gradually narrowed. In the same figure Tillyard included the veins of the cubital-anal area, although I find that there are only vague suggestions of them in the specimen. This area is not clear in any of the Elmo specimens of *obtusus*, either, but it is well preserved in one of the Midco specimens of *Misthodotes ovalis*, mentioned below.

The body structure is not so well known for *Misthodotes* as it is for *Protereisma*. One of the Elmo specimens of *obtusus* in the Peabody Museum (YPM 1100) does show some details. In his description of this specimen Tillyard stated that the tarsi were entirely missing. However, one hind tarsus has now been completely exposed by removal of some of the rock matrix, and its structure

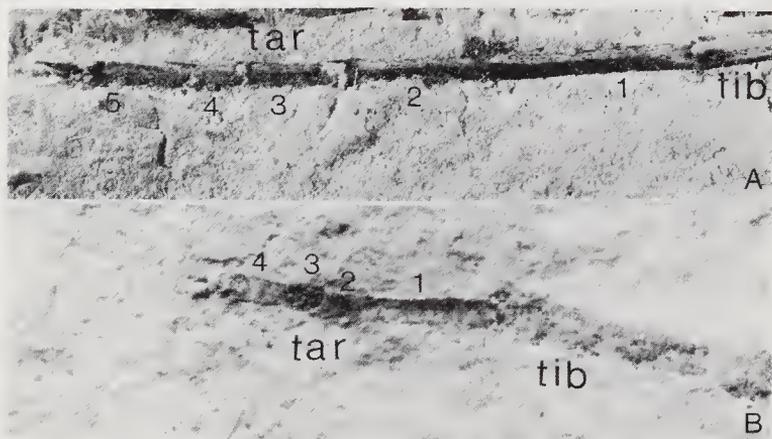


Figure 13. Photographs of tarsi of Protereismatidae and Misthodotidae: A, *Protereisma permianum*, MCZ 3402, Permian of Kansas. Length of tarsus, 8 mm. B, *Misthodotes obtusus*, MCZ 3402, Permian of Kansas. Length of tarsus, 1.5 mm. TIB, tibia; TAR, tarsus.

turns out to be like that which I described in one of the MCZ specimens (Carpenter, 1939): relatively short and consisting of only four segments, the middle two being much shorter than the others (figure 13). This is in marked contrast to the protereismatid tarsi, which were very long and included five segments, the first being the longest and the others subequal.

In this connection it should be noted that Tschernova has described (1965) the tarsal structure of a specimen of a mayfly from the Permian of Chekarda. The species (*sharovi*) was placed in the genus *Misthodotes* and its venation, as noted above, appears to be typical of that of the Misthodotidae. However, the tarsal segmentation is apparently different from that of *M. obtusus*, there being five segments, the fifth being the longest, according to Tschernova's description. Unfortunately, it is not clear from the description whether that segmentation is very distinct or only vaguely preserved. Of course, generic and family definitions are difficult to decide on for the few Permian species of mayflies that are known and it could well be that tarsal segmentation is not significant for the definition of these particular genera or families. However, for the present it seems advisable to consider the assignment of *sharovi* to *Misthodotes* as doubtful.

Of the seven specimens of *Misthodotes* in the Midco collection three belong to the following new species:

***Misthodotes edmundsi*, n.sp.**

Figures 14 and 15

Hind wing: length, 10 mm; maximum width, 3.5 mm. Costal margin straight near mid-wing and curving towards SC well before the midpoint of the costal brace, the costal area gradually tapering towards the base; hind margin smoothly curved, the wing broadest at the level of mid-wing; venation essentially as in *obtusus*; two large, irregular maculations, one at mid-wing, its center about at the fork of R2+3 and R4+5; the other one smaller, just beyond the fork of R2+3. Holotype: No. MCZ 5184ab, collected at locality 15, lower layer, Midco insect bed, Noble Co., Oklahoma, by F. M. Carpenter (1940). This is a perfectly preserved hind wing (figure 14). Paratypes: no. MCZ 5194, a hind wing, complete but not so well preserved as the holotype; length, 10 mm., width, 3.5 mm.; no. MCZ 313ab, a hind wing, complete; length 9 mm.; width, 3 mm.

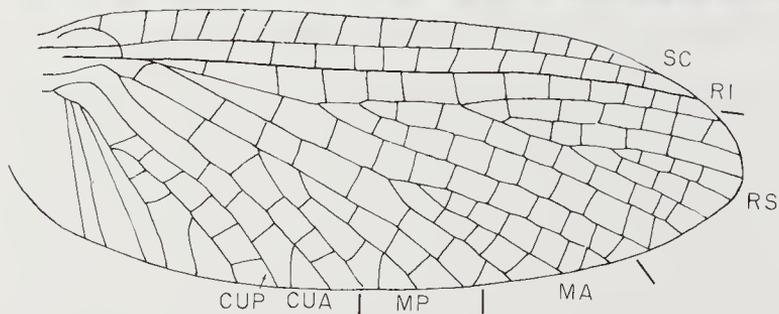


Figure 14 (above). *Misthodotes edmundsi*, n.sp. Photograph of holotype, MCZ 5184 (hind wing). Length of wing, 10 mm. Permian of Oklahoma.

Figure 15 (below). *Misthodotes edmundsi*, n.sp. Drawing of holotype. Lettering as in figure 12. Permian of Oklahoma.

This species is named for Dr. George F. Edmunds, Jr., University of Utah, in recognition of his outstanding contributions to the study of mayflies. The species is close to *obtusus* but differs in the wing shape; in *obtusus* the costal margin is consistently slightly concave, and the costal area remains wide until the very base of the wing; the maximum width of the wing of *obtusus* is nearer the base. Also, the wing of *obtusus* lacks maculations. In addition to wing shape, *edmundsi* differs from *biguttatus* (from Elmo) in having the center maculation much larger and irregular.

Two other specimens from the Midco beds are apparently *Misthodotes ovalis* Tillyard, a species described from Elmo on the basis of a single wing. This is the largest species of *Misthodotes* known;

the wing of the type was 15 mm long and the Midco specimens are fully that size. One of these, a forewing (MCZ 5193) has the cubital-anal area very well preserved and it also shows the large humeral plate at the base of the costal area, as in the holotype specimen of *ovalis*. The two remaining specimens of *Misthodotes* are too incomplete for generic determination.

The Families Eudoteridae and Doteridae

Eudoter delicatulus, described by Tillyard from the Elmo beds (1936), was based on a very poorly preserved specimen. It was placed by him in the family Doteridae Handlirsch (1919), the status of which is discussed below. In 1954 Demoulin proposed the family name Eudoteridae for the genus. He considered it to be close to the Protoreismatidae, from which he thought it differed by its "simplified venation." The type specimen of *delicatulus* (YPM 1014ab), which I have examined on several occasions, consists of part of the body and three folded and badly distorted wings. That the insect is a mayfly is shown by the presence of the median caudal filament between the paired cerci. However, its wing venation, so far as it is preserved, is no more simplified or reduced than that of the Misthodotidae. Indeed, a comparison of Tillyard's drawing of the wing of *delicatulus* (1936, fig. 3) with that of the wing of *Misthodotes* (1932, fig. 20) shows that the *preserved* parts of the wing of *delicatulus* are virtually identical with the corresponding parts of the *Misthodotes* wing. Tshernova (1965), accepting the family Eudoteridae, thought that its cross veins were more poorly developed than in the Misthodotidae. However, in the type of *delicatulus* the cross veins are as abundant and distinct as they are in some specimens of *Misthodotes obtusus*. In his restoration of the wing of *delicatulus* Tillyard represented CUA with a deeply forked triad—but only by broken lines, which he stated in the legend to the figure meant that he was not certain that the triad was present. From my own examination of the specimen under various types of illumination, I am convinced that the veins of the cubital-anal area are simply not preserved, and that there is no indication of the triad on CUA (as Tshernova, 1965, correctly inferred). I am therefore of the opinion that *delicatulus* is a misthodotid and even a member of the genus *Misthodotes*. The species is distinguished by its small size; its wings are only 6 mm long, a little more than half the size of *obtusus*.

The status of the family Doteridae Handlirsch is a more difficult problem. The original specimen of *Doter minor* Sellards (1907) consisted of two folded and twisted wings (both apparently fore wings) and part of the body, including the abdomen (Sellards, 1907, figure 13). When I examined the type in 1926 in Dr. Sellards' laboratory, I was surprised by its poor preservation. As Sellards correctly stated, the median caudal filament was not present and the clear preservation of the two cerci is almost conclusive evidence that the caudal filament was not present in the living insect. Its absence, in even vestigial form, would seem to eliminate the insect from the Ephemeroptera, since it is present in all the specimens of Palaeozoic and Mesozoic mayflies in which the abdomen and cerci are preserved. It is also present, at least in reduced form, in virtually all existing mayflies. The venation of the type specimen of *minor* was so poorly preserved that I would have doubted that the specimen was actually the one described by Sellards, if the abdomen and cerci had not been formed as they were figured by him. The presence of well-developed cerci and the absence of the caudal filament are characteristic of a number of Elmo insects, such as the Asthenohymenidae (Diaphanopteroidea) and Protohymenidae (Megasecoptera). The poorly preserved wings of *minor* did in fact have some resemblance to those of *Asthenohymen* Tillyard, as previously pointed out by Martynov (1930), and in my first account of that genus (1930) I considered *dunbari*, the type of *Asthenohymen*, to be a synonym of *Doter minor*. Since Tillyard did not accept that synonymy and since the type of *Doter minor* had been destroyed by then,⁶ I suggested (1932) that *Doter minor* be regarded as an unrecognized species and that *Asthenohymen dunbari* be accepted as the valid name for the species described by Tillyard. That proposal has subsequently been generally followed, although Demoulin has continued to recognize the family Doteridae as belonging to the Ephemeroptera, regardless of the absence of the median caudal filament. It is highly probable that we may never find a specimen in the Elmo or Midco beds that fits Sellards' description of *minor*. Some 20,000 insects from those two beds have now been examined and none agree with his account of that insect. For this reason I believe that

⁶A few weeks after my return to Cambridge from the University of Texas in 1927, Professor Sellards informed me that during the process of renovating the building in which his laboratory was housed some workmen, thinking that the pieces of the Elmo limestone were fragments of the old walls, threw them out with the general debris.

we should consider *Doter minor* as a species *incerti ordinis* within the Palaeoptera, instead of trying to fit it into the Ephemeroptera.

Order Palaeodictyoptera

The Palaeodictyoptera were apparently already on the wane even by the early Permian. In terms of both species and individuals the members of the order are only sparsely represented in Permian deposits. Only three species of the order have been found in the Elmo beds in Kansas. Two of these, *Calvertiella permiana* Tillyard and *Elmobia piperi* Carpenter, are known only by the holotypes. The third species, *Dunbaria fasciipennis* Tillyard, is represented in the collections of the Museum of Comparative Zoology and the Peabody Museum by ten specimens.⁷ Only one specimen of the order appears to be in our collection from the Midco beds. This is undescribed and is a member of the family Calvertiellidae.

Family Calvertiellidae Martynov

This family includes three species: *Calvertiella permiana*, from the Permian of Kansas, *Moravia convergens* Kukalova (1964), from the Permian of Moravia, and *Carrizoptera arroyo* Kukalova-Peck (1976), from the late Upper Carboniferous of New Mexico. Among the peculiar features of this family is the presence of intercalary veins, which are secondary veins inserted in forks of main veins and which have the opposite topography of the forked veins. They are consistently present in the Protodonata, Odonata, and Ephemeroptera, and occur sporadically in some other orders (e.g., Neuroptera). The presence of intercalary veins in insects that otherwise appeared to be Palaeodictyoptera was first noted in the family Syntonopteridae, which had such veins between the branches of RS, MA, MP, and CUA (Handlirsch, 1911; Carpenter, 1938).⁸ Their occurrence between branches of RS and MP in *Calvertiella* was responsible for Tillyard's placing the genus in the Protodonata. In *Moravia conver-*

⁷Although *Permonera lameerei* Carpenter was originally described as a palaeodictyopteron (1931), it now seems preferable to assign it to the category *incerti ordinis* until more is known about the insect (see Carpenter, 1976).

⁸This has led some students of the Ephemeroptera to conclude that the Syntonopteridae were mayflies, instead of Palaeodictyoptera. This question will probably not be settled until the mouthparts of the syntonopterids are known to be either haustellate as in the Palaeodictyoptera or mandibulate as in the Palaeozoic mayflies.



Figure 16. *Moravia grandis*, n.sp. Photograph of holotype, MCZ 8647a; maximum length of preserved part of wing, 74 mm. Permian of Oklahoma.

gens the intercalary veins were also confined to the branches of RS and MP but were very irregular and formed by alignment of the sides of the two rows of cells bordering the main veins. In *Carrizoptera arroyo* they are so short and irregular as to be hardly recognizable. In the new species, *Moravia grandis*, described below, the radial sector is not preserved, but the intercalary veins are not present between the branches of MA, MP, or CUA, the spaces between the veins being filled with a reticulate archedictyon. The nature of the intercalary veins in the Calvertiellidae, therefore, would seem to suggest that these veins developed in that family quite independently of their occurrence in other orders or families. They appear to have arisen by the alignment of the sides of the cells forming the archedictyon between the main veins. The development of such intercalary veins, in association with the increased fluting along the veins, may have provided more support for the wing membrane than the original archedictyon. In any case, I believe that the presence or absence of the intercalary veins should not be given very much weight in considering evolutionary relationships.

Genus *Moravia* Kukalova

Moravia Kukalova, 1964: 162; Kukalova-Peck & Peck, 1976:83.

This genus is characterized by the presence of an arched cuticular strut, formed by the alignment of the basal parts of R1 and CUA, connected by a strong cross vein. It has previously been known only by the type-species, *convergens*, from the Lower Permian of Obora, Czechoslovakia.

***Moravia grandis*, n.sp.**

Figures 16 and 17A

Hind wing: maximum length of preserved portion, 72 mm; maximum width, 48 mm; estimated length of complete wing, based on *M. convergens*, 90 mm. The basic pattern of the main veins, so far as preserved, is very similar to that of *convergens* (figure 17B). CUA, CUP, and 1A are not so strongly curved as in *convergens* and the spaces between the main veins are filled with several rows of cells forming the archdictyon in the distal portion or by fine, irregular crossveins in the basal portion. This is a very distinct species and may eventually require a separate genus. However, until the distal part of the wing is known, it seems preferable to assign the species to the genus *Moravia*.

Holotype: no. MCZ 8647ab, collected at locality 1, lower layer, in the Midco beds, Noble County, Oklahoma, by F. M. Carpenter in 1940. This consists of the basal two-thirds or three-fourths of a hind wing, with all details very well preserved. The distal part of the wing appears to have been torn away before preservation. This species is by far the largest known in the family Calvertiellidae, being apparently more than twice the size of *convergens* and more than three times the size of *permiana* or *arroyo*.

Comparison of the Species of Palaeoptera in
the Elmo and Midco Beds

In my introduction to Part 1 of this series of papers (1947) I pointed out that the Elmo beds in Kansas and the Midco beds in Oklahoma originated as deposits formed by lakes about 140 miles apart. Both deposits are part of the Wellington Formation of the Leonardian Stage of the Permian and, in geological terms, were

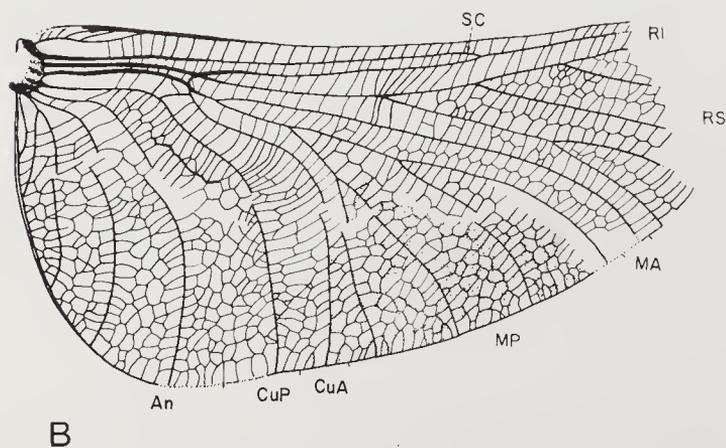
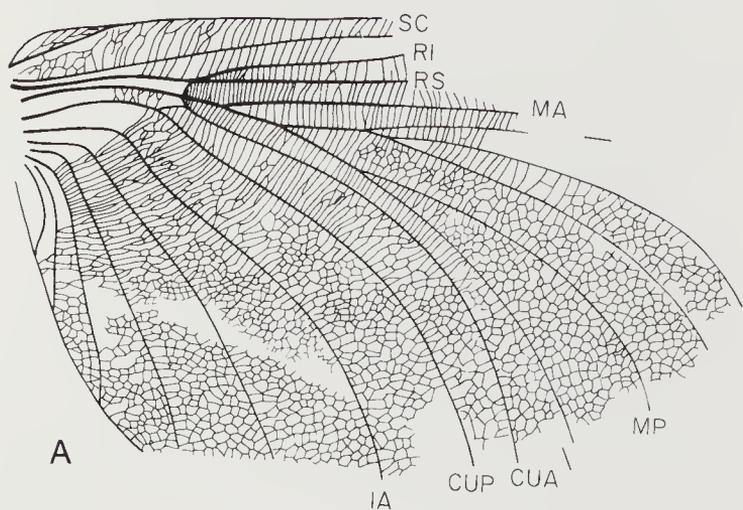


Figure 17A. *Moravia grandis*, n.sp. Drawing of holotype. Lettering as in figure 12. Permian of Oklahoma.

Figure 17B. *Moravia convergens* Kukulova. Drawing of paratype (hind wing). Lower Permian of Moravia. [From Kukulova, 1964].

Table 1 Comparison of Paleopterous Species from Elmo and Midco Beds

ORDERS	NUMBERS OF SPECIES		
	<i>Elmo</i>	<i>Midco</i>	<i>Elmo & Midco</i>
Palaeodictyoptera	3	1	0
Megasecoptera	5	5	1
Diaphanopteroidea	7	14	3
Protodonata	5	3	1
Odonata	4	5	2
Ephemeroptera	8	5	1
	32	33	8

apparently contemporaneous. However, there appear to have been differences in the environments of the lakes (Raasch, 1946). The one in Kansas contained fresh water, derived from an earlier swamp, with plants growing close to the water's edge and with some insect nymphs living in the water. The Midco lake was essentially a playa, containing algae and Conchostraca; plants did not grow near it and insect nymphs did not live in it.⁹

Now that the study of the Palaeoptera in the Midco beds has been completed, it is of some interest to compare the numbers of species represented in each deposit and common to both deposits. These figures are given in the accompanying table (Table 1). The total number of species in each of the beds is very close, and the number of species in each order corresponds closely except for the Diaphanopteroidea, of which there are twice as many in the Midco beds as at Elmo. It appears that, on the average, about one-quarter of the Midco species collected also occur at Elmo.

REFERENCES CITED

- CARPENTER, F. M.
 1930. The Lower Permian insects of Kansas. Part 3. The Protohymenoptera. *Psyche* 37:343-374.
 1932. The Lower Permian insects of Kansas. Part 5. Psocoptera and additions to the Homoptera. *Amer Journ Sci* 24:1-22.
 1933. The Lower Permian insects of Kansas. Part 6. Delopteridae, Protelytroptera, Plectoptera, and a new collection of Protodonata, Odonata, Megasecoptera, Homoptera, and Psocoptera. *Proc Amer Acad Arts Sci* 68:411-503.

⁹The fossil mayfly nymphs discussed above were apparently the cuticular remains shed by the nymphs at moulting and carried down streams to the lake.

1938. Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Amer Journ Sci* 36:445-452.
1939. The Lower Permian insects of Kansas. Part 8. Additional Megaseoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plectoptera, and Protoperlaria. *Proc Amer Acad Arts Sci* 73:29-70.
1947. Lower Permian insects from Oklahoma. Part 1. Introduction and the orders Megaseoptera, Protodonata, and Odonata. *Proc Amer Acad Arts Sci* 76:25-54.
1976. The Lower Permian insects of Kansas. Part 12. Protorthoptera (continued), Neuroptera, additional Palaeodictyoptera, and families of uncertain position. *Psyche* 83:336-378.
- DEMOULIN, G.
1954. Essai sur quelques Éphéméroptères fossiles adultes. Vol Jubil Vict Van Straelen 1:549-574. Bruxelles.
1970. Remarques critiques sur des larves "Ephemeromorphes" du Permien. *Bull Inst R Sci Nat Belg* 46 (3): 1-10.
- GUTHÖRL, P.
1965. Zur Arthropoden-Fauna des Karbons und Perms. 21. *Protereisma rossenrayensis*-Fund (Insecta) aus dem niederrheinischen Zechstein. *Paläont Zeitschr* 39:229-233.
- HANDLIRSCH, A.
1911. New Palaeozoic insects from the vicinity of Mazon Creek, Illinois. *Amer Journ Sci* 31:297-326, 353-377.
1919. Revision der Paläozoischen Insekten. *Denkschr Acad Wiss Wien Math-Naturw Klasse* 96:1-82.
- KINZELBACH, R.
1970. Eine fossile Eintagsfliege aus dem Perm des Saar-Nahe-Pfalz-Gebietes. *Mainz Naturw Archiv* 9: 323-334.
- KUKALOVA, J.
1964. Review of the Calvertiellidae, with description of a new genus from Permian strata of Moravia (Palaeodictyoptera). *Psyche* 71:153-178.
1968. Permian mayfly nymphs. *Psyche* 75:310-327.
- KUKALOVA-PECK, J. AND S. PECK
1976. Adult and Immature Calvertiellidae (Insecta: Palaeodictyoptera) from the Upper Palaeozoic of New Mexico and Czechoslovakia. *Psyche* 83: 79-93.
- MARTYNOV, A. V.
1928. Permian fossil insects of North-East Europe. *Trav Musee Geol Acad Sci URSS* 4:1-118.
1938. Etudes sur l'histoire geologique et de phylogenie des ordres des insectes (Pterygota) 1, Palaeoptera et Neoptera-Polyneoptera. *Trav Inst Paleon, Acad Sci USSR* 7:1-119 [Russian].
- OWEN, D. F.
1971. *Tropical Butterflies*. Pp. 1-214, 40 figs., plates 1-40. Oxford Press.
- RAASCH, G. O.
1946. The Wellington Formation in Oklahoma. Doctoral Dissertation, Univ. Wisconsin, Pp. 1-154.

- SELLARDS, E. H.
1907. Types of Permian insects. Part II. Plecoptera. *Amer Journ Sci* 23:345-355.
1909. Types of Permian insects. Part III. Megasecoptera, Oryctoblattinidae and Protorthoptera. *Amer Journ Sci* 27:151-173.
- TASCH, P. AND J. R. ZIMMERMAN
1962. The Asthenohymen-Delopterum bed—a new Leonardian insect horizon in the Wellington of Kansas and Oklahoma. *Journ Paleont* 36: 1319-1333.
- TILLYARD, R. J.
1932. Kansas Permian insects. Part 15. The order Plecoptera. *Amer Journ Sci* 23:97-134; 237-272.
1936. Kansas Permian insects. Part 16. The order Plecoptera (cont'd.): the family Doteridae, with a note on the affinities of the order Protohymenoptera. *Amer Journ Sci* 32:435-453.
- TSHERNOVA, O. A.
1965. Some fossil mayflies (Ephemeroptera, Mithodotidae) from Permian beds of the Ural. *Ent Rev USSR* 44:353-361 [Russian]; English edition pp. 202-207.
1970. On the classification of fossil and Recent Ephemeroptera. *Ent Rev* 49:124-145 [Russian]; English edition pp. 71-81.
- ZALESSKY, G. M.
1946. A new mayfly from the Permian deposits of the Urals. *Doklady Acad Sci USSR* 54:351-352.

THE COURTSHIP CALL OF *CHRYSOPA DOWNESI* BANKS
(NEUROPTERA: CHRYSOPIDAE):
ITS EVOLUTIONARY SIGNIFICANCE*

BY CHARLES S. HENRY
Biological Sciences Group, Box U-43
University of Connecticut
Storrs, CT 06268

INTRODUCTION

Tauber and Tauber (1977a) suggest that the conifer-associated green lacewing *Chrysopa downesi* Banks evolved sympatrically in northeastern North America from its holarctic sibling *C. carnea* Stephens. The proposed mechanism of speciation follows the general theoretical model of Maynard Smith (1966) and specifically involves simple allelic changes at three loci, one controlling body color and two altering the insect's response to photoperiod (Tauber and Tauber, 1977b). Gene substitution at the first locus initially induced divergence in habitat association, while later substitutions at the other loci produced complete reproductive isolation of the two populations by causing each to breed at a slightly (but sufficiently) different time of year (Tauber and Tauber, 1976).

An alternative explanation of *C. downesi's* origin from *C. carnea* is proposed which invokes the concept of allopatric speciation (Mayr, 1963): two portions of a previously contiguous *C. carnea* population became physically isolated from one another for a period of time, perhaps by glaciation events; subsequently, removal or disappearance of the geographic or climatic barrier re-established contact between the two populations, but intervening, independent evolutionary changes prevented much or any gene flow (Hendrickson, 1978). Tauber and Tauber (1978) argue that allopatric or geographical speciation is a less parsimonious explanation of the existing data than the sympatric model, although they admit that their evidence does not truly discriminate between the two hypotheses. However, my studies of courtship and mating behavior in the two lacewing species indicate that, in this case, a traditional allopatric model may in fact be preferable to the more intriguing sympatric one.

*Manuscript received by the editor February 20, 1980

Implicit in most models of geographical speciation is the strengthening of reproductive isolation between imperfectly isolated populations after contact is re-established; in animals, behavioral patterns associated with courtship are thought to be particularly subject to alteration, since premating barriers are presumed to be less wasteful of reproductive effort, gametes, or offspring than those that intervene after copulation (Dobzhansky *et al.*, 1977). In lacewings of the genus *Chrysopa* Leach, I have shown that short-distance acoustical communication by substrate transmission of abdominal vibration or jerking is a necessary component of successful courtship (Henry, 1979, 1980). A different "calling" pattern characterizes each of the eight sympatric lacewing species that I have studied in detail, suggesting that abdominal jerking is or has been important to the reproductive isolation of lacewing species in eastern North America. This view is strengthened further by the fact that the most closely related species, particularly those of the subgenus *Chrysoperla* Steinmann,¹ predictably show the most distinctive and elaborate patterns. Since *C. carnea* and *C. downesi* are members of this latter taxon, the nature of their acoustical signals could indicate how they speciated. If their separation occurred within a single contiguous population by the simple genetic changes postulated by Tauber and Tauber, one would predict identity or at least similarity of calling pattern in both species, since (1) barriers to gene flow are presumed complete after the three allelic substitutions and (2) even casual attempts at interspecific matings are precluded by the Taubers' model. On the other hand, allopatric speciation followed by re-established sympatry should produce unmistakably different patterns of abdominal jerking in the two species, since different calls would terminate heterosexual interactions between them before copulation could occur. I propose that the latter alternative is consistent with the extreme calling differences that exist between the two siblings.

METHODS AND MATERIALS

Lacewing calls consist of discrete bursts or volleys of abdominal strokes (jerks); the call itself is actually a sequence of one or several different kinds of volleys repeated in characteristic temporal pat-

¹This taxon has been given full generic status by Y. Semeria (1977).

terns. The frequency with which the abdomen is jerked or vibrated during each volley is quite low and may be modulated (changed) during the brief course of the volley. A sexually receptive male and female of a given species will establish a duet of abdominal jerking during courtship; in such a duet, partners will alternately trade volleys, or whole sequences, without overlap or interference.

I recorded and photographed jerking activity using the equipment and techniques of a previous study (Henry, 1979). A ceramic transducer (crystal phonograph cartridge) picked up substrate vibrations produced in a thin plastic membrane by calling lacewings and fed these signals to a storage oscilloscope. Conclusions regarding the patterns of *C. carnea* were based on observations of many (more than 30) successful courtships performed by numerous pairs of individuals drawn from populations in Connecticut, New York, Illinois, and California; those concerning *C. downesi* were based on six successful and 15 unsuccessful courtships by eleven pairs (7 males and 10 females) from the northern Catskill mountains of New York State, observed for 69 hours. The source population of *C. downesi* was sympatric with that of *C. carnea* at the Catskill site. I did not find any geographical variation in *C. carnea's* calling patterns.

RESULTS

Chrysopa carnea's call (Fig. 1) consists of a long sequence of 40 or more short (approximately 1/2 second) volleys of vibration; volleys are separated by 1-2 second intervals, and the sequences of two insects are interdigitated during duets—i.e., partners alternate volleys (Fig. 1A). The frequency of abdominal vibration is modulated during each volley, from around 100 strokes per second at inception to 35 or 40 per second at termination (Fig. 1B). Additionally, there is a gradual but significant change in the spacing of volleys during each solo or duet sequence (Henry, 1979). The calls of this species are not markedly sexually dimorphic.

In contrast, the call of the *C. downesi* male or female is more elaborate than and totally unlike that of *C. carnea* (Fig. 1C and Table 1). A sexually receptive individual will periodically release a 5-8 second (or longer) sequence of closely-spaced jerking volleys, punctuated by a sharp discontinuity where the duration of and interval between volleys abruptly change. Part one of each sequence consists of four to seven identical (except for gradually increasing

overall amplitude) volleys at $1/2$ second intervals; each volley itself lasts about $1/3$ second and is divided into a short, relatively intense initial section of 5-8 abdominal strokes and a longer, weaker portion of 20 or more strokes, every other one of which is usually emphasized (Fig. 1D). Part two consists of 10-20 distinctly different, shorter, simple volleys repeated every $1/5$ - $1/4$ second and each made up of 6-8 strokes of the abdomen; overall intensity is high at the onset of part two, but steadily declines almost to a null. Frequency of abdominal vibration is held fairly constant throughout, averaging 68-80 strokes/second. Duetting insects, rather than interdigitating their solo sequences in the manner of *C. carnea*, alternate entire sequences politely with one another. Again, sexual differences are not profound in *C. downesi*, although during duets female sequences are nearly always shorter than those of males (99 out of 127 sequences).

DISCUSSION

In summary, the calls of *C. carnea* and *C. downesi* differ greatly in overall complexity, duration, volley amplitude and frequency structure, and manner of exchange in heterosexual duets. Whereas *C. carnea* adults produce long homogeneous sequences of indeterminate length and rapidly exchange volleys of jerking when duetting, those of *C. downesi* produce more structured sequences composed of two distinct classes of volleys and patiently exchange entire sequences when duetting. Additionally, pronounced frequency modulation characterizes single volleys of *C. carnea* but not of *C. downesi*. If, as is likely, the divergent calls function primarily to prevent interbreeding², an allopatric origin of the two species is implicated. An alternative explanation of the observed dissimilarity in their "songs," genetic drift following sympatric speciation, is not as convincing. It requires that two species showing grossly different calling patterns also display striking morphological similarity (Tauber, 1974) and complete interfertility in the laboratory (Tauber and

²Species-specific calls can also originate in response to selective pressures unrelated to reproductive isolation—e.g., one type of call might communicate information more efficiently than another in a particular habitat. However, I am unable to identify any features of the two lacewings' normal habitats that are simultaneously important to the production of sound and sufficiently different to account for the divergent calling patterns.

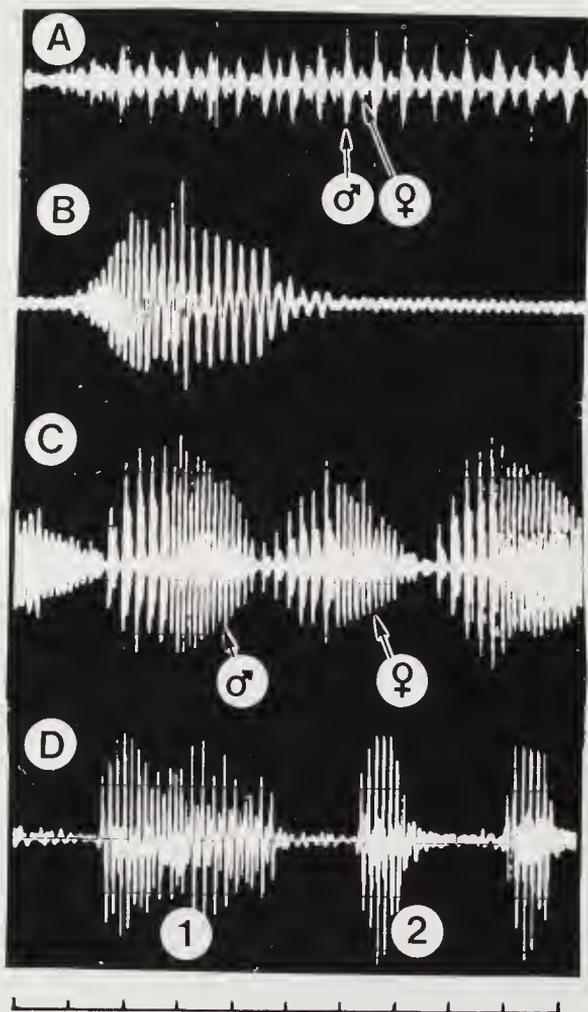


Figure 1. Oscillographs of abdominal vibration patterns produced by courting individuals of *Chrysopa carnea* (A, B) and *C. downesi* (C, D). Duets between a sexually receptive male and female are recorded in (A) and (C) at an oscilloscope writing speed of 2 seconds/major division; in *C. carnea*, each insect exchanges single volleys of abdominal jerking with its partner, while in *C. downesi*, whole sequences of volleys are exchanged. Individual volleys for each species are shown in B (*C. carnea*, male) and D (*C. downesi*, male), recorded at a writing speed of 0.10 second/major division. For *C. downesi*, volleys typical of part 1 and part 2 of the sequence are indicated.

	NUMBER OF VOLLEYS	INTERVAL BETWEEN VOLLEYS	NUMBER OF ABDOMINAL STROKES/VOLLEY	FREQUENCY OF ABDOMINAL VIBRATION	OVERALL DURATION OF CALL	INTERVAL BETWEEN CALLS
MALES						
PART 1	5.29±1.32 (214, 7)	0.56±0.05 (241, 7)	25.69±4.46 (31, 3)	78.29±5.49 (31, 3)	6.76±1.48 (182, 7)	13.47±2.21 (142, 7)
PART 2	15.41±4.57 (190, 7)	0.25±0.02 (246, 7)	7.02±0.84 (45, 3)	70.74±5.28 (47, 3)		
FEMALES						
PART 1	4.92±1.01 (169, 10)	0.55±0.05 (196, 10)	26.88±4.02 (36, 3)	74.50±2.75 (35, 3)	5.78±1.12 (153, 10)	13.33±2.19 (138, 10)
PART 2	13.04±4.30 (164, 9)	0.25±0.02 (218, 9)	6.84±0.85 (79, 4)	69.32±4.86 (77, 4)		

Table 1. Important measurable characteristics of the calls (sequences) of males and females of *Chrysopa downesi*. Data from heterosexual, homosexual, and solo calls are pooled due to insignificant differences. Mean values and their standard deviations are tabulated; intervals and duration are in seconds, frequency in abdominal strokes per second. Sample sizes are entered parenthetically; the larger figure represents the number of calls measured, while the smaller one is the number of different individuals producing more than 10 of such calls. Parts 1 and 2 as in Fig. 1.

Tauber, 1977), whereas one expects random processes to affect all aspects of an organism's genotype more or less equally. This same interfertility and morphological similarity of the two species argue strongly for their close relationship to one another and against their having other closest relatives and other evolutionary histories.

ACKNOWLEDGEMENTS:

This study was supported by N.S.F. award number DEB77-12443, C. S. Henry, principal investigator. I thank the following colleagues from the University of Connecticut: R. Pupedis, J. O'Donnell and S. Cohen for help in the field collection and laboratory maintenance of lacewings; and R. J. Schultz, E. Brighty, and G. Clark for constructive comments on the paper and its concepts. C. Tauber, Cornell University, kindly supplied six of the *C. downesi* adults from a young laboratory colony.

REFERENCES:

- DOBZHANSKY, TH., F. J. AYALA, G. L. STEBBINS, AND J. W. VALENTINE. 1977. *Evolution*. Freeman Press, San Francisco. 572 pp.
- HENDRICKSON, H. T. 1978. Sympatric speciation: evidence? Letter to *Science* **200**:345-346.
- HENRY, C. S. 1979. Acoustical communication during courtship and mating in the green lacewing *Chrysopa carnea* (Neuroptera: Chrysopidae). *Ann. Entomol. Soc. Am.* **72**(1): 68-79.
- HENRY, C. S. 1980. Acoustical communication in *Chrysopa rufilbris* (Neuroptera: Chrysopidae), a green lacewing with two distinct calls. *Proc. Entomol. Soc. Wash.* **82**(1): 1-8.
- MAYNARD SMITH, J. 1966. Sympatric speciation. *Am. Nat.* **100**: 637-650.
- MAYR, E. 1963. *Animal Species and Evolution*. Belknap Press, Cambridge, Mass. 797 pp.
- SÉMÉRIA, Y. 1977. Discussion de la validité taxonomique du sous-genre *Chrysoperla* Steinmann (Planipennia, Chrysopidae). *Nouv. Rev. Entomol.* **7** (2): 235-238.
- TAUBER, C. A. 1974. Systematics of North American chrysopid larvae: *Chrysopa carnea* group (Neuroptera). *Can. Entomol.* **106**: 1133-1153.
- TAUBER, C. A. AND M. J. TAUBER. 1977a. Sympatric species based on allelic changes at three loci: evidence from natural populations in two habitats. *Science* **197**: 1298-1299.
- TAUBER, C. A. AND M. J. TAUBER. 1977b. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature* **268**: 702-705.
- TAUBER, C. A. AND M. J. TAUBER. 1978. (Reply to Hendrickson). Letter to *Science* **200**: 346.
- TAUBER, M. J. AND C. A. TAUBER. 1976. Environmental control of univoltinism and its evolution in an insect species. *Can. J. Zool.* **54**: 260-265.

The illustration on the front cover of this issue of *Psyche* is a reproduction of the published figure of a myrmicine ant from Bolivia, *Tingimymex mirabilis*, described by W. M. Mann in *Psyche* (1926, vol. 33, p. 105).

CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room 154, Biological Laboratories, Divinity Avenue, Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

BACK VOLUMES OF PSYCHE

Requests for information about back volumes of *Psyche* should be sent directly to the editor.

F. M. CARPENTER
Editorial Office, *Psyche*
16 Divinity Avenue
Cambridge, Mass. 02138

FOR SALE

REPRINTS OF ARTICLES BY W. M. WHEELER

The Cambridge Entomological Club has for sale numerous reprints of Dr. Wheeler's articles that were filed in his office at Harvard University at the time of his death in 1937. Included are about 12,700 individual reprints of 250 publications. The cost of the reprints has been set at 5c a page, including postage; for orders under \$5 there will be an additional handling charge of 50c. A list of the reprints is available for \$1.00 from the W. M. Wheeler Reprint Committee, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138. Checks should be made payable to the Cambridge Entomological Club.

P54
6182

ISSN 0033-2615

MUS. COMP. ZOOI.
LIBRARY

NOV 24 1980

HARVARD
UNIVERSITY

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 86

December, 1979

No. 4

CONTENTS

Worker Compatibilities within and between Populations of <i>Rhytidoponera metallica</i> . Caryl P. Haskins and Edna F. Haskins	301
Notes on the Nesting Behavior of the Bethyloid Wasp, <i>Epyris eriogoni</i> Kieffer, in Southern Texas. William L. Rubink and Howard E. Evans	313
Nymphal Habitat of <i>Oliarus vicarius</i> (Homoptera:Cixiidae), and Possible Association with <i>Aphaenogaster</i> and <i>Paratrechina</i> (Hymenoptera: Formicidae). C. R. Thompson, J. C. Nickerson, and F. W. Mead	321
Sexual Competition for Space of the Parasite <i>Xenos pallidus</i> Brues in Male <i>Polistes annularis</i> (L.) (Strepsiptera, Stylopidae, and Hymenoptera, Vespidae). S. W. Dunkle	327
A Remarkable New Species of <i>Proceratium</i> , with Dietary and Other Notes on the Genus (Hymenoptera: Formicidae). William L. Brown, Jr.	337
Observations on Swarm Emigrations and Dragging Behavior by Social Wasps (Hymenoptera: Vespidae). Ruth Chadab and Carl W. Rettenmeyer	347
Notes on the Russian Endemic Ant Genus <i>Aulacopone</i> Arnoldi (Hymenoptera:Formicidae). Robert W. Taylor	353
Variation in Distribution, Morphology and Calling Song of Two Populations of <i>Pterophylla camellifolia</i> (Orthoptera: Tetigoniidae). Robert C. North and Kenneth C. Shaw	363
Comparative Anatomy of the Ventral Region of Ant Larvae and Its Relation to Feeding Behavior. Ronald S. Petralia and S. B. Vinson	375
Mating Behavior of Three Species of Coniopterygidae (Neuroptera). Victor Johnson and William P. Morrison	395
Observations of Seed-Bug (Hemiptera: Lygaeidae) Parasitism by a Species of <i>Catharosia</i> (Diptera: Tachinidae). Kevin W. Thorpe and B. Jane Harrington	399
<i>Argyrodes attenuatus</i> (Theridiidae): A Web That Is Not a Snare. William G. Eberhard	407
Index to Authors and Subjects	415

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1979-1980

<i>President</i>	NORMAN WOODLEY
<i>Vice-President</i>	MATTHEW DOUGLAS
<i>Secretary</i>	HEATHER HERMAN
<i>Treasurer</i>	FRANK M. CARPENTER
<i>Executive Committee</i>	WILLIAM A. NEIL ROGER SWAIN

EDITORIAL BOARD OF PSYCHE

- F. M. CARPENTER (Editor), *Fisher Professor of Natural History, Emeritus, Harvard University*
W. L. BROWN, JR., *Professor of Entomology, Cornell University and Associate in Entomology, Museum of Comparative Zoology*
P. J. DARLINGTON, JR., *Professor of Zoology, Emeritus, Harvard University*
B. K. HÖLLDOBLER, *Professor of Biology, Harvard University*
H. W. LEVI, *Alexander Agassiz Professor of Zoology, Harvard University*
R. J. MCGINLEY, *Assistant Professor of Biology, Harvard University*
ALFRED F. NEWTON, JR., *Curatorial Associate in Entomology, Harvard University*
R. E. SILBERGLIED, *Associate Professor of Biology, Harvard University*
E. O. WILSON, *Baird Professor of Science, Harvard University*

PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: \$9.50, domestic and foreign. Single copies, \$3.50.

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

Orders for missing numbers, notices of change of address, etc., should be sent to the Editorial Office of Psyche, 16 Divinity Avenue, Cambridge, Mass. 02138. For previous volumes, see notice on inside back cover.

IMPORTANT NOTICE TO CONTRIBUTORS

Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

Authors are expected to bear part of the printing costs, at the rate of \$24.50 per printed page. The actual cost of preparing cuts for all illustrations must be borne by contributors: the cost for full page plates from line drawings is ordinarily \$18.00 each, and for full page half-tones, \$30.00 each; smaller sizes in proportion.

The Sept.-Dec., 1979, Psyche (Vol. 86, No. 2-3) was mailed June 25, 1980

PSYCHE

Vol. 86

December, 1979

No. 4

WORKER COMPATIBILITIES WITHIN AND BETWEEN POPULATIONS OF *RHYTIDOPONERA METALLICA**

BY CARYL P. HASKINS, EDNA F. HASKINS
Haskins Laboratories, Inc.,
New Haven, Connecticut 06510

INTRODUCTION

The markedly diffuse nature of the colonial structure of *Rhytidoponera metallica*, associated with the rarity of true females and the usual presence of multiple fertilized egg-laying "workers" in the community, blurs the spatial distinction between naturally occurring "colonies" to an unusual degree. This condition coupled with the indefinite nest-form frequently typical of the species, which commonly occupies leaf-litter and superficial layers of soil, makes it difficult on occasion to distinguish a mosaic of neighboring "colonies" from what often superficially appears as merely a rather highly "viscous" population of socialized individuals. This situation lends special interest to the question of how far one mechanism commonly involved in the maintenance of integrity in formicid communities, that of colony "identification" among workers, is developed in *R. metallica*, and, if it is developed, what may be its basic characteristics. This interest has led to a preliminary investigation of those questions over the past several years.

MATERIALS AND METHODS

Preliminary tests of compatibilities between workers of *R. metallica* taken from widely separated populations amply demonstrated:

Manuscript received by the editor November 8, 1979.

(a) That there is indeed a sharp behavioral distinction between "home" and "alien" populations, and

(b) That *R. metallica* is sufficiently aggressive so that a simple confrontation of such "alien" workers, in the field, in the artificial nest, or simply in such "arenas" as laboratory finger bowls is sufficient to elicit sharp and unmistakable reactions at once. Thus, while observations involving compatibility reactions within and between colonies of some hypogeaic or semi-hypogeaic Ponerinae (such as members of the genus *Amblyopone*) must be undertaken with great care, and should be conducted within arenas, such as artificial nests, which are thoroughly familiar to the subjects and preferably have been occupied by them for many months beforehand, such precautions appear unnecessary with this active, aggressive epigeaic ectatomine.

Three well-separated Australian populations of *R. metallica* were selected for the investigation. The first group was drawn from a rather small area in Southern Queensland, bounded by a rough triangle marked by the towns of Nambour, Montville, and Paramount Point, in the coastal Blackall Range. Nambour is approximately 59 miles north of Brisbane, and the distance between Nambour and Montville is approximately 7 miles. A second population was drawn from a limited area in Ashton Park,* a municipal reserve on the outskirts of Sydney, N.S.W. separated by an arm of Sydney Harbor, and located approximately 560 miles from the Nambour-Montville region. This Ashton collection area included a roadside strip approximately one-half mile in greatest length by some sixty feet in width. The third area was located outside of the town of Sutherland, N.S.W., near the proximate border of the National Park of New South Wales, separated from the Ashton population by approximately 20 miles. It included strips of roadside verge approximately three miles in length by one-half mile in width.

Colonies were collected from these areas in 1959, 1963, 1968, 1973, and 1977, and maintained in the laboratory in glass earth-filled Lubbock-type nests, kept in arenas where workers could forage at all times. Some individual colonies were maintained continuously under these conditions for as long as 14 years, so that, when desirable, reactions could be tested of workers more than one "generation" removed from the group originally collected.

*Now Sydney Harbor National Park

Mode of Testing:

As mentioned, reactions of workers on meeting were usually immediate and quite clear cut, although some anomalies were observed. The procedure used was simply to introduce the individual to be tested into the colony tested against, or, alternatively, to place two workers together in a confined space, and to observe their behavior over periods ranging from less than a minute (when incompatibility was unquestionably evident, as in immediate and violent attack) up to an hour if necessary to be sure of compatibility. Reactions were arbitrarily (but, it is believed, reasonably accurately) scored in four "envelope" categories:

A. Extreme incompatibility, accompanied by attack, vigorous attempts to sting, and frequently tight body "closure".

B. Evident incompatibility, usually with seizure of antennae or legs, but without the violent "closure" of *A*. Both *A* and *B* were taken to mean marked incompatibility.

C. Initial "starting back" or alarm on first encounter, and sometimes brief running, but no threat or attack. The situation is commonly followed by fraternization and complete compatibility.

D. Complete compatibility from the outset, lasting permanently, and frequently accompanied by vigorous antennal cleaning and sometimes mutual body licking. *C* and *D* may be justifiably interpreted, we believe, as ultimate compatibility, although obvious distinctions initially recognized in the *C*-type reactions were sometimes interesting.

Categories *A* and *D* were very clear cut. Inevitably, some observer subjectivity entered into assignments of *B* and *C* categories, but every effort was made to estimate them accurately. Very occasionally a reaction was sufficiently indefinite, or changed sufficiently with time, so that it had to be judged a "border case" and was so designated — as, for example "*C/D*".

The tests summarized below were designed to test several aspects of the whole question, as indicated.

Controls

Two sets of controls were run where the results to be expected were obvious, primarily to test the validity of the experimental conditions. One was between workers drawn from within a small contiguous area, the second between two fairly well-separated populations within a single collection location.

Ashton-Ashton

Populations from three colonies (#3, #4, #5), were collected at Ashton Park on January 3, 1973, and tested on January 5. Colonies #3 and #4 were taken about 100 yards apart. Colony #5 was separated from the other two by about 1/2 mile. Following are the results:

- #3 × #4 Test #1—Divaricated mandibles, no attack. (C)
 Test #2—Same, close mutual examination, then mutual grooming, entire compatibility. (C)
- #3 × #5 Test #1—Opened mandibles for a moment, then entire compatibility (D)
 Test #2—Opened mandibles, then entire compatibility. (D)
- #4 × #5 Test #1—Entire compatibility. (D)
 Test #2—Brief pursuit, with opened mandibles. (C)

Sutherland-Sutherland

Two colonies were used, taken in this case approximately 3 miles apart in the study area on January 23, 1973, and tested two days later, on January 5, 1973. They were labeled #1 and #2:

- #1 × #2 Test #1—Entirely compatible (D)
 Test #2—Initial alarm with open mandibles and momentary seizure, passing to entire compatibility (C)

Ashton-Sutherland

When workers from the two populations were tested against one another, the results were very different. These tests were performed on the same day as those above.

- #1 × #3 Test #1—Extreme incompatibility, with active fighting (A)
 Test #2—Extreme incompatibility. Pursuit but no seizure. (B)
- #1 × #4 Test #1—Continuous open-mandibled aversion (B)
 Test #2—Open-mandibled aversion. (B)
- #1 × #5 Test #1—Open-mandibled aversion, no actual attack. (B)
 Test #2—Continuous attacks, with frequent seizures (A)
- #2 × #3 Test #1—Vigorous and continuing attacks (A)
 Test #2—Open-mandibled encounters frequently repeated (B)

- #2 × #4 Test #1—Instant attack and seizure (A)
 Test #2—Open-mandibled encounters (B)
 #2 × #5 Test #1—Aggression; open-mandibled encounters (B)
 Test #2—Immediate aggression and attack (A)

SUMMARY

Six tests among the Ashton populations were rated 3 each C and D. Two tests between Sutherland-location colonies were rated D and C. There was thus a notable degree of compatibility among colonies drawn from within both study areas, although within the Sutherland area collections were made over a fairly wide range (about 3 miles apart).

In marked contrast, among 12 tests made between the Ashton and the Sutherland populations 5 were rated A, and 6 B. Incompatibility here was the general rule, varying only in the vigor of its expression.

Tests within a single "colony":

As a final test of the adequacy of the method, tests were run on the same day between workers taken in the same *collection*. The results were:

- #1 × #1 Entire compatibility (D)
 #2 × #2 Entire compatibility (D)
 #3 × #3 Entire compatibility (D)
 #4 × #4 Entire compatibility (D)
 #5 × #5 Entire compatibility (D)

It thus seemed clear (a) that the method itself was workable, and (b) that compatibility does diminish with distance, though "colonies" situated as much as three miles apart within the same study area (far beyond the likely bounds of daily worker encounters) can remain reasonably compatible, although at this distance there were often signs that workers were briefly "uncomfortable" in proximity, though they quickly adjusted. By contrast, members of widely separated populations (New South Wales and Queensland) uniformly behaved in an antagonistic fashion.

Is Compatibility a Conditioned or an Innate Perception and Reaction?

This question was approached in two ways:

- (a) By introducing workers which had been eclosed from cocoons and had matured away from the parent "colony" (under

the guardianship of one of two "home" adult workers) into that colony and noting the reactions of the "hosts".

(b) By testing reactions between colonies drawn from the same or different populations long enough after they had been separated (three to four years in most cases) so that at most a very small proportion of the workers living at the time of collection survived to participate. Thus the participants entirely or for the most part, had never been *individually* subjected to such tests. Thus, while the individual might itself have been conditioned by the distinctive colony odor of its own community, that distinction must persist over more than one worker generation. Results were as follows:

1. *Young Ants Returned to Parent Colony*

Young workers of *R. metallica* normally eclose from cocoons in a quite advanced stage of pigmentation and actively participate in colony functions within one or two days. This facilitated experimental procedures considerably, though the question remained open, of course, as to whether the "receiving" adults in the main community might distinguish their younger sisters or progeny on an age basis.

The colony used in this work (Y-1) had been collected from the Sutherland population on December 30, 1959, and maintained as a laboratory group thereafter.

Test #1

A group of cocoons from colony Y-1 was isolated on September 17, 1962, with 2 adult and 2 callow nurses.

On March 10, 1963, 20 workers (at least 18 of which must have been "strangers" to the home community) were reintroduced to the main colony with clean forceps. All were entirely compatible as shown.

Test #1

<i>Test No.</i>	<i>Reaction</i>
1	Fully compatible (A)
2	Fully compatible (A)
3	Fully compatible (A)
4	Fully compatible (A)
5	Fully compatible (A)
6	Fully compatible (A)

7	Fully compatible (A)
8	Fully compatible (A)
9	Fully compatible (A)
10	Fully compatible (A)
11	Fully compatible (A)
12	Fully compatible (A)
13	Fully compatible (A)
14	Fully compatible (A)
15	Fully compatible (A)
16	Fully compatible (A)
17	Fully compatible (A)
18	Fully compatible (A)
19	Fully compatible (A)
20	Fully compatible (A)

Test #2

On September 17, 1962, a second group of cocoons from Y-1 was isolated in the care of two adult nurses. They eclosed and matured there.

On March 11, 1963, 17 workers were transferred with clean forceps, as before, back to the main colony. At the most, two of these workers (the two nurses) would previously have been exposed to the main group. In these tests, there was some low-order alarm as indicated, quickly passing to entire compatibility.

Test #2

<i>Date</i>	<i>Trial</i>	<i>Reaction</i>
3/11	1	Slight hostility—opening of mandibles, some “starting back”, no attack. Individual shortly accepted in home colony. (C)
3/11	2	Identical reaction to above. (C)
3/11	3	A little suspicion and obvious “starting” with open mandibles by two or three “home” individuals, but quick and complete acceptance. (C/D)
3/11	4	Identical reaction to above (C/D)
3/11	5	Identical reaction to above. (C/D)
3/12	6	Identical reaction to above. (C/D)
3/12	7	Identical reaction to above. (C/D)
3/12	8	Identical reaction to above. (C/D)
3/12	9	Identical reaction to above. (C/D)

- 3/12 10 Here the hostility was a bit more pronounced, many individuals "starting" with open mandibles, but no actual attacks occurring. (C).
- 3/13 11 Identical reaction to 9. (C/D)
- 3/14 12 Identical reaction to 9. (C/D)
- 3/14 13 Identical reaction to 9. (C/D)
- 3/14 14 Identical reaction to 9. (C/D)
- 3/14 15 Identical reaction to 9. (C/D)
- 3/14 16 Identical reaction to 9. (C/D)
- 3/14 17 Identical reaction to 9. (C/D)

Experiments Repeated on October 7, 1962

- 10/7 18 Some "chasing," but no attack. Some "startle" effect. (C)
- 10/7 19 Identical to above. (C)

(b) Reactions Between Adult Members of the Same Populations After Several Years of Separation—Intervals Greater than the Average Life-span of Workers.

(b1) Ashton-Ashton

On January 4, 1973 a collection of two groups of workers was made from under adjacent stones at a specifically marked location in Ashton Park. They were separately colonized in the laboratory, and kept entirely isolated, being maintained under identical conditions of environment and diet on adjacent tables but not being permitted contact until March 20, 1977, more than four years later. These colonies were labeled X and 4.

On March 2, 1977, an additional collection was made from precisely the same spot in Ashton Park, and brought to the laboratory. Tests among all three of these colonies were conducted on March 20, 1977, with the following results:

- D × #4 Test #1—Complete compatibility (D)
 Test #2—Complete compatibility (D)
- D × X Test #1—Complete compatibility (D)
 Test #2—Complete compatibility (D)
- 4 × X Test #1—Complete compatibility (D)
 Test #2—Slight initial "starting back", followed by complete compatibility. (C)

It is rather striking that after more than four years of separation, in one case between two populations in the laboratory maintained under identical regimens, in the other between these colonies and a

wild population taken in the same location more than four years later, which must have existed under significantly divergent environmental conditions, these three populations remained wholly compatible.

(b2) *Sutherland-Sutherland*

A similar series of four tests was made on January 17, 1973 between colonies collected in the same marked area within the Sutherland arena, respectively on January 12, 1968 (maintained thereafter in isolation) and January 3, 1973.

Test #1—Initial "startle", followed by entire compatibility (C/D)

Test #2—Initial "startle", followed by entire compatibility (C/D)

Test #3—Initial "startle", followed by entire compatibility (C/D)

Test #4—Initial "startle", followed by entire compatibility (C/D)

(b3) "*Blind*" Tests between Individuals of Colonies from Sutherland and from Queensland in the Nambour-Montville-Paramount Point Triangle

These tests involved colonies collected in the Queensland area on December 23, 24, and 26, 1963, and a single colony collected in the Sutherland area on January 12, 1968. All had been housed since capture in earth-containing Lubbock nests in five-gallon aquaria with screened tops, as previously described, within a month of the time of collection. All had reared broods continuously over the nearly nine years that the Queensland collections were held before these tests, and the nearly five years for the Sutherland collection. During this time there had been numerous broods of males matured, and extensive male flights occurred within each arena, with presumed periodic re-fertilization of the successive broods of laying females. It is virtually certain that none of the workers tested from the Queensland collections were in existence when those collections were made, and extremely probable that the same was true for the Sutherland population.

For purpose of the tests, the locality label on each of the nests was obscured and replaced by an arbitrary designation, A1-A7 for the Queensland colonies, B1 for that from Sutherland.

A series of tests were run among the Queensland colonies and between them and the Sutherland colony, in all possible combinations, on October 23, 1972. As a result, three compatibility groups could be distinguished.

Queensland colonies A1; A2; A6; and A7 showed entire compatibility. They were designated as *Group I*.

Queensland colonies A3; A4; and A5 showed entire compatibility. They were designated as *Group II*.

Members of Group I and Group II were consistently incompatible *inter se*.

Members of both Group I and Group II were consistently incompatible with B1, the Sutherland population.

When the specific locality label for each colony was uncovered, it was found that the members of Group I (A1; A2; A6; A7) had been closely associated geographically when collected nine years before:

A1 and A2 had originally been taken a few feet apart at Paramount Point.

A6 had been taken a few feet from A1-A2 at Paramount Point.

A7 had been taken at Montville, a short distance away. Thus all of these had originally been parts of a closely circumscribed population.

The members of Group II (A3; A4; A5) had likewise been collected in close proximity, near the town of Nambour, approximately 7 miles from the first group.

These tests were repeated with the same colonies on March 20, 1977, when the Queensland colonies had been maintained in the artificial nest for more than thirteen years and that from Sutherland for more than nine years, and one of the Ashton colonies, collected January 4, 1973, was added. Colonies were renumbered as follows:
#1— Montville, Queensland (A7 in the October 23, 1972 tests recorded above.—Group I).

#2— Nambour (Group II in 10/23/72 tests above).

#3— Colony A1 in the 10/23/72 tests above (Group I).

#4— "X" in the Ashton-Ashton tests described above. Ashton, January 4, 1973.

#5— Sutherland, January 12, 1968 (B1 in the 10/23/72 test above).

#1 × #2 (Old Group I × Group II)—Violent attack (A)

#1 × #3 (Old Group I × Group I)—Complete compatibility (D)

#1 × #4 (Old Group I × Ashton)

Test #1—Violent attack (A)

Test #2—Extreme avoidance (A/B)

#1 × #5 (Old Group I × Sutherland)—Extreme "startle" reaction and avoidance (B)

- #2 × #3 (Old Group II × Group I)—Violent attack (A)
 #2 × #5 (Old Group II × Ashton)—Agitation, mutual repulsion,
 no actual attack (B)
 #3 × #4 (Old Group I × Ashton)—Violent attack (A)
 #3 × #5 (Old Group I × Sutherland)—Violent attack (A)
 #4 × #5 (Ashton × Sutherland)
 Test #1—Violent attack (A)
 Test #2—Violent attack (A)

SUMMARY AND CONCLUSIONS:

These tests seem to point to three conclusions:

1. The capacity to make compatibility distinctions between well-separated populations is highly developed in *R. metallica*, a normally aggressive species, despite the "diffuseness" of its colonial structure, characterized by the physical nature of the colonies themselves, the circumstance that communities consist only of monomorphic workers showing a minimum of morphological or habitus differentiation *inter se* even between ordinary and fertile laying workers, rather numerous in populous colonies.
 However, consistent with this "looseness" of colony structure, groups of workers taken from the same general area but at distances clearly too great to permit continual communal contact under natural conditions retain some compatibility, the tolerance seeming to decrease with distance. Thus a picture of a rather "viscous" population seems more applicable in this context than that of well-defined colonial entities.
2. Compatibility distinctions were found to be consistently retained between groups originally drawn from the same natural populations but then isolated under identical laboratory conditions for up to more than thirteen years. Similar compatibility was exhibited between a group collected from a specific field location when tested shortly after capture against other groups collected at the same locality more than four years earlier and maintained in the laboratory over the interval under environmental conditions obviously very different. Thus differing environmental and nutritional histories do not seem to influence compatibility reactions in any observable way.

3. Individuals eclosed apart from a given community and returned to it after maturity, though "strangers" to the parent community as individuals, are characteristically accepted as compatible. This suggests that the qualities affecting compatibility are here innately determined (cf. Crozier and Dix, 1979) though further work with "alien" nurses remains to be done.

All this suggests a genetic basis for the characteristics determining compatibility in *R. metallica*. The fact that the males of the species fly actively, and probably over some (though limited) distances, and mate, as we have demonstrated, with "calling" "laying workers" of neighboring colonies (Hölldobler and Haskins, 1977; Haskins, 1978), seems to fit this picture, suggesting an "interlaced" population, in which the frequencies of given matings between hypothetical colonies A and B diminish as some function of their spatial separation. The degree to which compatibility patterns can be maintained in isolated populations suggests that several generations (one would guess, of course, thousands or more) may be required to achieve significant shifts of compatibility.

ADDENDUM*

As a final test designed to distinguish genetic from environmental factors in colony—or population—discrimination in *Rhytidoponera metallica*, a colony of this species, collected in the Blackall Range at Montville, Queensland, Australia on December 23, 1963, and maintained in the laboratory since that time in a stacked group of modified, earth-containing Lubbock-type artificial nests in a plastic arena was divided into two approximately equal moieties by placing half of the nest stack in each of two identical plastic arenas arranged side by side on the laboratory bench. Conditions of temperature, light, and humidity were virtually identical for the two groups. Each remained in nests familiar to it, and each continued to breed normally during subsequent months. The only difference in treatment was in feeding. One moiety was given fresh mealworms at the rate of twice a week. The other was supplied with fresh crickets at the same intervals. The moiety given mealworms was supplied with dilute sugar water as a carbohydrate source; the "cricket fraction" with dilute honey.

*Addendum manuscript received by the editor September 22, 1980.

The separation and differential feeding was begun on November 4, 1979, and continued until September 16, 1980. At that time individual pairs of workers from each moiety were tested for interactions in four inch fingerbowls, in the same manner as described in the main paper. Testing was carried out from 1:40 p.m. until 3:15 p.m. on September 16, 1980.

One hundred workers were tested, in fifty pairs of one from each moiety. Of these, 47 pairs, or 94 individuals, showed completely neutral (or "amicably interacting") reactions. In two pairs there was a slight initial hostile reaction, but no attack. In only a single case one individual seized the other by the base of an antenna, maintaining the grip for a few seconds before spontaneously releasing it with no further aggression.

As a control, workers from this same colony were tested on the same day against members of a colony of *R. metallica* collected at Sutherland, New South Wales, Australia, on January 12, 1968. These two colonies had been housed in similar Lubbock nests in arenas which had been maintained next to one another on the same laboratory bench for twelve years. Throughout this period, they had been fed identical diets: mealworms as a protein source, dilute sugar water as a source of carbohydrate. Thus diet, as well as all environmental conditions, had been maintained essentially identical for these two colonies over a twelve year period.

Seventeen pairs, involving thirty-four workers, were tested in the same manner as in the preceding case. In fifteen of these there was an almost instantaneous and violently hostile reaction, the pairs quickly becoming "locked" in a mutually stinging posture which quickly results in fatalities to one or both participants unless they are forcibly separated. In one case the members of a pair showed no reaction; in a second pair there was a distinct "startle" reaction when the two individuals met, but no actual attack.

The contrast between the behaviors of the members of a single genetically highly related population maintained on different diets in the one case and genetically separated populations maintained on identical diets in the other was very striking, and appeared to demonstrate quite unequivocally the predominant role of genetic factors in enabling colony (or "population") discrimination in this species, as against the role of nutritional factors, further reinforcing the conclusions drawn from the evidence presented in the main portion of the paper.

The rare but conspicuous exceptions recorded in both series may hint at a multiple-allele genetic control mechanism, but further investigation and analysis of such a situation, if present, must await the future.

LITERATURE CITED

- HÖLLDOBLER, B. AND C. P. HASKINS
1977. Sexual calling in a primitive ant. *Science* **195**: 793-794.
- HASKINS, C. P.
1978. Sexual calling behavior in a highly primitive ant. *Psyche*: **85**: 407-415.
- CROZIER, R. H. AND M. W. DIX
1979. Analysis of two genetic models for the innate components of colony odor in social Hymenoptera. *Behavioral Ecology and Sociobiology* **4**: 217-224.

NOTES ON THE NESTING BEHAVIOR OF THE
BETHYLID WASP, *EPYRIS ERIOGONI* KIEFFER,
IN SOUTHERN TEXAS

BY WILLIAM L. RUBINK¹ AND HOWARD E. EVANS
Department of Zoology and Entomology
Colorado State University
Fort Collins, Colorado 80523

In spite of its cosmopolitan distribution and large size, the family Bethylidae remains relatively poorly known, especially from a behavioral viewpoint. This is particularly unfortunate because of the presumed phylogenetic importance of this group (e.g., Malyshev, 1968) and a growing appreciation of the possible value of these wasps in biological control (e.g., Yamada, 1955; Schaefer, 1962; Gordh, 1976; Gordh and Evans, 1976). Evidently there is a great diversity in the behavior of members of this family. (For reviews see Richards, 1939; Yamada, 1955; Evans, 1964; Gordh, 1976). The present paper concerns a species exhibiting behavior remarkably similar to that of some of the more generalized fossorial wasps of the families Sphecidae and Pompilidae.

The genus *Epyris*, one of the largest in the family, is found in all zoogeographic regions. They are small wasps (2–10 mm in length) and have been little studied aside from a brief report by Bridwell (1917), and a somewhat more detailed account by Williams (1919). Bridwell observed a female of a South African species carrying a tenebrionid larva. Williams studied the Hawaiian species *E. extraneus* Bridwell, also a predator on tenebrionid larvae, and described stinging behavior, prey carriage, larval development, and certain aspects of its nesting behavior. He found that prey were hunted and stung before a nest site was selected, and were dragged to the nest site using what Williams described as a unique form of carriage, "the prey being borne rapidly along on the wasp's back".

Our studies are the first conducted on a North American species of *Epyris* and confirm Williams' observations while adding some details. They were conducted on the shores of the Rio Grande, approximately one mile west of the Bentsen-Rio Grande State Park,

¹Present address: Department of Entomology, Ohio Agricultural Research and Development Center, Wooster, Ohio 44691.

Manuscript received by the editor February 26, 1980.

Hidalgo County, Texas, on May 19, 27, and 28, 1979. *E. eriogoni* Kieffer males and females were common in sandy, bare areas among the vegetation within 10–20 meters of the shoreline (Fig. 1). Males, in loose aggregations, were observed to be active from mid-morning to early afternoon. They were observed to fly just above the soil surface, landing and digging occasionally, and seemed to stray little from an area of a few square meters. Females were most abundant in areas where males were observed; however, no copulations were seen. Other females were observed primarily on low-lying vegetation. In most cases the females flew little. Most of their activity was devoted to scurrying along the soil surface, entering cracks and crevices, or exploring under clods of earth and other debris scattered on the soil surface. Female activity was restricted to early to mid morning hours; few were observed in the afternoon.

Two field observations were made of *E. eriogoni* nesting behavior. At 1030 hours, May 19, we observed a female carrying its tenebrionid prey up a slight incline in a bare expanse of beach sand. Prey transport consisted of pulling the prey backwards over the sand (Fig. 2a), or carrying it alongside, and sometimes slightly above (Fig. 2b).



Fig. 1. Typical nesting habitat of *Epyris eriogoni* in southern Texas.

In both cases the wasp grasped the larva in the head region, apparently by the palps. A similar mode of transport was described by Williams (1919) for *E. extraneus* in Hawaii.

After experiencing much difficulty in carrying the relatively larger prey the wasp carried it under a clod of sand. She emerged after approximately one minute and was captured and preserved. Subsequent excavation recovered the prey at about 1 cm depth. Since no egg was found on the prey, we hypothesize that this site probably represented a temporary location to be utilized until a suitable nest site could be found.

At 0930 hrs on May 28 a second female, *E. eriogoni*, was observed dragging its larval tenebrionid prey up a gradual sandy incline. Again the same two forms of prey carriage were noted (Fig. 2). The wasp abandoned the prey several times and, in a 50 to 100 cm radius, investigated numerous cracks and depressions in the soil surface. She appeared to experience some difficulty in relocating the prey after each of these forays. On the third foray the bethylid entered a tiny hole in the sand (which later proved to be the temporarily closed burrow of a sand wasp), remained several seconds, and then returned directly to the prey and began transporting it towards the hole. Upon reaching the burrow, she deposited the prey outside, a few millimeters distant, and entered the burrow. Within a few seconds she reemerged, grasped the head (palps?) of the prey, and backed into the burrow with it. Shortly after the prey and bethylid had disappeared into the burrow, a *Bembix troglodytes* entered the same burrow with its dipterous prey; this caused the bethylid to leave the burrow momentarily. After re-entering the burrow the bethylid remained for at least two hours (until 1200 hours), when observations were discontinued.

Excavation of the sand wasp nest revealed a small horizontal tunnel (approx. 1–2 mm diam.) leading off at a right angle from the sand wasp burrow. It extended about two centimeters where it enlarged to a "C" shaped cell only slightly larger than the partially curled tenebrionid prey it contained. The *Epyris* "nest" was located at approximately 25 cm depth and immediately before the internal closure of the sand wasp nest (leading to the cell of the latter nest). The female bethylid was not found in the nest. The prey contained a single egg (Fig. 3) in a position nearly identical to that pictured for *E. extraneus* in Hawaii (Williams, 1919). The egg died before hatching.

The two preserved tenebrionid larvae were identified as *Blastinus* sp., which are apparently very close taxonomically to the prey

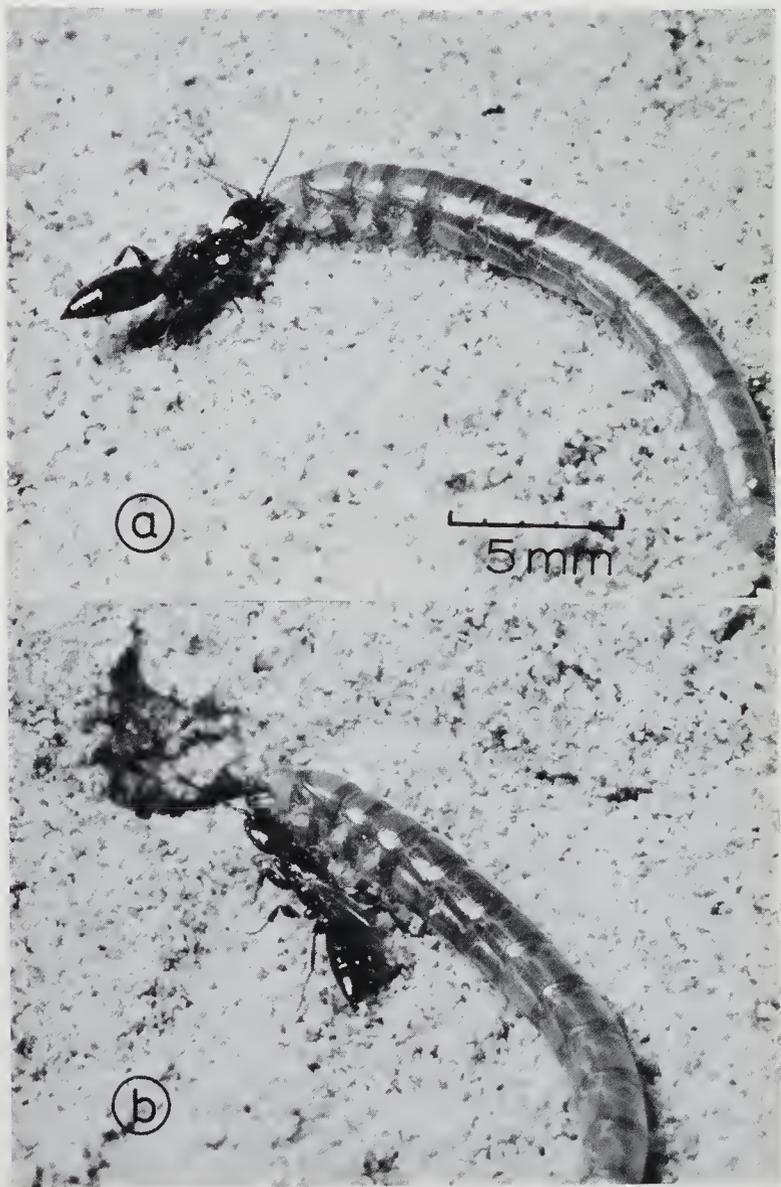


Fig. 2. *Epyrus eriogoni* dragging its *Blastinus* sp. prey: a) backwards along the soil surface, and b) forward along the soil surface and toward the nest opening.

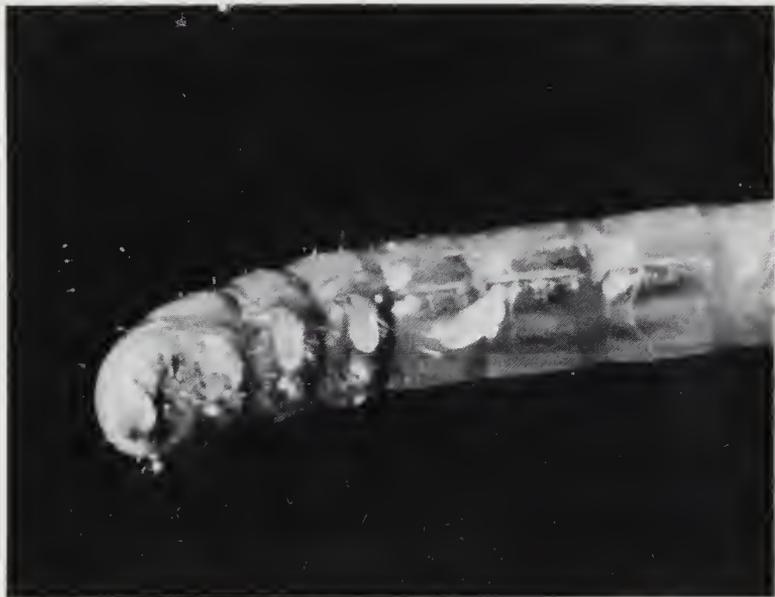


Fig. 3. *Blastinus* sp. larval prey of *Epyris eriogoni* showing egg on the first abdominal segment.

(*Gonocephalum seriatum* (Boisduval)) Williams (1919) found to be used by *E. extraneus* (T. J. Spilman, pers. comm.).

Four female and five male wasps were returned to the laboratory in an attempt to further study their biology. The males survived for several days and the females for a period of two months on a 5% honey-water diet. Captive females would not accept *Tenebrio molitor* L. larvae of the appropriate size class as prey. Although they did appear to be searching for prey in the available cracks and crevices in the rearing chamber, no interest in mealworms was apparent.

DISCUSSION

Based on this report and that of Williams (1919), the habits of *Epyris* are seen to parallel remarkably those of some of the primitive fossorial wasps. Certain Pompilidae, for example, commonly build cells from the sides of digger wasp burrows (e.g., Evans, 1974) and some Sphecidae of genera such as *Chlorion* regularly nest from pre-existing burrows (e.g., Peckham and Kurczewski, 1978). Man-

dibular prey carriage over the ground also occurs in both of these families, and the manner of dragging the prey backward (Fig. 2a) is remarkably like that of many Pompilidae. Williams was, however, correct in characterizing carriage such as that shown in Figure 2b as unique.

Members of other genera of Bethylidae are known to carry their prey to a second site for oviposition after being stung; this includes *Bethylus*, *Holepyris*, *Parascleroderma*, and to a certain extent *Allepyris* (Yamada, 1955). However, only *Epyris* actually constructs a nest. Further work regarding the comparative ethology of *Epyris*, as well as other members of this family should prove very rewarding.

ACKNOWLEDGMENTS

This work was partially supported by National Science Foundation grants DEB75-17142 and BNS78-17818 to Howard E. Evans. We thank T. J. Spilman of the USDA Systemic Entomology Laboratory for identifying the tenebrionid larvae.

LITERATURE CITED

- BRIDWELL, J. C.
1917. A note on *Epyris* (Hymenoptera, Bethylidae) and its prey. Proc. Haw. Ent. Soc. III(4):262-263.
1919. Some notes on Hawaiian and other Bethylidae (Hymenoptera) with the description of a new genus and species. 2nd paper. Proc. Haw. Ent. Soc. IV(2):291-314.
- EVANS, H. E.
1964. A Synopsis of the American Bethylidae (Hymenoptera, Aculeata). Bull. Mus. Comp. Zool. 132(1):1-222.
1974. Digger wasps as colonizers of new habitat. J. N.Y. Ent. Soc. 82(4):259-67.
1978. The Bethylidae of America north of Mexico. Mem. Am. Ent. Inst. No. 27. 332 pp.
- GORDH, G.
1976. *Goniozus gallicola* Fouts, a parasite of moth larvae, with notes on other bethylids: (Hymenoptera: Bethylidae, Lepidoptera, Gelechiidae). U.S.D.A. Tech. Bull. 1524, 27 pp.
- GORDH, G. AND H. E. EVANS
1976. A new species of *Goniozus* imported into California from Ethiopia for the biological control of pink bollworm and some notes on the taxonomic status of *Parasierola* and *Goniozus* (Hymenoptera: Bethylidae). Proc. Ent. Soc. Wash. 78(4):479-89.
- MALYSHEV, S. I.
1968. Genesis of the Hymenoptera and the Phases of their Evolution. Methuen & Co., Ltd., London. 319 pp.

PECKHAM, D. J. AND F. KURCZEWSKI

1978. Nesting behavior of *Chlorion aeriarium*. Ann. Ent. Soc. Am. 71(5):758-61.

RICHARDS, O. W.

1939. The British Bethylidae. Trans. Roy. Ent. Soc. London. 89(8):185-344.

SCHAEFER, C. H.

1962. Life history of *Conophthorus radiatae* (Coleoptera: Scolytidae) and its principal parasite, *Cephalonomia utahensis* (Hymenoptera: Bethylidae). Ann. Ent. Soc. Am. 55(5):569-77.

WILLIAMS, F. X.

1919. *Epyris extraneus* Bridwell (Bethylidae), a fossorial wasp that preys on the larva of the tenebrionid beetle, *Gonocephalum seriatum* (Boisduval). Proc. Haw. Ent. Soc. IV(1):55-63.

YAMADA, YASUJI

1955. Studies on the natural enemy of the woollen pest, *Anthrenus verbaci* Linne (*Allepyris microneurus* Kieffer) (Hymenoptera, Bethylidae). Mushi. 28(3):13-29.

NYMPHAL HABITAT OF *OLIARUS VICARIUS*
(HOMOPTERA: CIXIIDAE), AND POSSIBLE ASSOCIATION
WITH *APHAENOGASTER* AND *PARATRECHINA*
(HYMENOPTERA: FORMICIDAE)¹

BY C. R. THOMPSON,² J. C. NICKERSON,³ AND F. W. MEAD³

Oliarus is a cosmopolitan genus represented in North America north of Mexico by 51 species (Mead 1968). The most recently published key is found in a preliminary revision by Ball (1934) in which 31 species of *Oliarus* are recognized. Mead (1968) showed that *O. vicarius* (Walker) and *O. quinquelineatus* (Say) are so similar in morphology and habits that misidentifications are made. Mead stated that *O. vicarius* ranges only from North Carolina southward to Florida and, with few exceptions, is restricted to the coastal plain. *O. quinquelineatus* is widespread in the eastern half of North America. Its range overlaps that of *O. vicarius* as far south as Gainesville, Florida.

Little is known of the nymphal habitat and behavior of *O. vicarius*. Prior to the report of Sheppard *et al* (1979) nymphs of *O. vicarius* were unknown. They were found by Sheppard *et al* (1979) in unoccupied galleries in mounds of the red imported fire ant, *Solenopsis invicta* Buren, and also in rotten stumps and logs. We here give further information on nymphal habitat and adult flight patterns. In addition, observations are given for 2 ant species frequently found with *O. vicarius* nymphs.

METHODS

In 1976, *O. vicarius* nymphs and adults were found ca. 30 km east of Silver Springs, Florida, in stands of sand pine, *Pinus clausa* (Champm.) Vasey. Also present were saw-palmetto, *Serenoa repens*

¹Florida Agricultural Experiment Station Journal Series No. 2139 and Contribution No. 462, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services.

²Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611.

³Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P. O. Box 1269, Gainesville, FL 32602.

Manuscript received by the editor January 18, 1980

(Bartr.) Small, and one or more species of scrub oak, *Quercus spp.*, typical of sand pine forest. *O. vicarius* nymphs were found beneath the numerous logs and stumps in mature stands of sand pine and oak. Records were made of nymphal chamber construction, log dimensions, and state of decay.

Late-instar nymphs were brought to the laboratory for rearing. *O. vicarius* nymphs, along with the rotten wood and wax fibers of their original chambers, were placed on moist cotton in Wilson cells. The ambient temperature was held at ca. 21°C. A mass of eggs was kept in a tightly sealed shell vial with material from beneath the logs.

O. vicarius adults were recorded for the years 1969–76 from a blacklight trap located adjacent to turkey oak and pine woods at the Division of Plant Industry, Doyle Conner Building, Gainesville, Florida.

RESULTS AND DISCUSSION

When oak and pine stumps and logs were overturned, masses of wax fibers invariably indicated an *O. vicarius* chamber. The white, opaque, fluffly lining of the chambers consisted of numerous wax fibers (1–3 mm long) produced from wax plates on the abdomen of the nymphs (Mead 1968). When nymphs were disturbed, they appeared to drop their wax fiber “tails” or to knock them off while escaping.

Nymphs were found beneath logs and stumps ranging from dry and relatively decay-free to almost fully decayed and easily pulled apart; all were partially buried in the duff of the forest floor. Nymphal collection data are presented in Table 1.

The ant, *Aphaenogaster carolinensis* Wheeler, was collected on 5 occasions in or near the cixiid nymphal cells. When one stump was overturned, an *Aphaenogaster* worker grasped an *O. vicarius* nymph and attempted to escape. Nymphs were not attacked when placed in vials with unfed *Aphaenogaster* workers. Nymphs were also collected twice with another ant, *Paratrechina vividula* Nylander. These observations parallel those of Myers (1929) who found an association between *Odontomachus brunneus* Patton and cixiid nymphs of *Mnemosyne cubana* Stål.

Backlight collections of *O. vicarius* adults are summarized in Fig. 1. This trap was located approximately 80 km northwest of the study area. Adults were collected only from April through July. Nymphs

Table 1. *Oliarus vicarius* collection data for 1976, in the Ocala National Forest.

Date	# Nymphs	# Adults	# Cells	Cell Dia. (cm)	Log Dia. (cm)	Notes
22 January	13	0	0	—	—	<i>Aphaenogaster carolinensis</i> colony adjacent (A2cm) to each of the 3 <i>O. vicarius</i> chambers. Turkey oak stumps.
22 March	0	2	—	—	—	On sand pine trunk in mature stand bordering large clearing.
31 March	1	1	1	—	—	Late instar (wing pads extended to 2nd abdominal segment). <i>A. carolinensis</i> workers nearby. Oak stump.
	0	0	3	5.5, 5.8, 6.1	7.15-13.0	1 exuvia. Oak saplings.
	0	1	1	2.5	—	Teneral adult with <i>A. carolinensis</i> workers and pupae. Oak stump.
	2	1	2	10	10	<i>Paratrechina vividula</i> workers in both cells. Pine log.
	1	0	2	—	13, 15	1 exuvia. Pine log.
9 April	0	0	7	2.5, 2.5, 3.8, 1.3, 5.1, 3.8	—	Pine logs. An exuvia was found in each of 2 cells, 3 exuviae were found in the large cell. 1 exuvia found under log without cell.
12 October	11	0	2	—	7.6, 3, 10, 7, 7, 5, 6.3	Most not in distinct cells. 1 nymph with <i>P. vividula</i> . Nymphs medium sized.

were found in rotten wood chambers January through March. One hundred seventeen nymphs hatched ca. 4 June from a mass of eggs collected 31 March beneath a log. In late March, a late-instar nymph and a teneral adult were collected, while only exuviae were found under the logs in early April. In October, medium-sized nymphs were found beneath logs. These data suggest a univoltine cycle in which these insects overwinter as late-instar nymphs, emerge, and mate during March–July. Eggs deposited under logs hatch, and the nymphs develop during the summer and fall.

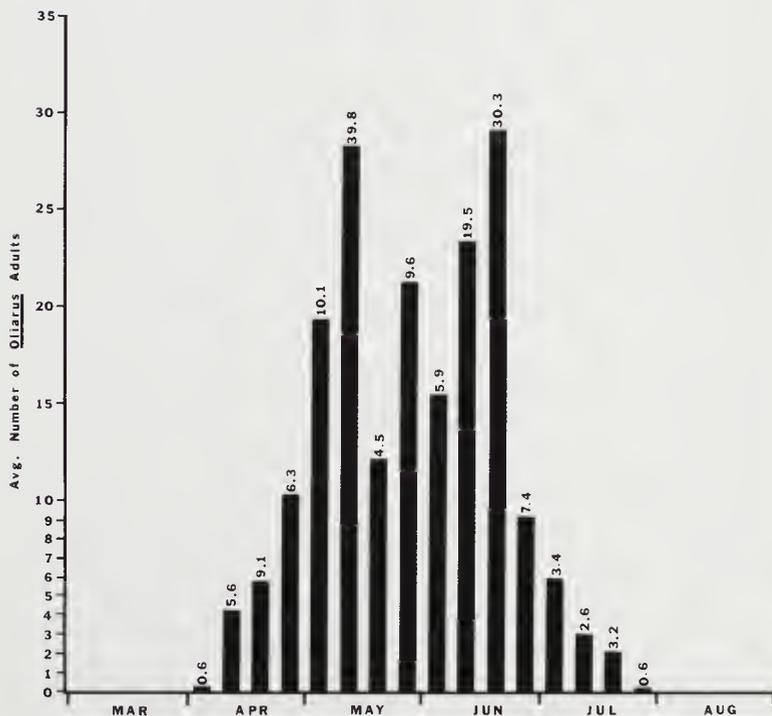


Fig. 1. Average weekly catch of *Oliarus vicarius* adults collected from a blacklight trap maintained at the Division of Plant Industry, Gainesville, for the years 1969-1976. No *O. vicarius* adults were captured during the months not shown. Confidence intervals are given for each average weekly collection.

CONCLUSIONS

Wax-fiber lined chambers found beneath pine and oak logs or stumps indicate the habitat of the nymphs and teneral adults of *O. vicarius*. We suggest that some type of symbiotic relationship exists between *O. vicarius* and the ants, *Aphaenogaster carolinensis* and *Paratrechina vividula*. Such a relationship is indicated by the repeated collections of the ants, especially *Aphaenogaster*, and *Oliarus* in close proximity. It is also possible that the presence of *Aphaenogaster* and *Oliarus* under the same logs is the result of similar habitat requirements. We suspect that the *Oliarus* nymphs feed on the exposed roots of pine, saw-palmetto, or oak that are beneath the logs.

ACKNOWLEDGEMENTS

We thank Mr. G. Hemingway of the U. S. Forest Service for permission to work within the Ocala National forest; and Dr. William F. Buren for identifying the ants.

LITERATURE CITED

- BALL, E. D.
1934. The genus *Oliarus* and its allies in North America. J. Wash. Acad. Sci. 24(6):268-276.
- MEAD, F. W.
1968. A revision of the genus *Oliarus* in North America, north of Mexico (Homoptera:Cixiidae). Ph.D. Dissertation. North Carolina State University. Raleigh, North Carolina xxxiv, 398 p., 595 fig.
- MYERS, J. G.
1929. Observations on the biology of two remarkable cixiid plant-hoppers (Homoptera) from Cuba. Psyche 36(4):283-292, 1 pl.
- SHEPPARD, C., P. B. MARTIN, AND F. W. MEAD.
1979. A planthopper (Homoptera:Cixiidae) associated with red imported fire ant (Hymenoptera:Formicidae) mounds. J. Georgia Entomol. Soc. 14(2):140-144.



SEXUAL COMPETITION FOR SPACE OF THE PARASITE
XENOS PALLIDUS BRUES IN
MALE *POLISTES ANNULARIS* (L.)
(STREPSIPTERA, STYLOPIDAE, AND
HYMENOPTERA, VESPIDAE)*

BY S. W. DUNKLE
Department of Entomology, University of Florida
Gainesville, Florida 32611

INTRODUCTION

Xenos pallidus Brues is the only known stylopid parasite of *Polistes annularis* (L.) and is apparently restricted to this host (Bohart, 1941, and personal communication, 1979). *X. pallidus* within the host abdomen absorb nutrients directly from the blood. When mature the head and thorax is protruded between two of the wasp's abdominal segments. The female remains a permanent larviform parasite while the male metamorphoses to pupa and adult. The male emerges and flies in quest of a female for his lifespan of a few hours. Eggs hatch within the body of the female and the larvae crawl from her brood chamber onto the surface of the host. Eventually they find and bore into larvae of *P. annularis*. Two or more generations of parasites develop per season and apparently overwinter as adult females in queen *annularis*.

During the period 7 October-12 November 1979 I collected *P. annularis* on Newnan's Lake, near Gainesville, Florida. The colonies collected contained a total of 13372 queens and 11542 males. The queens were used for venom extraction and are not included in the following discussion, but my subjective impression while sexing the wasps was that the males were more often parasitized. Between 17 November and 23 November 1979, 1691 queen and 331 male *annularis* were collected at several other lakes near Gainesville. These queens were also used for venom extraction, and since only 3 of the males were parasitized by *pallidus*, only males from Newnan's Lake are used in the analysis which follows.

*Florida Agricultural Experiment Station Journal Series, number 2267.

Manuscript received by the editor April 3, 1980.

METHODS

The *annularis* colonies collected were built over the water, primarily under branches of bald cypress, *Taxodium distichum*. Plastic bags were carefully slipped around the nests, and the bag was tied shut and placed in a cooler. The wasps were killed by freezing, and the parasitized males preserved in alcohol. The abdominal sclerites were separated with a dissecting needle while the wasps were examined at 20 \times to locate all exerted *pallidus*, including collapsed male puparia. Statistical analysis was performed using chi-square tests applied to contingency tables as described by Siegel (1956). Considerable lumping of data was necessary to perform the test in some categories.

RESULTS

Sex ratio of *Polistes annularis*:

Sex ratios of both wasp and parasite in this study are of course the ratios only at the time of collection in the life cycle of each. The ratio of male to female *annularis* at Newnan's Lake was 1.04:1 on 23 Oct. but decreased to 0.21:1 on 12 Nov. 1979 as the males died or left the nests at a greater rate than the females. Few of the wasps were foraging during the collection period. Therefore one would expect parasitized and unparasitized males to be otherwise equal with respect to predation pressure and energy consumption, and the parasitized individuals to die sooner. The per cent of parasitized males should decrease with time, but the data available for 4 dates show no clear trend. The per cent of males parasitized on 23 Oct. was 2.1, on 26 Oct. 8.4, on 5 Nov. 5.6, and on 12 Nov. 2.5, from 529, 309, 321, and 279 males collected on those days respectively.

Number of *Xenos pallidus* in individual male *Polistes annularis*:

Table 1 shows the number of male wasps with various combinations of male and female parasites. Only 1 host had as many as 6 female *pallidus*, while 6 had 6-8 males, possibly indicating that the male parasite extracts less nourishment from the host, because males are smaller. Bohart (1941) stated that males may decrease host survival due to evaporation of water from the empty puparia and invasion of fungi into the puparia. In the present study all but 6 of the 423 male *X. pallidus* had emerged. Fungus invasion did not appear to be a major cause of host mortality. Only a few of the puparia were slightly

moldy, and 3 of the male still in pupal cases had apparently died and become moldy. The average number of parasites per infested host was 2.1.

Table 2 compares the number of hosts observed with each parasite load to the number expected from a truncated negative binomial distribution obtained by modifying the method of Crofton (1971). This method predicts the number of hosts for each parasite load by referring to the pattern established with small parasite loads, in this case the number of hosts observed with 0-3 parasites. Table 2 shows an extremely close correspondence between observed and expected numbers of hosts until the parasite load reaches 9 and 10 per host. Thus 9 or more parasites probably kill the host relatively rapidly.

Sex ratio of *Xenos pallidus*:

The *Xenos* sex ratio was 423 males to 772 females or 1:1.83. This ratio probably results from the more rapid death rate of hosts carry-

Table 1. Number of male *Polistes annularis* with each combination of male and female *Xenos pallidus* parasites, collected at Newnan's Lake, Alachua Co., Florida, 7 Oct-12 Nov 1979.

Males per host	Females per host							Hosts
	0	1	2	3	4	5	6	
0	10973	246	56	15	3	4	1	325
1	55	55	24	13	6	2		155
2	9	13	11	5	2	3		43
3	6	5	7	4	2	2		26
4	1	2	3	1	2			9
5	1	2	2					5
6		1	1					2
7			1					1
8	1	1	1					3
Total Hosts	73	325	106	38	15	11	1	569

Table 2. Number of male *Polistes annularis* observed with 0 to 10 *Xenos pallidus* parasites compared with the number expected from a truncated negative binomial distribution, truncated at 3 parasites per host.

	Parasites per host										
	0	1	2	3	4	5	6	7	8	9	10 or more
Observed	10973	301	120	58	33	25	14	9	6	2	1
Expected	10972	302	118	60	34	21	13	9	6	4	8

ing male parasites. At first sight, this sex ratio seems contradicted by the higher maximum number of male parasites per host. I account for this discrepancy by postulating a short emergence season for the male *pallidus*. If, in a host with several male parasites, all the males emerged in rapid sequence before the host could die from the effects of desiccation, a situation would exist in which relatively fewer of the hosts that had carried males would be alive at any one time, but some of them could show high numbers of males per host. Other data from table 1 agree with this explanation of the sex ratio in that there were 325 hosts with just females and 244 with just males or with both males and females present. Antagonistic to this explanation is the probability that over 6 female *pallidus* kill the host outright so that we do not see these in the sample at all.

Location of *Xenos pallidus* in the host:

The *Xenos* exerted themselves under the edges of the sclerites of the second to the sixth abdominal segments posterior to the waist. The parasites showed a strong preference for a dorsal position on the abdomen, for several probable reasons. First, the parasite could force its way out more easily dorsally because the tergites separate when the wasp flexes its abdomen, while the sternites are compressed. Second, the tergites cover more of the surface of the abdomen than the sternites. Third, it would seem that natural selection would select for females to locate dorsally because they would be easier for males to fly to and mate with, especially if the female were located posteriorly. How mature stylopids penetrate the intersegmental membranes of the host has not been described.

No *pallidus* were located in segment 1 of the host in this study. However, Pierce (1909) did find one male protruding between the first and second tergites. As seen throughout the following discussion male *pallidus* are characteristically located more anteriorly than females. Only 1 female was found in segment 2 and only 1 male in segment 6. The maximum number of males under tergites 2, 3, 4, and 5 was 3, 4, 3, and 1 respectively, for males under sternites 2-5 the maximum numbers were 1, 2, 2, and 1 respectively. The maximum numbers of females under tergites 3, 4, 5, and 6 were 1, 3, 3, and 2 respectively, for females under sternites 3-6 the maximum numbers were 2, 2, 2, and 1 respectively.

Data on parasite position in the host was divided into 5 categories: (1) Only females in host, (2) Only males in host, (3) Equal numbers of both sexes in host, (4) Fewer males than females in host, and (5) More males than females in host. These categories had subcategories based on the sex combination of the parasites in each host.

Parasite position with only female *Xenos pallidus* in the host:

Table 3 shows that as the number of female parasites in a host changes, the location of the parasites under the tergites of the host significantly changes ($p < 0.001$). When only one female is present in a host, 90.8% of the dorsally located females had a preference for the fifth tergite. As the number of females in a host increases, the proportion under tergite 5 decreases, while the proportion under tergite 4, and possibly tergite 6, increases. Only 3 females were located under the third tergite in this category.

Table 3. Contingency table for correlation between number of female *Xenos pallidus* in male *Polistes annularis* and the tergite of the abdomen where the parasites were located. Parentheses indicate percentages of each row. $C = .41$, $X^2 = 78.4$, significant at $p < 0.001$, $DF = 6$, $N = 396$.

Number of females in host	Number of Abdominal Tergite			Total
	3 and 4	5	6	
1	12 (5.0)	217 (90.8)	10 (4.2)	239
2	18 (19.2)	69 (73.4)	7 (7.5)	94
3	10 (29.4)	23 (67.7)	1 (2.9)	34
4, 5, or 6	16 (55.2)	9 (31.0)	4 (13.8)	29
Total	56	318	22	396

Just 45 females in this category were located under the sternites, compared to 396 under the tergites. If females located ventrally are added to Table 3, the change in parasite location is still significant ($p < 0.001$). Most of the females (32/45) under the sternites were under the fifth sternite. As the number of females in a host increases, the proportion under sternite 5 increased similar to the proportion under tergite 4.

Thus intrasexual competition causes a tendency for the "losing" females to be shifted first to the fourth tergite, then others to the fifth sternite. One might expect the preferred fifth tergite position to be filled before the other positions were accepted. If we assume that 2 females fill the fifth tergite position, only 29 of 79 hosts with 2 or more

females show the filled condition. However, 72 of the 79 hosts had at least 1 female under the fifth tergite. Thus perhaps only 1 female under the fifth tergite fills that location so far as intrasexual competitive effect is concerned.

Parasite position with only male *Xenos pallidus* in the host:

Table 4 shows that the position of male parasites significantly changes as the number of parasites changes ($p < 0.02$). Most of the male *pallidus* present alone in a host prefer a location under the fourth tergite. Only 7 of the males were in the second segment, and only 6 in the fifth segment. Nine of the 14 males located under sternites were under sternite 4. The proportion of those under sternite 4 increases as the number of males per host increases. When 2 males are present in a wasp, one goes to the fourth tergite and the other to the third tergite. With 3 to 8 males present in a host the preferred location is the third tergite. Thus the males exhibit the same pattern of intrasexual competition as the females. The losing males are shifted from the preferred tergite 4 to the next anterior tergite and then to sternite 4. As in the females, only 1 parasite seemed to fill the preferred position, since only 1 of the 18 hosts with 2 or more males had 2 males under the fourth tergite, but 14 of the 18 had at least one male there.

Position of male relative to female *Xenos pallidus* in the host:

Clearly the male *pallidus* tends to extrude from the host more anteriorly than the female. This tendency is probably related to the fact that males are shorter than females. Ten adult females had a head-thorax length of about 1.5mm, an abdomen length of 6-7mm. Three of the females contained larvae. The 3 male pupae retaining puparium caps had a head-thorax length of 2mm, an abdomen length of 2.5-3mm. Comparing the total length of the *Xenos* to the abdomen of the host, it appears that both sexes of parasites usually brace themselves near the base of the second abdominal segment of the host to extrude the cephalothorax.

Position of *Xenos pallidus* in the host when the number of each sex is equal:

Not enough data were available to test the position of females in this category. The males did not show a significant change of position in the host as number of parasites per host increased ($p > 0.05$). However, the trends seemed to be for the males to prefer segment 3

Table 4. Contingency table for correlation between number of male *Xenos pallidus* in male *Polistes annularis* and the abdominal sclerite where the parasites were located. Parentheses indicate percentages of each row. $C = .29$, $X^2 = 10.1$, significant at $p < 0.02$, $DF = 3$, $N = 108$.

Number of males in host	Abdominal Tergite or Sternite		Total
	2 and 3	4 and 5	
1	19 (34.5)	36 (65.5)	55
2	9 (50.0)	9 (50.0)	18
3	10 (55.6)	8 (44.4)	18
4, 5, or 8	13 (76.5)	4 (23.5)	17
Total	51	57	108

Table 5. Contingency table for correlation between number of female *Xenos pallidus* in male *Polistes annularis* and the abdominal sclerite where the parasites were located when one male parasite was also present. Parentheses indicate percentages of each row. $C = .25$, $X^2 = 8.3$, significant at $p < 0.05$, $DF = 3$, $N = 121$.

Number of males (m) and females (f)	Abdominal Tergite or Sternite		Total
	4	5 and 6	
1m2f	6 (12.5)	42 (87.5)	48
1m3f	5 (12.8)	34 (87.2)	39
1m4f	8 (33.3)	16 (66.7)	24
1m5f	4 (40.0)	6 (60.0)	10
Total	23	98	121

and the females segment 5 in all subcategories. These data could mean that intersexual competition prevents the change in parasite position due to intrasexual competition that we saw above.

Position of *Xenos pallidus* in the host when the number of males was less than the number of females:

Table 5 indicates that an increasing number of females in hosts with one male caused a significant shift in position of the parasites (< 0.05). With an increasing number of females, the proportion in segment 5 decreases while the proportion in segment 4 increases. This is basically what we see in Table 3 where only female *pallidus* were present in a host, and suggests that mostly intrasexual competition is occurring. In this category, 2 or 3 females more often filled the preferred position at tergite 5 than when only females were present in a host, because 1 host had 3 females at tergite 5, 22 had 2, 17 had 1,

and 5 had 0 there. This filling effect may be due to intersexual competition, in which more females pile up at the preferred location before overcoming the effect of the male present.

Not enough data were available to test the effect on position of increasing number of males or when two or more males were present in a host in this category, but generally the females preferred segment 5 and the males segment 3 as before. When all the data for females in this category were lumped into three subcategories in which either 1, 2, or 3 males were present with the females, there was no significant change in the positions of females as number of males increased ($p > 0.05$). In other words, the data analyzed this way indicated either no intersexual competition, or that the intersexual competitive effect of 1 male was as strong as the effect of 3 males.

Position of *Xenos pallidus* in the host when the number of females was less than the number of males:

With one female present in a host, increasing number of males from 2 to 8 had no significant effect on position of the males ($p > 0.05$). This result is different from that of the preceding section where we saw more intrasexual competition between females in hosts with one male. In addition, with 2 females in a host with 3 to 8 males, no significant position changes in the males were observed ($p > 0.05$). These data seem to mean that the intersexual competitive effect on position is stronger than the intrasexual effect and the intersexual and intrasexual competitive effect of females is stronger than that of males.

There were not enough data to test female position in this category, but where one female was present with 2 to 8 males, 17 of 23 females were under the fifth tergite. Where two females were present with 3 to 8 males, 25 of 33 females were under the fifth tergite. In this category, males were rather scattered among segments 2-4. In summary, no intrasexual competition is seen in this category, but females seem to take their preferred position and suppress position changes of the males.

DISCUSSION

Notes on small collections of *pallidus* have been given by several investigators. Hubbard (1892) confined and studied a nest of Florida *P. annularis* for three weeks. He noted that parasitized hosts rarely left the nest, and states that the parasites extrude from the abdomen

before the wasp emerges from the pupa. Brues (1905) compared a nest of *annularis* taken in July with one collected in October in Texas. In the adult October wasps he found *X. pallidus* larvae as well as adults. Thus possibly in the present study non-extruded *Xenos* may have been missed. However, I dissected 49 male *P. annularis* whose abdomens looked abnormal, but no *X. pallidus* were found. Brues suggested that all the wasps carrying male *Xenos* die before the next spring since he saw none with male pupal cases in the spring. This would also mean the death of the female *pallidus* in the same wasp carrying males. If this is so, the effect on the populations of both host and parasite could be severe.

Pierce (1909) reported on two large colonies of Texan *annularis* taken in September and kept alive through October containing 1311 male and 242 female wasps. The males were 19.8% parasitized by *pallidus*, the females 2.9% parasitized. One male wasp carried 15 male *pallidus*, whereas the highest parasite load in the present study was 8 males with 2 females. Pierce states that several queen wasps with empty male *pallidus* puparia were found hibernating, but whether such queens could reproduce the next spring remains unproved. Pierce (1909) also states that male *pallidus* did not protrude from the host until several days after the host left its pupal cell, a contradiction with Hubbard (1892). The winged males left the host 10–17 days after the host became adult.

Pierce (1918) points out that in *Delphax* (Homoptera) the female strepsipteran is located more anteriorly in the host than the male probably because the female is smaller than the male, the reverse of the case in *pallidus*. Salt (1927) found no morphological change at all in a small series of *annularis* carrying *pallidus*, nor was any change except deformation of the abdomen noted in the present study.

According to Bohart (1941) only two strepsipterans are known to parasitize *Polistes* in North America, *pallidus* in *annularis* and *X. peckii* Kirby in several other species. The most extensive study of *X. peckii* was done by Schrader (1924). She found extreme differences in infestation rates, from 0 to 25%, in different localities in New England. The parasites extruded from the host after the wasps emerged from pupae, the males 5–10 days before the females. The sex ratio of larval *X. peckii* was 38 male: 37 female. Further work on both species of *Xenos* in North America, and comparison between them, is certain to provide much new information on the evolution of parasite/host interactions in a very interesting system.

ACKNOWLEDGEMENTS

I thank Gary Fritz and particularly Sandra Skar for help in collecting the wasps. Special thanks are due Carmine Lanciani for criticizing the manuscript and performing the truncated negative binomial distribution analysis.

LITERATURE CITED

- BOHART, R. M.
1941. A revision of the Strepsiptera with special reference to the species of North America. Cal. Univ. Publ. Entomol. 7:91-159.
- BRUES, C. T.
1905. Notes on the life history of the Stylopidae. Biol. Bull. 8:290-295.
- CROFTON, H.D.
1971. A quantitative approach to parasitism. Parasitology. 62:179-183.
- HUBBARD, H.G.
1892. The life history of *Xenos*. Can. Entomol. 24:257-261.
- PIERCE, W. D.
1909. A monographic revision of the twisted winged insects comprising the order Strepsiptera Kirby. U. S. Nat. Mus. Bull. 66:1-232.
1918. The comparative morphology of the order Strepsiptera together with records and descriptions of insects. Proc. U. S. Natl. Mus. 54:391-501.
- SALT, G.
1927. The effects of stylopization on aculeate Hymenoptera. J. Exp. Zool. 48:223-331.
- SCHRADER, S. H.
1924. Reproduction in *Acroschismus wheeleri* Pierce. J. Morph. Physiol. 39:157-205.
- SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y. 312 p.

A REMARKABLE NEW SPECIES OF *PRO CERATIUM*,
WITH DIETARY AND OTHER NOTES ON THE GENUS
(HYMENOPTERA: FORMICIDAE)¹

BY WILLIAM L. BROWN, JR.
Department of Entomology
Cornell University
Ithaca, New York 14853

INTRODUCTION

The primary purpose of this paper is to describe an extraordinary new insect from Madagascar. This ant has, in effect, two tail ends, one of which, the false end, is a logical extension of the tendency in certain *Proceratium* species (e.g., *P. pergandei* and *P. micrommatum*) for the second gastric segment to extend rearward, while the true gastric apex projects from its ventral aspect in an anterior direction. The adaptive reason for this down-and-forward orientation of the true abdominal apex is not entirely understood, though it is clear that the deployment of the sting is usually an important feature of prey-attack in ponerine ants.

***Proceratium diplopyx* new species**

Figs. 1, 2.

Holotype worker: TL 6.0, HL (including clypeus) 1.44, HW 1.25, ML (beyond clypeus) 0.15, scape L 1.12, eye diameter 0.12, WL 1.77, petiole L in side view 0.70, gaster L 1.97, hind tibia L 1.26, hind femur L 1.53 mm. CI 87, SI 90. (A single paratype worker hardly differs from the holotype by more than the usual errors of measurement, except that the head is slightly wider: HW 1.29 mm, CI 90.)

Habitus well portrayed in figures 1 and 2. Figure 2 shows the head tilted slightly back from the full-face view plane, so that the posterior cephalic margin appears straight and is slightly surpassed by the scapes laid back in repose. In perfect full-face view, the center of the posterior margin is feebly concave, and the scape laid back does not

¹A report of research from the Cornell University Agricultural Experiment Station, New York State College of Agriculture and Life Sciences. The research was supported in part by National Science Foundation Grant GB-31662

Manuscript received by the editor February 14, 1980

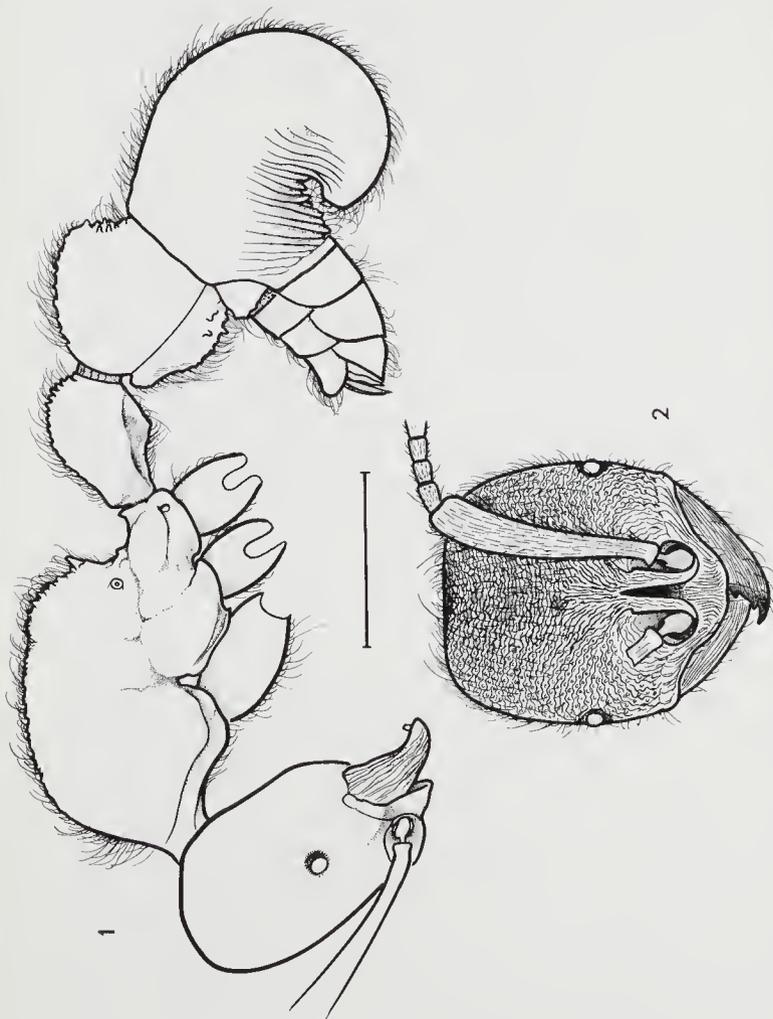


Fig. 1. *Procerattium diplopius* new species, nototype worker, side view; only the silhouetted body pilosity is shown, but that of head and cephalic appendages is omitted. Fig. 2. Same, front view of head tilted slightly back from full-face plane, showing sculpture and pilosity; right antenna mostly omitted. Drawings by Susan Poulakis. Scale bar 1 mm long.

quite attain it. Median clypeal lobe raised, broad and rounded, with a faint median sulcus and a tendency toward flattening, or even shallow emargination, of the middle of its anterior border, especially as viewed when the head is tilted back. Frontal area narrow-lanceolate and deeply impressed. Eyes each composed of a single, large, clear, convex facet that projects beyond the lateral margins of the head in full-face view.

Mandibles each with 4 sharp teeth, including the apical; because of full closure, the presence of an additional tooth at the basal angle cannot definitely be excluded as a possibility. Labrum retracted against the rest of the under-mouthparts, difficult to see, but appears to be medially sulcate on its visible (extensor) surface and weakly bilobate, with a median excision of its free apical margin. Outside the lateral labral margins can be seen clearly 3 segments of each maxillary palp and 2 segments of each labial palp, so that the palpi must include at least 4 and 3 segments respectively.

Underside of head shallowly concave and weakly rugulose, sunken between thick, rough, raised, ventrolateral cephalic margins ("occipital carinae") that originate near the mandibular insertions.

Antennae with segment II (pedicel) longer than broad; III-VIII about as long as broad to slightly longer than broad; IX-XI slightly broader than long; apical segment about $2\frac{1}{2}$ times as long as broad; the length-breadth ratios vary somewhat in different perpendicular views of the antennal axis.

Trunk as seen from dorsal view weakly pyriform, evenly convex and slightly broader across pronotum (0.94 mm in holotype) than across propodeum and metathorax (0.76 mm), with only a very feeble constriction near truncal midlength, but convexities of mesonotum and propodeum as seen in side-view profile separated by a slight but distinct metanotal impression. Propodeum strongly convex in both directions, passing into declivity through a smooth curve flanked on each side by a short, upturned tooth; declivity smooth and shining, flanked on each side by a low margin bearing a short denticle at the bottom of each concavity, and an upturned, triangular, metapleural tooth or lobe at its ventral extremity.

Propodeal spiracle small, with a nearly round aperture, directed posterolaterad. A curved and rather deep sulcus marks the approximate juncture of propodeum with meso- and metathoracic sclerites below it.

Petiolar node pyriform or subclavate, with feebly suggested peduncle, about 0.47 mm wide across the widest part (near posterior end) in holotype, and about 0.66 mm long. Ventral keel forming an obtuse tooth just behind midlength.

Postpetiole with broadly rounded sides, diverging caudad to the greatest width, a little before the posterior margin (W 0.89 mm in holotype), which is rather sharply constricted. Median posterodorsal surface of postpetiole weakly set off as a high, rounded boss; anteroventral shelf or lip well developed, trailing a short, septate carina caudad.

The remainder of the abdomen forms the most extraordinary structure of this body region known among the ants (figure 1). The second gastric (fourth true abdominal) tergum is grossly hypertrophied posteriad beyond the anteroventral opening, from which issues the true abdominal apex, with the exerted apical segments extending ventro-cephalad. The hypertrophied posterior extension of the second gastric tergum is permanently curled anteroventrad to form a short, bluntly rounded, false gastric apex, so that the real sternum of this segment is externally represented only by a small anteroventral piece, triangular in side view. The incurled ventral surface of the tergal extension is furnished with a series of coarse, sharp rugae that tend to extend vertically or obliquely part way up the lateral surfaces, and run partly transversely across the concavity in the holotype (in the paratype worker, the posterior rugae tend to run lengthwise, following the curve of the curl). From above, the hypertrophied tergum is cylindrical, 1.3 mm long, with almost straight (very feebly concave), parallel sides and a broadly rounded posterior outline, and is almost exactly (0.87 mm) as wide as the postpetiole. (In the paratype, maximum postpetiole W 0.92 mm, maximum second tergal W 0.90 mm.)

In both specimens the gastric apex is extended as 3 stout visible segments and the strong, exerted sting; undoubtedly these are all retractile to some degree.

Legs rather long and slender, though both femora and tibiae are gradually incrassated from base toward apex; hind leg: femur L 1.53, tibia L 1.26, metatarsus L 1.0 mm. Tibial spurs one on each leg (small on mid tibia), pectinate, but only feebly so on mid tibia. Claws on all legs slender, simple.

Head, trunk, petiole and postpetiole densely and moderately coarsely sculptured, opaque generally, but with minor glancing reflections here and there from individual rugulae or the bottoms of punctures. On the head, the sculpture is finest and most shallow, with rugulosity running in the directions shown in fig. 2, and more or less longitudinally on the sides of the head. Mandibles (except for their smooth, shining apices), median clypeus and frontal lobes rather coarsely and unevenly striate. Trunk, petiole and postpetiole densely rugose to scabriculous, becoming scabriculous-muriculate, or even denticulate on propodeum, petiolar node, and both tergum and sternum of postpetiole. Hidden throughout these roughly sculptured surfaces are numerous small but deep punctures with central, piligerous tubercles. The rugae of the postpetiole are longitudinal and subconcentrically curved as seen from above.

Second gastric (fourth true abdominal) tergum predominantly smooth and shining over most of its dorsal, lateral and posterior surfaces, but with numerous, spaced piligerous papillulae throughout, giving way to piligerous punctures caudad, and to the aforementioned rugae ventrad. Apical segments of gaster delicately strigulate, shining. Legs and antennae finely and densely reticulate-punctulate, the antennae distinctly so, and matt; the legs more superficially so, and weakly shining in part. Coxae obscurely rugulose in addition.

Body and appendages covered with an abundant pilosity consisting of fine, curved, tapered, whitish hairs, mostly 0.05 to 0.2 mm long and obliquely standing (straighter and more erect on clypeus, antennae and legs). A short, dense pubescence is also present and widespread, and especially noticeable on antennae and legs, where it is appressed or subappressed and lies longitudinally, and on posterior surface of large gastric tergite, where it is mostly decumbent. Apical gastric segments, especially the last two, with luxuriant bands or brushes of long, fine, pale hairs.

Body color deep reddish-brown, almost mahogany; second gastric (IV abdominal) segment brighter, more reddish; mandibles, antennae, legs and apical gastric segments ferruginous yellow.

Queen, male and larvae still unknown.

Holotype (Muséum National d'Histoire Naturelle, Paris) and one paratype worker (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA) taken in a leaf litter berlesate in "forêt dense humide de moyenne altitude" (about 1000 m) at

Iaraka, on the eastern side of the Baie d'Antongil, Province de Tamatave, Malagasy Republic, on 26 November 1969, by J. -M. Betsch.

This altogether extraordinary ant is distinguished at once from its congeners by the strongly produced and downcurved "false apex" of the second gastric segment, as well as by the form of the propodeum, and several minor characters of sculpture, etc. It is the first species of its genus to be taken on Madagascar, and its must be placed in a species group of its own. Its relatively large size, large but single-faceted eyes, elongate petiole, coarse sculpture and developed propodeal teeth ally it with the *stictum* group of primitive species more closely than any other group.

Proceratium micrommatum (Roger)

(=*P. convexiceps* Borgmeier) new synonym

Earlier (Brown 1974:82) I called attention to the doubtful status of *P. convexiceps* Borgmeier (1957:120-122, fig. 34). Not only do samples of this complex (including new collections from Honduras: Lancetilla, near Tela; and 14 km S. La Ceiba; both in rotten logs, W. L. Brown, Jr.) vary in the development of the median clypeal process, which may be absent, weakly projecting, or strong, but it seems clear that the "Arbeiter" of *micrommatum* against which Borgmeier (1957:118-120) compared *convexiceps* was actually an ergatoid queen of *micrommatum*, so that differences in head shape, eye size and petiolar thickness are apparently only allometric caste differences.

A worker specimen of *P. micrommatum* from Honduras was dissected and proved to have maxillary palpi of 3 segments, the second segment having the "hammer-head" form characteristic of *Proceratium*, i.e., it is stalked from the side, and the apical segment has 3 long apical sensilla. Labial palpi with each 2 segments: basal segment narrower, apical segment claviform, with 3 long apical sensilla.

KEY TO NEW WORLD *PROCERATIUM*, WORKERS

1. Petiolar node in the form of a thick, erect scale with nearly parallel anterior and posterior faces (posterior face may be concave), apex truncate or subtruncate in side view; second gastric (IV true abdominal) segment curved downward, but neither

- strongly inflated nor produced caudad 2
 Petiolar node low and bun-shaped, or at least broad at base, with anterior and posterior faces strongly covering to a rounded apex; second gastric segment strongly vaulted, inflated, and produced caudad behind the anteroventrally-protrusible true apical segments 3
2. Size larger, head width >0.75 mm (SE U.S.) *croceum*
 Size smaller, head width <0.75 mm (L. Ontario and Massachusetts s. to Florida and Honduras) *silaceum*
3. Apical segments and sting issuing from near anteroventral end of second gastric segment, so that the sternum of this segment is very short—as seen from the side, not or scarcely more than half as long as sternum of preceding (postpetiolar) segment ... 4
 Apical gastric segments issuing from second gastric segment nearer to its posterior end, so that its sternum as seen from the side is subequal in length to that of the preceding segment (California) *californicum*
4. Larger species; head width without eyes >0.80 mm; anterior clypeal border produced as a median lobe that is emarginate apically 5
 Smaller species; head width without eyes <0.80 mm; anterior median lobe of clypeus absent or reduced to a small, rounded or single-pointed tooth 6
5. Very large species; head width >1.0 mm; petiole longer than deep, and slightly longer than broad in worker (Central America) *goliath*
 Medium-sized species; head width without eyes <1.0 mm; petiole about as high as long, and broader than long (forested E. USA north to Massachusetts) *pergandei*
6. Trunk in side view with dorsal outline evenly convex from pronotum to top of propodeal declivity (Mexico to Ecuador, Cuba) *micrommatum*
 Trunk in side view with propodeal dorsum feebly concave in outline, then raised as a rounded angle or boss where it meets the declivity (SE Brasil) *brasiliense*

Proceratium numidicum in Europe

Baroni Urbani (1977) calls into question my 1958 identification of *Proceratium numidicum* from Tirana, Albania, saying that "appar-

ently this specimen has not been studied by Brown himself, but by Wilson . . ." He adduces other circumstantial evidence to conclude that the Albanian specimen is really *P. melinum*. But Baroni Urbani never called for a loan of the specimen in question, which resides in the Museum of Comparative Zoology at Harvard University, and if he had done so, he would have been forced to conclude, as I was originally (Brown, 1958:334) after my own *personal* study of the same example, that the Tirana specimen is morphologically *P. numidicum*, and not *P. melinum*. The two species are in fact members of different species-groups. At my request, in 1955 or 1956, E. O. Wilson did compare the Albanian specimen with a type of *P. numidicum* (Brown, 1974: 82) in the Emery Collection. This comparison was based on my previous suspicion that the Albanian specimen (then under my care in MCZ) belonged to *numidicum*. Since that time, I have had ample opportunity to compare the relevant types directly with the Albanian specimen and to confirm once more my own opinion of its identity. Finzi's old determination as "*europaea*," as well as Baroni Urbani's conjecture, are both wrong. Unless the label data are in error, *P. numidicum* must be considered to occur in Balkan Europe.

EGG PREDATION IN *PROCERATIUM* AND SOME OTHER ANTS

The species of *Proceratium* are arthropod egg predators as far as is known. In *Proceratium*, *P. silaceum* has been observed feeding upon and storing eggs of spiders and (rarely) of another, unknown arthropod (Brown, 1958; the determination of *P. silaceum* was inadvertently omitted from the field and artificial nest observations). Since then, I have observed *P. pergandei* in Mississippi feeding on and storing spider eggs in a rotten-wood nest in nature; *P. micrommatum* from rotten-wood colonies from Lancetilla, near Tela, Honduras, feeding on spider eggs of two different kinds offered in the artificial nest; and *P. avium* carrying and storing eggs resembling spider eggs in Mauritius (Brown, 1974). Tests by me with all these species in the artificial nest failed to elicit any attempt by the ants to feed on sugary food, eggs of one or two kinds of millipedes, and various insect parts, but I did once get two *P. silaceum* workers to feed on a small droplet of yolk from a fresh hen's egg for periods of up to about 2 minutes at a time in the artificial nest.

Observations of *P. silaceum* in artificial nests indicate that in this species the reflexed gastric tip is used to tuck the slippery eggs forward toward the mandibles when the eggs are being carried by the ants. Eggs of prey are stored in the ant nest in large numbers, recalling seed storage by the true harvester ants in subfamily Myrmicinae. Since *Proceratium* conceivably may belong to a group not too distant from the parent stock leading to the Myrmicinae, one may wonder whether the egg-collecting habit could have served as a key preadaptation to seed harvesting.

Ants of the related ectatommine genus *Discothyrea* also feed on arthropod eggs, probably usually those of spiders (though one small, undetermined Australian species has been found in nests of other ants). *D. bidens* (or near) is one egg-feeder in the wet mountain forests of New South Wales (Brown, 1958; embryos found in eggs packed in 4 nests of this ant appear to be those of spiders). In 1960, I found tiny spherical ova resembling spider eggs in a small nest cavity of a *Discothyrea* species (group of *testacea*) on Barro Colorado Island in the Panama Canal Zone. In 1969, in wet mountain forest in Hogsback Reserve, eastern Cape Province, South Africa, I found numerous spherical eggs resembling those of spiders, and also a few more elongate ova, in a nest of *Discothyrea poweri* in rotten wood.

Oligomyrmex species (subfamily Myrmicinae) may often be specialist egg predators, particularly of eggs of termites in rotten wood. A populous colony of *O. urichi* that I found in rotten wood in forest along the Rio Don Diego, Guajira Dept., Colombia, contained many spherical eggs of an unknown arthropod, ranging in color from nearly white to reddish-brown in color, as though in different stages of cuticular tanning. These eggs were fed upon by soldiers and workers of the ant, and slowly disappeared during several months of captivity in a plaster-bottomed nest in the laboratory.

W. H. Gotwald has given me specimens of a small new West African species of *Plectroctena* recently described as *P. lygaria* by Bolton, Gotwald and Leroux (1976), that was found to have stored large number of millipede eggs in its nest. The adult of at least some of the larger *Plectroctena* species are predators of adult millipedes.

The above sampling, by no means exhaustive, should demonstrate that arthropod egg predation is a significant adaptive zone exploited by a variety of ants.

REFERENCES CITED

- BARONI URBANI, C.
1977. Les espèces européennes du genre *Proceratium* Roger (Hymenoptera: Formicidae). Mitt. Schweiz. Ent. Ges. **50**: 91-93.
- BOLTON, B., W. H. GOTWALD AND J.-M. LEROUX.
1976. A new West African ant of the genus *Plectroctena* with ecological notes (Hymenoptera: Formicidae). Ann. Univ. Abidjan (E) **9**: 371-381.
- BORGMEIER, T.
1957. Myrmecologische Studien. I. An. Acad. Sci. Brasil. Ci. **29**: 101-128.
- BROWN, W. L., JR.
1958a. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). Bull. Mus. Comp. Zool. Harv. **118**: 171-362.
1958b. Predation of arthropod eggs by the ant genera *Proceratium* and *Discothyrea*. Psyche **64**: 115.
1974. A remarkable new island isolate in the ant genus *Proceratium* (Hymenoptera: Formicidae). Psyche **81**: 70-83.
- SNELLING, R. R.
1967. Studies on California ants. 3. The taxonomic status of *Proceratium californicum* Cook (Hymenoptera: Formicidae). Contrib. Sci. Los Angeles Co. Mus. **124**: 1-10.

OBSERVATIONS ON SWARM EMIGRATIONS AND
DRAGGING BEHAVIOR BY SOCIAL WASPS
(HYMENOPTERA: VESPIDAE)*

BY RUTH CHADAB AND CARL W. RETTENMEYER
Biological Sciences Group, University of Connecticut
Storrs, Connecticut 06268, U.S.A.

Naumann (1975) reported the first evidence that several species of social wasps (Vespidae: Polybiini) use chemical trails to direct swarms to a new nest site. His observations were based on absconding swarms following army-ant raids. Those observations were corroborated by Jeanne (1975, 1980), and most recently by Forsyth (1978) and us. Incidental to investigating raids by army ants on social wasps, we observed that the movement of absconding wasp swarms did not always conform to the trail-following behavior as it has been described. In this report the typical emigrations of absconding swarms will be summarized followed by our observations on two unusual swarm movements and related dragging behavior.

Prior to the movement of a wasp swarm to a new site, some wasps run a few millimeters to centimeters on vegetation dragging their gasters in a zig-zag motion which deposits a chemical produced in Richards' gland (Naumann 1975, Jeanne 1980). Such dragging runs occur first on prominent vegetation near the swarm site and then in various directions from the swarm. Eventually dragging activity consolidates along a path to the new nest site. The behavior of subsequent wasps visiting the dragging sites differs: their gasters do not touch the substrate or move back and forth but they antennate the dragging sites. Those wasps use the chemical traces for orientation and are called "followers."

At the swarm site some workers returning to the swarm behave differently than do regular foragers. They run excitedly through, among, or over clusters of calm wasps. Since increased activity and flight follow, such behavior is considered important for stimulating the wasps to emigrate and is called "breaking behavior" (Naumann 1975).

Increasing numbers of wasps drag on vegetation along the route to the new nest and are gradually replaced by increasing numbers of follower wasps until numerous wasps are flying along the entire

*Manuscript received by the editor February 4, 1980.

route. After followers appear, the number of wasps at the swarm site dwindles rapidly, but there is continuous activity there as wasps fly in and out of the swarm. Movement of the swarm is completed in less than one hour. Since Naumann (1975) found similar behavior by species in four genera, *Angiopolybia*, *Leipomeles*, *Polybia* and *Stelopolybia*, it may be typical of all or most polybiines.

We have observed such behavior on several occasions in *Angiopolybia pallens* (Lepelletier) and *Polybia catillifex* Moebius when colonies moved after they were attacked by army ants. However, the behavior of the wasps was distinctly different following a raid by *Eciton rapax* Fr. Smith on a nest of *Polybia velutina* Ducke (colony V-535, Ecuador). The nest in a large *Codeum* bush was raided on 24-VI-1977 at 5:30 PM, and the wasps started a swarm on several leaves on the north side of the same bush 15–20 min after leaving the nest. The swarm consolidated on 2 leaves about 1.3 m north of the nest during the next 2 hours. Based on photographs of the swarm taken about 11:45 PM, there were 325–375 wasps in the colony.

At 1:40 PM the next day, 20 hours after the wasps absconded and more than 2 hours before the swarm moved, we located the new nest site on a wire under a nearby house. There were 17 wasps at the new location which was 8 m south of the swarm. Earlier in the day wasps were observed flying north and south from the swarm, but the northern flights were abandoned shortly after 1:00 PM. Despite the short distance between the swarm and the new nest, it was impossible for the wasps flying from the swarm at a height of 2.3 m to see the new site at a height of 1.8 m because it was hidden by the thick *Codeum* bush and an overhang on the side of the house. The new nest site would not be within sight of the wasps until they approached it at a height of about 1.5 m in the last 2 m.

The wasps did not fly directly to the new nest site but flew around the east or west sides of the *Codeum* shrub, a total flight distance of 9–10 m. Between the swarm and the new nest site there were approximately 3 m of *Codeum* foliage and 3 posts 1–2 m high. To see if we could stimulate dragging behavior, we placed a wooden chair in the flight path of the wasps at 2:36 PM in the area of about 3 m where there was no vegetation higher than a few centimeters and no posts. The wasps ignored this potential substrate for chemical marking.

At the swarm there was a high level of activity. A typical count at 2:22 PM showed 11 wasps arriving and 9 leaving per minute. Wasps were seen landing on the swarm and performing breaking behavior.

For example, a wasp with its wings raised at a 45° angle excitedly ran over the bodies of the wasps to the top of the leaf, turned and ran half the length of the leaf touching many wasps and again ran up through the center of the swarm before stopping to groom.

For more than 2 hr the number of wasps on the wire at the new nest site fluctuated from 7-25 (Table 1). Most were constantly palpating 35 cm of the wire with their antennae and mouthparts as they slowly walked back and forth over it. The activity was suggestive of cleaning since the wasps nibbled almost imperceptibly at the wire with mandibles that were barely open and moved their maxillae actively. No wasp was ever observed dragging its gaster on the wire.

Table 1. Timing of swarm movement of *Polybia velutina* on 25 June 1977.

Time PM	Swarm Site	Numbers of Wasps in Flight	New Nest Site
1:40	300 ^a	—	17
2:00	300 ^a	—	25
2:15	300 ^a	—	9
2:20	300 ^a	—	13
2:35	300 ^a	—	7
2:40	300 ^a	—	15
2:55	300 ^a	—	18-22
3:40	300 ^a	—	20-26
4:10	200 ^a	25-30	50 ^a
4:15	20	40-50	200 ^a
4:23	10	5-10 ^a	200 ^a
4:30	10	5-10 ^a	200 ^a
4:40	8	5-10 ^a	200 ^a
4:50	11	5-10 ^a	200 ^a
5:40	1	—	200 ^a
6:00	0	—	200 ^a

^aestimated

The number of wasps at the new nest site increased rapidly between 3:40 and 4:00 PM, indicating the beginning of the major emigration. At that time 25-30 wasps were also simultaneously in flight between the 2 sites. The first carton was added to the wire between 4:00 and 4:10 PM, and the number of wasps in flight increased to 40-50. The wasps hovered in the air making a diffuse cloud of wasps along the path between the swarm and the new nest. Several wasps landed briefly on leaves of the *Codeum*, and 2 wasps dragged their gaster, each on different leaves. On a third leaf, 3 wasps paused in what

appeared to be a dragger-follower-dragger sequence. With those exceptions no dragging or following behavior was observed during the afternoon while both of us were constantly present. By 4:15 PM the majority of wasps were at the new nest site, though until 5:40 PM a few wasps were constantly at the old swarm site.

There was no convincing evidence that the wasps used a trail of chemical spots to orient to the new site or that the nest site itself was chemically marked by Richards' gland. The limited dragging on 3 prominent leaves resulted in no systematic follower visits, with the exception noted above. Since polybiines are able to learn the location of food even a hundred meters away from the nest (Forsyth 1978), foragers active before the raid must have been familiar with landmarks within 10 m of their old nest. It, therefore, seems probable that many wasps could have learned the short route to the new nest site during the 2 hr before the emigration. The hovering wasps along the path to the new nest site at the peak of the emigration could have guided any naive wasps. It is also possible that pheromone from Richards' gland or some other source provided an aerial plume for orientation, although we saw no evidence of this in the behavior or posture of the wasps. Unfortunately, we did not record the wind direction at the time, but the prevailing winds are from the east to northeast or at a right angle to the flight path.

Another swarm, *Protopolybia exigua binominata* (Schulz) (colony V-346, Panama), also appeared to move to a new nest site without the use of a pheromonal trail. Immediately after the wasps were experimentally evicted from their nest (by placing a few army ants near the nest), several wasps dragged their gasters along the edges of leaves close to the abandoned nest. The tip of the gaster did not touch the substrate, but the distal sternites contacted the leaf as in typical dragging behavior. By 5:30 PM, 3 hr after the wasps had been ousted from their nest, the swarm of about 200 had consolidated on a nearby leaf, and the wasps were flying from the swarm into the distance. The next day at 9:35 AM there were many wasps landing on various leaves near the swarm. No dragging or following behavior was observed; the wasps merely landed momentarily on leaves. The new nest was located on the underside of a leaf only 2-3 m from the swarm leaf and about 1 m higher. There were many intervening leaves between the 2 sites, and the wasps did not follow any one path through the vegetation to get to or from the new nest site. By 9:45 AM the old swarm site

had been abandoned and only an occasional wasp appeared there afterward. Several wasps at the new nest site were observed dragging their gasters on the edge of the new nest leaf after 10:00 AM.

In only 10 min most of the wasps flew to the new site, less than 3 m from the swarm. The short distance and the large number of wasps enhanced the probability that the wasps were following other individuals visually or by an aerial pheromone trail. No systematic visits, marking, or antennation at specific sites were observed. Forsyth (1978) noted that visual cues may be important or used in conjunction with a pheromone trail during short movements of *Polybia occidentalis* (Olivier).

The shortest distance for a swarm emigration observed by Jeanne (1975) was 70 m and Naumann (1975) reported distances of 3–33 m. Perhaps a continuum of behavior exists; for short distances the wasps rely on learning and visual cues for orientation and as the emigration distance increases they rely increasingly on chemical-spot trails. Honey bees also shift their orientation-communication system as the distance to food increases (Frisch 1967:57).

Although Jeanne's (1980) recent research supports that secretions from Richards' gland deposited during dragging behavior form a scent trail, such behavior is not restricted to trail formation. The dragging at the new nest site by *P. exigua* well after the emigration was completed may have been an ill-timed part of the emigration process, or a method of reinforcing recognition of a new nest. Dragging behavior was also observed in a context other than swarm emigration in *Polybia scrobalis* Richards.

When army ants were placed on or held near 2 nests of *Polybia scrobalis* (colonies V-377, V-443, Panama), 50–100% of the adults flew. Wasps started returning to the nest immediately, and 10–20% of those returning dragged their gasters in the typical manner on the nest carton, nest leaf, adjacent leaves, and occasionally on their nest-mates. This response could not be elicited by holding *Paraponera clavata* (F.) or *Ectatomma tuberculatum* (Olivier) next to the wasps' nest, but on one occasion when a worker of *Camponotus sericeiventris* (Guerin) was held up to the nest a similar evacuation was accompanied by dragging both before and after flight. Such frequent dragging behavior by alarmed wasps and wasps which have left their nest for less than one minute was not observed during similar experiments performed with 30 species of polybiines in Panama and Ecua-

dor (Chadab 1979). This suggests that in at least *Polybia scrobalis* gaster-dragging behavior or chemicals deposited as a result of that behavior, may have other functions than identifying the path to a new nest site.

ACKNOWLEDGMENTS

We thank O. W. Richards for identifying the wasps, R. L. Jeanne, C. S. Henry, and B. Hölldobler for criticizing the manuscript, The Smithsonian Tropical Research Institute (STRI) for providing facilities on Barro Colorado Island, Panama, and the Summer Institute of Linguistics for providing facilities at Limoncocha, Ecuador. Ruth Chadab was funded by a Visiting Research Appointment from STRI and a National Science Foundation Doctoral Dissertation Improvement Grant; Carl W. Rettenmeyer was funded by NSF Grant BMS 75-03389.

LITERATURE CITED

- CHADAB, R.
1979. Army-ant predation on social wasps. Unpublished Ph.D. Thesis. Univ. of Connecticut. 260 p.
- FORSYTH, A. B.
1978. Studies on the behavioral ecology of polygynous social wasps. Unpublished Ph.D. Thesis. Harvard Univ. 226 p.
- FRISCH, K. V.
1967. The dance language and orientation of bees, Belknap. Harvard Univ. Press, Cambridge, xiv + 566 p.
- JEANNE, R. L.
1975. Behavior during swarm movement in *Stelopolybia areata*. (Hym.: Vespidae). *Psyche* **82**: 259-264.
1980. Evolution of social behavior in the Vespidae. *Ann. Rev. Entomol.* **25**: 371-396.
- NAUMANN, M. G.
1975. Swarming behavior: Evidence for communication in social wasps. *Science* **189**: 642-644.

NOTES ON THE RUSSIAN ENDEMIC ANT GENUS
AULACOPONE ARNOLDI
(HYMENOPTERA: FORMICIDAE)*

BY ROBERT W. TAYLOR
Australian National Insect Collection
CSIRO, Division of Entomology
P. O. Box 1700, Canberra City, A.C.T.
Australia

INTRODUCTION

The ponerine ant genus *Aulacopone*, and its only known species *A. relict*a, were described by Arnoldi (1930) from a unique dealate female collected at Alazapin, near Lenkoran (38° 45'N., 48° 50'E.), in Azerbaydzhan S.S.R., near its border with Iran. The specimen was taken in galleries of the formicine ant *Lasius emarginatus* (Olivier), under the bark of an oak stump, in Talisch mid-montane forest. The holotype, which I have not seen, is reportedly in the collection of the Zoological Institute, Leningrad. A second, previously unreported dealate female of *A. relict*a, now in the Arnoldi collection at the Institute of Evolutionary Animal Morphology, Moscow, was taken by Arnoldi on Mt. Gugljaband, near Alekseevka, Azerbaydzhan, in 1936. The only important reference to this species, apart from Arnoldi's paper, is in Brown's (1958a) reclassification of tribe Ectatommini. These articles by Arnoldi and Brown are essential references to this paper.

Aulacopone is the only extant genus of subfamily Ponerinae with known distribution limited to some part of Holarctica. In addition it is one of only two ant genera known exclusively from the Soviet Union, the other being *Rossomyrmex* Arnoldi (subfamily Formicinae).

Following a recent visit to Moscow (under the Australia/U.S.S.R. Science Exchange Agreement) I was permitted by Dr. Arnoldi and Dr. A. A. Zakharov to carry the over-glued Mt. Gugljaband specimen to Australia on loan, there to re-mount, clean and prepare it for examination by scanning electron microscopy. This paper is the result. The general accuracy of Arnoldi's original description is con-

*Manuscript received by the editor April 18, 1980

firmed and some additional features are described, though the risk of damage to the specimen precluded dissection of its mouthparts or sting. The relationship of *Aulacopone* to *Heteroponera* Mayr, suggested by Brown, is supported. This has interesting evolutionary and biogeographical implications.

TAXONOMIC AND BIOGEOGRAPHIC RELATIONSHIPS OF
AULACOPONE

The allocation of *Aulacopone* to tribe Ectatommini is unquestionable, and is further supported by the absence of arolia from the tarsi of the available specimen. Within subfamily Ponerinae the absence of arolia is apparently unique to species of tribe Ectatommini, except *Paraponera clavata* (Fabricius) (J. Freeland and R. D. Crozier, *pers. comm.*).

In order to understand in modern terms Arnoldi's discussion on the possible affinities of *Aulacopone*, the following synonymies by Brown are relevant: *Gnamptogenys* Roger = *Alfaria* Emery = *Stictoponera* Mayr; *Proceratium* Roger = *Sysphincta* Mayr; Ectatommini = Proceratiini = Stictoponerini.*

Arnoldi considered *Aulacopone* close to *Gnamptogenys*, a genus of somewhat diverse content now strongly and disjunctly represented (a) in the Indo-Australian area (from Ceylon and Western China to the Philippines and Fiji, with one New Guinean species on far northern Cape York Peninsula providing the only known Australian records), and (b) in the New World (from Texas south to Tucumán and Buenos Aires, including the Antilles and Peru, but as yet not Chile). The genus is not known from Africa. Brown recognised 26 Indo-Australian species, and more are now known. Sixty-four neotropical species were listed by Kempf (1972). One extinct species, *G. europaeum* (Mayr), is known from Oligocene Baltic Amber, and according to Brown, *Archiponera wheeleri* Carpenter, of the North American Oligocene Florissant Shale, seems close to *Gnamptogenys*. Arnoldi indicated specific resemblances between *Aulacopone* and the palaeogeane "Stictoponera" and neogeane "Alfaria" species groups of Brown's *Gnamptogenys* classification. He considered these three taxa, comprising his spurious subtribe Stictoponerini, to represent a

*The name Stictoponerini was proposed by Arnoldi (1930); it seems not to have been used subsequently, or formally synonymized under Ectatommini, where it belongs following Brown's reclassification.

“grade” standing parallel to *Proceratium* in ectatommine evolution, especially to those species then assigned to *Sysphincta*.

Brown, however, related *Aulacopone* to *Heteroponera*, a genus which has its distribution somewhat more peripheral to the main northern continents than that of *Gnamptogenys*, especially in the Old World. There are two faunistic elements: one in eastern and south-western mainland Australia, Tasmania and New Zealand; the other in South America, from Panama south to Uruguay and Chile (Kempf and Brown 1968). *Heteroponera* is unknown from the Palearctic, Oriental and Ethiopian regions, or from Melanesia. It has no known fossil record. Undescribed species known from Australia could at least treble its continental fauna of three species recognised by Brown, and the name *H. imbellis* (Emery), as applied by Brown, certainly refers to a partly intractable complex of several Australian species. New Zealand has a single known endemic species. Kempf (1972) listed 13 Neotropical species.

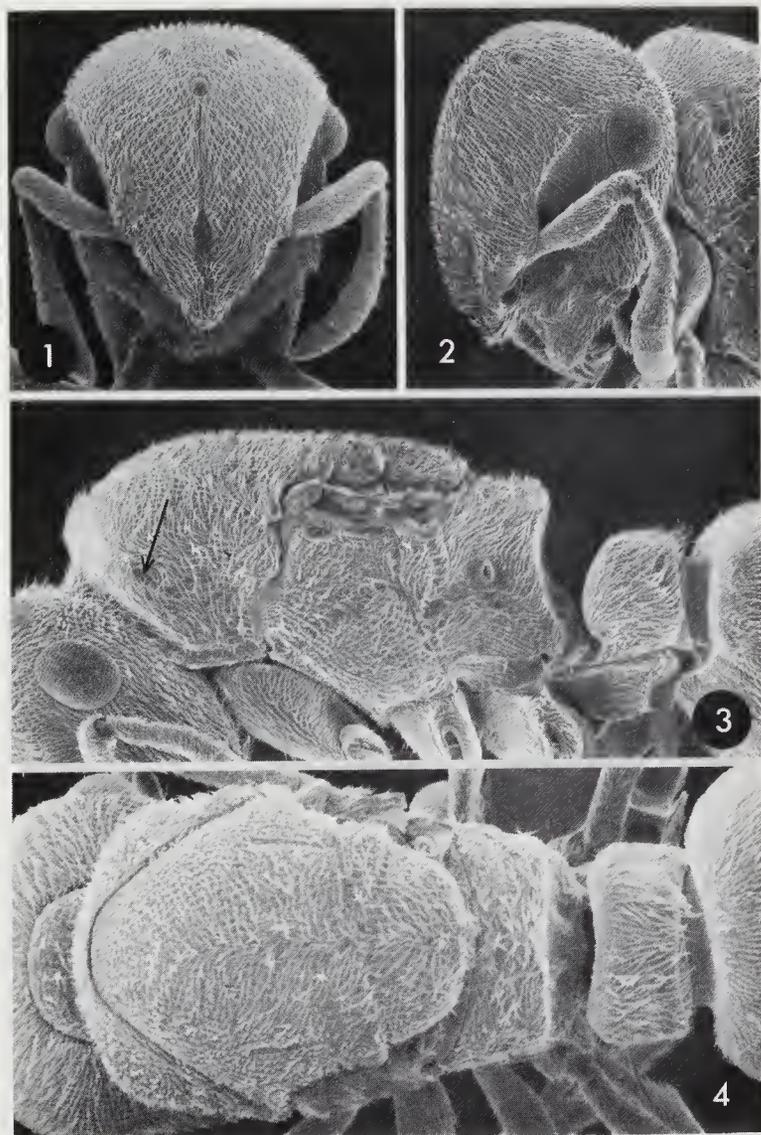
The *Aulacopone* female (Figs. 1–4) is very like her counterparts in species of the *Heteroponera imbellis* complex, in size, general habitus, structure of the mesosoma, and colour. *Aulacopone* and *Heteroponera* share several major features distinguishing them from *Gnamptogenys*, including the presence of a median longitudinal costa, distinct from other sculpture, on the head (terminating in front of the anterior ocellus in females), and the absence of a tooth or spine on the upper surface of each posterior coxa (a feature of almost all *Gnamptogenys* species, found nowhere else among the Ectatommini). *Aulacopone* also shares with *Heteroponera* those features distinguishing the latter from the neotropical genus *Acanthoponera*; these include the absence of long propodeal spines and a strong tooth or spine on the petiolar summit, and the lack of a prominent basal lobe accompanying a distinct submedian tooth on each tarsal claw. Basal lobes are characteristic of *Acanthoponera*. Submedian teeth are vestigially represented on the claws of some neotropical *Heteroponera* species, though they are lacking from all Australian species, and from *Aulacopone*. The lack of submedian teeth on the tarsal claws also distinguishes *Aulacopone* and *Heteroponera* from the prominent and diverse Australia-based genus *Rhytidoponera*, the species of which, in addition, almost all have a strong tooth-like process on each lateral pronotal margin. Such structures are lacking in other ectatommine genera, including *Aulacopone*, and all *Hete-*

roponera species except *H. relict*a (Wheeler). The latter could stand close to the *Rhytidoponera* ancestry.

Aulacopone resembles *Heteroponera* in all fundamental structural details referred to in Brown's discussion of features diagnosing or characterising ectatommine genera, except those related to cranial and petiolar structure, and other minor features, as detailed below.

In discussing likely relationships among the ectatommine genera Brown considered *Acanthoponera* to be "the genus surviving with the greatest number of primitive characters". *Heteroponera* was considered "a rather conservative stock" that "can be derived directly from *Acanthoponera*", and *Rhytidoponera* was represented as a genus "very closely related to *Heteroponera*" which "may have originated in the Australian region from some *Heteroponera*-like stock". According to Brown these genera stand apart as a lineage separate from that of the exclusively neotropical genera *Ectatomma* Fr. Smith and *Paraponera* Fr. Smith. *Gnamptogenys*, while difficult to relate precisely to other genera, "seems closer to the *Acanthoponera*/*Heteroponera* line than to *Ectatomma*". All the above genera are essentially epigeaic, in contrast to the two further ectatommine genera, *Proceratium* Roger and *Discothyrea* Roger, which are cryptobiotic and "seem, on the basis of adult characters, to be closest to *Heteroponera*", while "the Baltic Amber species *Bradoponera meieri* (Mayr) looks like a reasonable step in this line".

Workers of *Proceratium* and *Discothyrea* are notable for their possession of cryptobiotic attributes, including medium to small size, with relatively small eyes, reduced sculpture and pilosity, and depigmented coloration. In particular the mesosomal structure is streamlined, through ankylosis of its component sclerites, and the frontoclypeal structure is highly modified. The antennal sockets are exposed in full-face view, through elevation of the lobes of the frontal carinae, and they have migrated anteromedially, carrying the clypeus and frontal area forwards to form a shelf-like process over the mandibles. This is especially prominent in *Discothyrea*, which usually has an erect vertical plate separating the antennal sockets, a structure which in some species is "T" shaped in transverse section and extends back along the head to enclose an antennal scrobe on each side, usually accompanied by a weak parallel longitudinal concavity of the frons. Both *Proceratium* and *Discothyrea* have their tubulate abdominal segment IV reflexed downwards or forwards under the body, a characteristic shared with various *Heteroponera*



Figures 1-4. *Aulacopone relicta*, female, Mt Gugljaband, Azerbaydzhan. Fig. 1, head, full-face view. Fig. 2, Head, oblique frontal view. Fig. 3, mesosoma and petiole, lateral view (position of humeral pits indicated by arrow). Fig. 4, mesosoma and petiole, dorsal view. Scanning electron micrographs; see text for dimensions.

species and with *Bradoponera*. In some *Discothyrea* species, in particular, the petiole is transverse in dorsal view and only slightly constricted behind, at its articulation with the following (postpetiole) abdominal segment. These attributes are doubtless adaptations to life in confined moist and irregular spaces in soil or rotting wood, where effective use of the antennae and sting would otherwise be compromised. The clypeal shelf probably functions with the mandibles to aid transport of arthropod eggs, upon which several species of both genera (including the remarkable secondarily epigaecic Mauritian *Proceratium avium* Brown) are known to feed (Brown 1958b, 1974). Females generally resemble workers, though the eyes are usually less reduced, and the mesosoma non-ankylosed, at least in those species with winged gynes.

The structural features of *Aulacopone* are, of course, known only for the female; those of the worker must be surmised. *A. relict*a nonetheless shows clear cryptobiotic tendencies. The female is of small to medium size for an ectatommine*, with fine sculpture comparable to that of various *Proceratium* and *Discothyrea* species, and relatively pale yellowish brown colour. The pilosity is dense, though short and not unlike that of some *Discothyrea* species, and the eyes are smaller than would be expected in an epigaecic ectatommine. The really distinctive features of the genus have to do with its cephalic structure (Figs. 1, 2), in which the fronto-clypeal part of the head is extended forwards to form a strong triangular process, partly covering the closed mandibles. The antennal fossae are carried forwards on this process almost to the level of the mandibular bases. The resulting structure is, however, very different from that of any *Proceratium* or *Discothyrea* species, for here the lobes of the frontal carinae are not elevated; they are instead extended laterally and posteriorly to form, on each side, the upper enclosure of a strong, deep scrobe, in which the folded antenna can be stowed. Such strong antennal scrobes are unusual in ectatommine ants, though those of *Heteroponera relict*a and of some *Discothyrea* species (discussed above) are almost as well developed. Each frontal carina is narrowed immediately above the appropriate antennal socket. This might facilitate anterior extension

*The measurements (mm) of the Mt Gugljaband specimen are: aggregate total length 4.25; maximum head length 1.08; head width across eyes 1.02; chord length of scape 0.59; maximum diameter of eye 0.24; Weber's length of mesosoma 1.36; scutum width 0.82; petiole width 0.52; petiole height 0.58; width of postpetiole (abd. II) 0.96.

of the scapes, as is so generously accommodated in *Proceratium* and *Discothyrea*. Immediately behind this section the carina is laterally expanded and partly reflexed, to form an obtuse lobe, which appears to partially lock the scape into position when the antennae are folded (Arnoldi, Fig. 3). These modifications cause the frons and posterior parts of the clypeus to form a regularly convex, more-or-less triangular shield-like face to the cranium, a configuration not unlike that of other small cryptobiotic ants, such as some in the myrmicine tribes Dacetini and Basicerotini. The fronto-clypeal structure of *Aulacopone* is unlike that of any other ponerine ant, and thus immediately diagnoses the genus. The extent to which it might be associated with specialised trophic behaviour, like egg-feeding, is quite unknown. In addition the petiolar node (Figs. 3, 4), though relatively broad, is structured similarly to those of some *Discothyrea* females, and is quite unlike those of any *Heteroponera* species. The structure is somewhat like that typical of the primitive ponerine tribe Amblyoponini, and might represent a holdover from a remote amblyoponine ancestry. Abdominal segment IV is somewhat reflexed (Arnoldi, Fig. 1), though less strongly so than in *Proceratium*, *Bradoponera* or *Discothyrea*; or even some *Heteroponera* species (notably *H. leae* (Wheeler), in which segment IV is more strongly reflexed than in *A. relictata* and relatively short compared to segment III). Other descriptive details are covered by Arnoldi and illustrated in Figs. 1-4. Several points deserve further discussion. (1) The eyes are notably hairy (Figs. 1, 2). This might not be the case in workers. However, the only similar condition I have seen in tribe Ectatommini is that of a worker of an undescribed species of *Heteroponera* (aff. *H. leae*) from southwestern Western Australia. No other Australian *Heteroponera* has hairy eyes. (2) The scanning electron microscope has revealed an unusual structure on each pronotal humerus of the subject specimen, positioned as shown in Fig. 3. One of these structures is illustrated in detail in the stereoscopic pair of micrographs comprising Fig. 5. Each consists of a small shallow depression, without pilosity, enclosing several irregular troughs which each contain a number of minute pores. These are presumably the ducts of some previously unreported prothoracic gland. A detailed survey by stereoscopic light microscope has revealed no comparable structure in any other of the several hundred ectatommine species, of all known genera, represented in the Australian National Insect Collection.

Aulacopone thus emerges as a genus close to *Heteroponera* which, like *Proceratium* and the *Bradoponera/Discothyrea* line, shows adaptations to a cryptobiotic lifestyle, though these have probably been separately, and convergently evolved in the three lineages. The full degree of cryptobiotic specialisation cannot be assessed until workers of *Aulacopone* are collected, and checked for fronto-clypeal structure, palpal formula, mesosomal ankylosis, and relative development of the eyes, pilosity and gastral reflexion. The genus can reasonably be considered an ancient ectatommine relict, very restricted in distribution, and perhaps more readily analagous to the extinct Baltic Amber and Florissant ectatommines than to extant species. Incidentally, in addition to *Bradoponera meieri* and *Gnamptogenys europaea*, the Baltic Amber fauna includes *Electroponera dubia* Wheeler, which might link the *Acanthoponera/Heteroponera* and *Ectatomma/Paraponera* lineages, according to Brown. In addition I have seen, courtesy of Drs. G. D. Dlussky and A. P. Rasnitsyn, an indubitably ectatommine male from the Miocene of Kirgiziya S.S.R., in Soviet Central Asia.

The presence of these extinct or extant palearctic relicts supports Brown's view that ectatommine evolution has occurred mainly on the larger continental land masses of Eurasia, North America, and perhaps Africa; with the various lineages successively retreating, under pressure from more recently evolved groups, into the peripheral southern land areas of Australasia and South America. This model satisfactorily explains the present distribution of *Gnamptogenys* and the less derived and more peripheral *Heteroponera*, especially in the Indo-Australian area. The absence today of epigaecic ectatommines in Eurasia, Africa and much of North America is explained as a result of their past retreat under pressure from the rising subfamily Myrmicinae, which itself seems derived from an ectatommine stock, with the Baltic Amber *Agroecomyrmex duisburgi* Mayr providing a plausible intermediate. *Proceratium* and *Discothyrea*, unlike the epigaecic ectatommine genera, are both represented in North America, Eurasia (including Japan), and Africa, in addition to the other peripheral southern continents, where *Discothyrea* has its richest development. The recluse habits of these ants might explain their survival in areas which now lack, and perhaps have lost, epigaecic ectatommines. These were certainly once present in Eurasia and North America at least, as evidenced by the fossil record.

The likely cryptobiotic habits of *Aulacopone relict*a might also

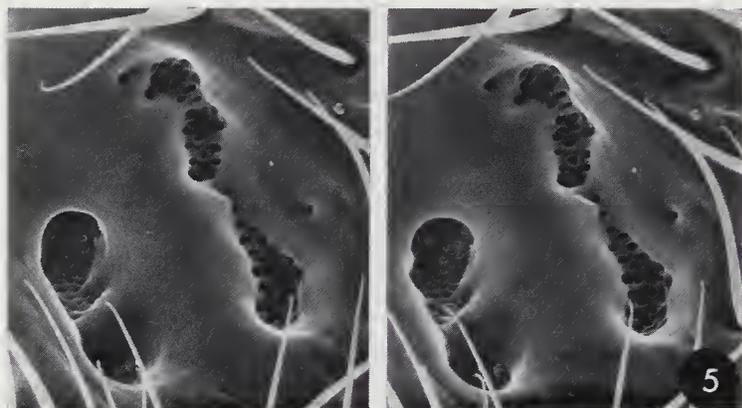


Figure 5. *Aulacopone relict*, female, Mt Gugljaband, Azerbaydzhan. Details of left-hand humeral pits. Steroscopic pair, scanning electron micrographs, magnification ca. $\times 1,000$.

explain the remarkable survival of this species as an apparently rare relict in Azerbaydzhan.

Despite the circumstances of its original collection, there is little reason to suppose that *A. relict* is a social parasite of *Lasius emarginatus*, although its bionomics might include cleptobiosis or lestobiosis, and the clypeal structure could be related to the latter.

The desirability of collection and study of further material of this exceptional ant provides a great challenge to Soviet myrmecology.

REFERENCES

- ARNOLDI, K. V.
1930. Studien über die Systematik der Ameisen. IV. *Aulacopone*, eine neue Ponerinen-gattung in Russland. Zool. Anz., 89 : 139-144.
- BROWN, W. L. JR.
1958a. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). Bull. Mus. Comp. Zool. Harv., 118 : 175-362.
1958b. Predation of Arthropod eggs by the ant genera *Proceratium* and *Discothyrea*. Psyche, 64 : 115.
1974. A remarkable new island isolate in the ant genus *Proceratium*. Psyche, 81 : 70-83.
- KEMPF, W. W.
1972. Catálogo abreviado das Formigas da Região Neotropical (Hymenoptera: Formicidae). Studia Ent., 15 : 3-344.
- KEMPF, W. W. AND W. L. BROWN, JR.
1968. Report on some Neotropical ant studies. Papéis Avulsos Zool. S. Paulo, 22 : 89-102.

VARIATION IN DISTRIBUTION, MORPHOLOGY AND
CALLING SONG OF TWO POPULATIONS OF
PTEROPHYLLA CAMELLIFOLIA
(ORTHOPTERA: TETTIGONIIDAE)¹

BY ROBERT C. NORTH² AND KENNETH C. SHAW
Department of Zoology
Iowa State University
Ames, Iowa 50011

INTRODUCTION

There are more than 200 species of singing katydids, crickets, and cicadas in the eastern United States. Among these, *Pterophylla camellifolia* (Fabricius) is unique in that several populations, identifiable by differences in song and morphology, are separated by zones of intergradation (Alexander 1968). This unique situation is associated with a history of taxonomic confusion.

Fabricius (1775) described two species of the genus *Locusta*: *camellifolia* and *perspicillatus*. *L. camellifolia* (female specimen) was described in the sentence preceding *L. perspicillatus* (male specimen). Subsequently, Kirby and Spence (1828) placed *camellifolia* and *perspicillatus* in the genus *Pterophylla*. Burmeister (1838) placed *perspicillatus* within the new genus *Cyrtophyllus*. Caudell (1906) divided *Cyrtophyllus* into three genera, *Cyrtophyllus*, *Paracyrtophyllus* and *Lea*, and described three new species of *Cyrtophyllus*: *elongatus*, *furcatus* and *intermedius*, as well as retaining *perspicillatus*. Kirby (1906) synonymized *Cyrtophyllus* with *Pterophylla*. Rehn and Hebard (1916) combined Caudell's *C. perspicillatus* and *elongatus* into *Pterophylla camellifolia camellifolia*, and *C. intermedius* became *P. camellifolia intermedia*. Hebard (1941) recognized two species of *Pterophylla*, *camellifolia* and *furcata*, with *camellifolia* divided into three subspecies (*P. c. camellifolia*, *P. c. intermedia*, and *P. c. dentifera*) and *furcata* into two subspecies (*P. f. furcata*, and *P. f. laletica*). Hebard believed there were racial differences among specimens col-

¹Part of a thesis submitted by the first author to the Graduate College, Iowa State University, in partial fulfillment of the requirements for the degree of Master of Science, June 1978.

²Present address: Department of Entomology, Iowa State University, Ames, Iowa 50011.

Manuscript received by the editor February 22, 1980

lected from the northern (Pennsylvania to Virginia), southern (South Carolina to Florida), and southwestern (Oklahoma, Arkansas, southwest Missouri) ranges of *P. c. camellifolia*. Apparent intergradation of subgenital plate dimensions, along with similar appearance of male cerci in southeastern material and specimens from Pennsylvania, precluded his recognizing these three populations as subspecies.

Alexander (1956) noted that specimens from Ohio and North Carolina differ in the shape of the male subgenital plate and pulse rate of the calling sound. Subsequently, on the basis of these differences, Alexander and Shaw (unpublished) differentiated three populations. Two of these probably correspond to Hebard's (1941) northern and southern populations of *P. c. camellifolia*. A third population, whose geographic distribution has not been determined in detail, occurs in Louisiana, Mississippi, southwestern Georgia and probably Tennessee. On the basis of intergradation in calling sound parameters (pulse rate and chirp pulse number), and subgenital plate dimensions, Alexander and Shaw hypothesized a zone of hybridization, forming an inverted Y-shape, among the three populations (Alexander 1968).

Shaw and Carlson (1969) used differences in chirp length of calling sounds and length of male subgenital plate to distinguish two populations of *P. camellifolia* in Iowa. For one population, representing the westward extension of the northern population of Alexander and Shaw, they reported subgenital plate lengths of 11.8 to 13.2 mm and two- to three-pulse chirps. A previously unreported western population in Iowa possesses subgenital plates 14.7 to 16.8 mm in length and chirps of 8 to 15 pulses.

Shaw and Carlson's (1969) characterization of the two populations of *P. camellifolia* was based on relatively little data; namely, song records from three counties (Boone, Hardin, Story), and subgenital plate measurements from 13 specimens representing seven counties (Boone, Hardin, Linn, Marion, Story, Van Buren, Worth). Since this publication we have been unable to confirm two of the geographic locations of western *P. camellifolia* based on subgenital plate measurements of specimens in the Iowa State University insect collection. Several visits to Worth County failed to uncover any *P. camellifolia* in this northern county. We have heard only northern males singing in Van Buren County in southeast Iowa.

This study is a detailed analysis of the geographic distribution of *P. camellifolia* in Iowa and a more extensive characterization of population differences based upon both behavioral (parameters of male calling sounds) and morphological characters.

METHODS

We determined the distribution of *P. camellifolia* in Iowa during the summers of 1975–1978. Colonies (disjunct groups of katydids) were located by driving at reduced speeds along rivers and stopping at approximately 1/2 km intervals to listen for the loud choruses of calling sounds. Forest preserves and state and county parks were also surveyed throughout the state.

Surveys in 1975 and 1976 indicated that northwestern and north central Iowa, areas with relatively little forested lands, were void of *P. camellifolia*. These surveys, as well as records of previous investigators (Froeschner 1954, Shaw and Carlson 1969), suggested that an extensive survey of gallery forests along certain rivers, e.g., Cedar, Des Moines, Iowa, Racoon, Skunk, in central, southern, and eastern Iowa would be most productive. During the surveys, exact locations of katydid colonies were recorded on county maps. Other data taken included: 1) written records of chirp pulse numbers from 10 to 20 katydids per colony, 2) tape recordings of calling sounds for 5 to 10 katydids per colony, and 3) collection of specimens whenever possible.

P. camellifolia is a large, flightless, green katydid that resides near the tops of tall trees in oak-hickory forests. Males stridulate only at night and in Iowa this takes place from the last of July until the first or second frost in October. Thus, it was necessary to locate the calling male in a tree, climb the tree, spot the katydid with a light, and capture it by hand.

Calling sounds were recorded on a Nagra III tape recorder. An American electrodynamic microphone (Model D33) mounted in a 38 cm aluminum parabolic reflector allowed recordings of individual katydids. Ambient temperature was taken at the site of each tape recording.

Pulse rate was determined from audiospectrograms made with a sonograph (Kay Vibralyzer). Pulse intervals and lengths were determined to the nearest 0.01 second.

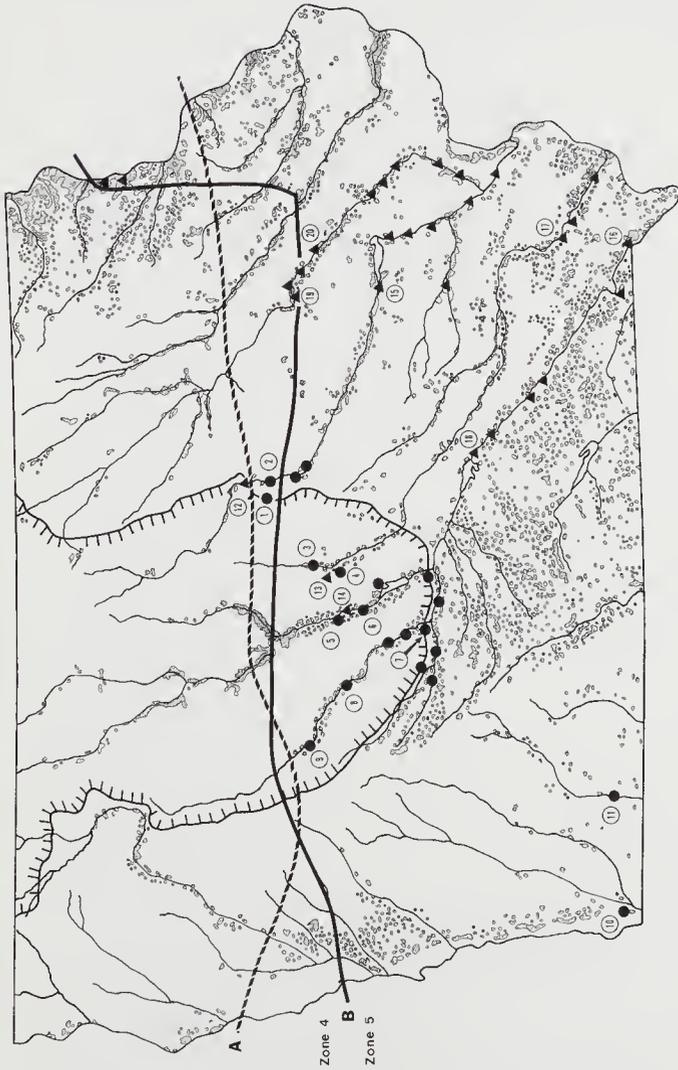


Fig. 1. Present forest in Iowa redrawn from remote-sensing, satellite photographs, as presented in *Land-Use in Iowa, Miscellaneous Map Series 5, Iowa Geological Survey, 1976*.

A. Isotherm of January mean temperature (-7.2°C), 1931-1960, (Shaw and Waite 1964).

B. Plant hardiness in Iowa. Approximate range of average annual minimum temperatures for each zone; zone 4 = -34.4 to -28.8°C ; zone 5 = -28.8 to -23.3°C . From plant hardiness zone map (Fowells 1965).

Colonies of *P. camellifolia* in Iowa. ●—western population. ▲—northern population. Unnumbered colonies are based on pulse number per chirp data taken from less than 10 individuals. JJJJ—border of the Wisconsin drift.

Morphological characters were determined from 13 previously collected specimens and from 192 males collected from 15 different colonies in 1977 and 1978. We examined characters used previously: length of body, length of metathoracic femur, length and width of tegmina, length and width of subgenital plate, length of the subgenital plate slit, and shape of cerci (Beutenmuller 1894, Caudell 1906, Blatchley 1903, 1920, Walden 1911, Hebard 1941, Shaw and Carlson 1969). In addition we measured the distance from the frons to the distal end of the tegmina. Measurements were made with calipers and an ocular micrometer.

RESULTS

In Iowa, *P. camellifolia* is restricted to gallery forests along major rivers, and colonies in central Iowa are disjunct from those of eastern Iowa (150 to 200 km). In western Iowa, distribution of *P. camellifolia* is limited to two colonies, one in Waubonsie State Park in Fremont County (colony number 10), and another in a county park in Page County (colony number 11) (Fig. 1).

Table 1. Nested ANOVA. A = Subgenital plate length. B = Subgenital plate slit length. C = Pulse number per chirp.

Source	d.f.	MS	% of total variation
A. Colonies	14	34.33	87.33
Individuals (Colonies)	190	0.37	12.67
B. Colonies	14	9.36	76.99
Individuals	190	0.21	23.01
C. Colonies	19	1976.53	79.50
Individuals (Colonies)	191	34.39	14.52
Records (Individuals Colonies)	4009	0.69	5.98

All characters showed significant F values (ranging from 2.54 to 74.02, $p \leq .01$). However, of the 11 morphological and behavioral parameters measured, only subgenital plate length (SPL), subgenital plate slit length (SPSL) and number of pulses per chirp (P/C) showed greater variation between colonies than within colonies (Table 1). Also these three characters were the only ones by which the colonies were separated into two significantly different populations by the Duncan's multiple range test (Table 2). SPSL is not shown in Table 2

because the groups delineated by this character were the same as by SPL. For population diagnosis, SPL would be simpler to measure than SPSL.

Duncan's test for P/C delineates the same two groups (Table 3) as analysis of SPL (Table 2). However, in the former case, additional colonies are included in both groups because specimens were not collected from all colonies. Western katydids, those with long subgenital plates (colonies 1-10; Table 2), produce long chirps (colonies 1-11; Table 3). In contrast, northern katydids, those with short subgenital plates (colonies 12-16), produce short chirps (colonies 12-20).

Table 2. Duncan's multiple range test for variable SPL (subgenital plate length). Means with the same letter and overlapping ranges of means designated by two or more letters are not significantly different. The range of means designated F are significantly different from overlapping range of means designated A, B, C, D and E ($p < .05$).

Colony number	N	Mean \pm sd (mm)	Grouping
4	11	17.2 \pm .5	A
2	25	16.8 \pm .6	B A
3	23	16.6 \pm .6	B C
9	4	16.4 \pm .2	B D C
5	35	16.4 \pm .8	D C
10	42	16.3 \pm .5	D C
1	9	16.2 \pm .5	D C
7	4	15.8 \pm .6	E D C
6	7	15.2 \pm .3	E D
8	5	15.1 \pm .2	E
16	5	13.0 \pm .5	F
13	8	13.0 \pm .5	F
12	11	12.9 \pm .4	F
15	6	12.4 \pm .2	F
14	10	12.2 \pm .3	F

All 40 males collected from colonies believed to be members of the northern population have cerci the ventral arms of which bifurcate with dorsal and ventral arms pointed distally (Fig. 2A). In contrast, 135 of 165 males from the western population showed a slightly bifurcate, blunt ventral cercal arm (Fig. 2B). The remaining 30 males exhibited various cercal shapes (e.g., Figs. 2C and 2D), making them indistinguishable regarding population affiliation.

The ranges of population means for the distance from the frons to the distal end of the tegmina (western: 38.3–44.7 mm; northern: 37.4–39.7 mm), frons to distal end of subgenital plate (western: 35.7–38.6 mm; northern: 31.7–33.7 mm), tegminal length (western: 32.8–37.9 mm; northern: 31.4–33.7 mm), metathoracic femoral length (western: 17.9–20.6 mm; northern: 13.0–15.1 mm), and tegminal width (western: 13.7–15.1; northern: 13.0–15.1), indicate that western katydids are on the average larger than northern katydids (North 1978).

DISCUSSION

Iowa is the northwestern limit of the range of *P. camellifolia*. The distribution of oak-hickory forests, even in presettlement times, eliminates the availability of much of the western and northern part of the state (Fig. 1). Approximately 75% of the 6.5 million acres of woodland that greeted the state's first white settlers in the 1850's has been destroyed, leaving a sparse 1.6 million acres. Temperature also may be an important factor in limiting the northward extension of *P. camellifolia* south of available oak-hickory forest (Fig. 1). The same factors appear to affect the distribution of 17-year cicadas whose northern limits in Iowa mimic those of *P. camellifolia* even though suitable habitat is also available for range expansion of this species (Lloyd and Dybas 1966).

At the time of the original land survey in Iowa territory, the native vegetation was of two main types, prairie and deciduous forest. More than three-quarters of the state was open grassland and the remainder oak-hickory forest (Simonson et al. 1952). Since Caucasians arrived in Iowa, the removal of timber has been extensive. It is possible that in presettlement times *P. camellifolia* was more or less continuously distributed across eastern and southern Iowa. However, our failure to find any colonies between southwest and central Iowa (Fig. 1) argues against such a continuous distribution.

The western and northern populations of *P. camellifolia* may have differentiated during the Pleistocene. Deevey (1949) concluded that glacial chilling was so extensive that many species of plants and animals could have survived only in peninsular Florida and in Mexico. The existence of four or more populations of *P. camellifolia* in the eastern half of the United States (Hebard 1941, Alexander 1968, Shaw and Carlson 1969), as well as dispersion by flightless females argues against only these two glacial refugia.

Transeau (1941), Braun (1951), and Thomas (1951) believe that preglacial forests and associated animals have existed throughout the Pleistocene in the Allegheny Plateau within a short distance of the glacial boundary. Kemp (1979) suggests that the present distribution pattern of the primitive flightless *Grylloblatta* in western Canada was derived from stock that survived the Pleistocene glaciation relatively close to the glacial front, and that migration routes from Wyoming and Montana permitted refugium populations to reach their present locations. Alexander and Moore (1962) argue convincingly that periodical cicada populations survived in approximately their present locations. They believe the last glacial advance resulted in brood splitting of 17-year cicadas with the populations closest to the glacial border separating from their more southern members because of diapause summation resulting from repeated periods of exposure to

Table 3: Duncan's multiple range test for variable P/C (pulse number per chirp). Means with the same letter and overlapping ranges of means designated by two or more letters are not significantly different. The range of means designated F are significantly different from overlapping range of means designated A, B, C, D and E ($p < .05$). * = colonies from which specimens have been collected (see Table 2).

Colony number	N	Mean \pm sd	Grouping
1*	11	13.6 \pm 2.9	B A
3*	20	9.4 \pm 1.9	B
9*	10	9.4 \pm 1.8	B
5*	10	8.5 \pm 1.4	B C
8*	10	7.6 \pm 0.7	D C
4*	10	7.5 \pm 1.1	D C
2*	10	7.5 \pm 1.7	D C
11	10	7.4 \pm 0.9	D C
10*	10	6.7 \pm 0.6	E D
7*	10	6.6 \pm 0.9	E D
6*	10	6.1 \pm 1.7	E
20	10	3.7 \pm 0.5	F
19	10	3.6 \pm 0.6	F
18	10	3.5 \pm 0.5	F
14*	10	3.3 \pm 0.6	F
13*	10	3.3 \pm 0.6	F
15*	10	3.0 \pm 0.4	F
12*	10	2.9 \pm 0.6	F
17	10	2.8 \pm 0.7	F
16*	10	2.5 \pm 0.5	F

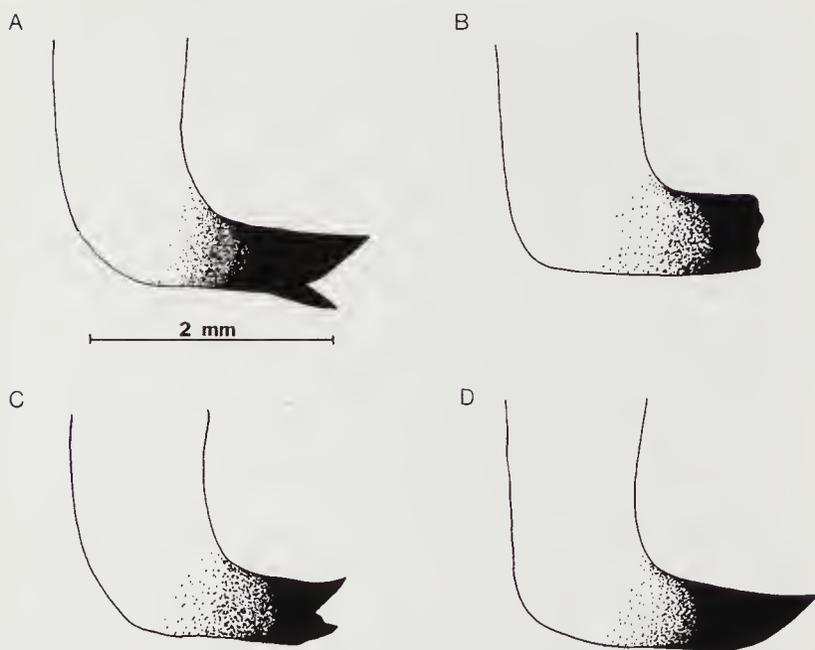


Fig. 2. Ventral arm of male cercus, ventral view. A. Northern population, colony #10. B. Western population, colony #3. C. Western population, colony #4. D. Western population, colony #5.

extreme cold. Such a brood-splitting could have resulted in brood III (central and southeast Iowa) and brood IV (southwest Iowa and south to Texas).

Smith (1957) takes a position intermediate to that of Deevy (1949) and that proposed by Transeau (1941), Braun (1951), Thomas (1951), and Alexander and Moore (1962). Smith's evidence is principally southern disjunct, relict populations of boreal vertebrates whose main contemporary distributions lie "partially or wholly within glaciated North America". These relict populations, widely separated from the main segment of their species ranges, occur in such states as Missouri, Arkansas, Kansas, Tennessee, and Georgia.

Such western (Missouri, Arkansas, Kansas) and eastern (Tennessee, Georgia) separation of a preglacial population of *P. camellifolia* could have been responsible for differentiation of the western and

northern populations of this species. Examination of subgenital plates and cercal arms of 12 specimens from Anderson County, Kansas, indicate they are western *P. camellifolia*. This would support Kansas as a possible glacial refuge and site of differentiation of western *P. camellifolia*.

Postglacial northern migration of oak-hickory forests with their accompanying fauna along the rivers of the Missouri and Mississippi drainage systems would have facilitated contact between western and northern katydids. Forest continuity in southern Iowa could have allowed the western population to cross from the Missouri to the Mississippi drainage system. During the Climatic Optimum Period (warm, moist period from approximately 6000–8000 B.P.), deciduous forest occurred more continuously and at slightly higher latitudes than at present (Smith 1957). Southward and eastward shrinking of the ranges of fauna and flora may have occurred during the warm and dry Hypsithermal (= Xerothermic Interval, ca. 4000–6000 B.P.) (Smith 1957). On the basis of the Climatic Optimum Period and boreal relicts, Smith argues for gallery forests or "islands" of forests along the major rivers as refugia for mesic-forest-inhabiting animals during this period. Although the drier-loving oak-hickory forests may have at first advanced during this period, they probably receded later and again may have remained only as gallery forests along rivers.

Assuming that the western and northern populations had come together during the Climatic Optimum Period, their present distribution could be explained by the effects of the Hypsithermal. The western and northern populations occur along or near river systems where they could have escaped the extreme conditions of the Hypsithermal. This could explain the existence of both western and northern populations within the Wisconsin drift area (Fig. 1), an area which contains protected ravines created by the actions of the Wisconsin glacier. The main bodies of these two populations could have been pushed southwestward and east-southeastward. The 150–200 km gaps between the southwestern and central colonies of western katydids and the eastern and central colonies of northern katydids could simply be the result of lack of forest and/or time to renew contact.

The fragmentation of animal ranges resulting from the activities of civilized man throughout his historic period has resulted in many

relict populations (Smith 1965). Such fragmentation facilitates population differentiation. As for *P. camellifolia*, fragmentation is most effective at the periphery of their range where habitat and animals are climatically limited. *P. camellifolia* in Iowa consists of a number of relatively small isolated colonies which are undergoing morphological and behavioral differentiation (a remarkable example is western colony #1 [Table 3] within which some males produce up to 30 pulses/chirp) and which may eventually become reproductively isolated populations.

The intrapopulation variation of colonies of western and northern *P. camellifolia* could be a result of 1) inbreeding of small isolated populations, and/or 2) gene exchange between formerly continuous western and northern populations. Further field studies are necessary to determine the extent of the distribution of the western and northern populations outside Iowa. Crossing experiments as well as choice and non-choice phonotaxis experiments, involving playbacks of calling sounds to virgin females of both populations, are necessary for a decision regarding the taxonomic affinity of northern and western *P. camellifolia*.

ACKNOWLEDGMENTS

We wish to thank Dr. D. F. Cox, Department of Statistics, Iowa State University, for assistance with the statistical analysis, and Dr. R. E. Lewis, Department of Entomology, Iowa State University, for reviewing the manuscript. Special thanks are due Ms Patti Hanson for prodigious assistance in the survey and the collection of specimens.

LITERATURE CITED

- ALEXANDER, R. D. 1956. A comparative study of sound production in insects, with special reference to the singing Orthoptera and Cicadidae of the eastern United States. Ph.D. Dissertation. Ohio State University. 529 pp.
- ALEXANDER, R. D. 1968. Arthropods. In T. A. Sebeok, ed. Animal communication, pp. 167-216. Indiana University Press, Bloomington, Ind.
- ALEXANDER, R. D. AND T. E. MOORE. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magiccada*). Misc. Publ. Mus. Zool. Univ. Michigan 121:1-59.
- BEUTENMULLER, W. 1894. Descriptive catalogue of the Orthoptera found within fifty miles of New York City. Bull. Amer. Mus. Nat. Hist. 6: 316 pp.
- BLATCHLEY, W. S. 1903. The Orthoptera of Indiana. 27th Ann. Rep. Ind. Dept. of Geol. and Nat. Resources. Indianapolis, Ind. 471 pp.

- BLATCHLEY, W. S. 1920. Orthoptera of Northeastern America. Nature Publ. Co., Indianapolis, Ind. 784 pp.
- BRAUN, E. L. 1951. Plant distribution in relation to the glacial boundary. Ohio J. Sci. **51**:139-146.
- BURMEISTER, H. 1838. Handb. Ent., II-Orthoptera. Berlin. 697 pp.
- CAUDELL, A. N. 1906. The Cyrtophylli of the United States. J. N. Y. Entomol. Soc. **14**:32-45.
- DEEVEY, E. S. 1949. Biogeography of the Pleistocene. Part I, Europe and North America. Geol. Soc. Amer. Bull. **60**:1315-1416.
- FABRICIUS, J. C. 1775. Systema entomologiae sistens insectoium, synonymis, locis, descriptionibus, observationibus. Flensburgi et Lipsiae. 832 pp.
- FOWELLS, H. A. 1965. Silvics of forest trees of the United States. U. S. Dept. Agr. Handb. 271. 762 pp.
- FROESCHNER, R. C. 1954. The grasshoppers and other Orthoptera of Iowa. Iowa State J. Sci. **29**:163-354.
- HEBARD, M. 1941. The group Pterophyllae as found in the United States (Tettigoniidae: Pseudophyllinae). Trans. Amer. Entomol. Soc. **67**:197-220.
- KEMP, J. W. 1979. Taxonomy, distribution, and zoogeographic evolution of *Grylloblatta* in Canada (Insecta: Notoptera). Can. Entomol. **111**:27-38.
- KIRBY, W. AND W. SPENCE. 1828. Introd. Ent. 5th ed. London. 607 pp.
- KIRBY, W. 1906. Syn. Cat. Orth. II. Orthoptera Saltatoria, Pt. I. London. 562 pp.
- LLOYD, M. AND H. S. DYBAS. 1966. The periodical cicada problem. II. Evolution. Evolution **20**(4):466-505.
- NORTH, R. C. 1978. *Pterophylla camellifolia* (Fabricius) (Orthoptera: Tettigoniidae) in Iowa: Variation in distribution, morphology and calling song. Master's Dissertation. Iowa State University. 39 pp.
- REHN, J. A. G. AND M. HEBARD. 1916. Studies in the Dermaptera and Orthoptera of the coastal plain and Piedmont region of the southwestern United States. Proc. Acad. Nat. Sci. Phil. **68**:187-338.
- SHAW, K. C. AND O. V. CARLSON. 1969. The true katydid, *Pterophylla camellifolia* (Fabricius) (Orthoptera: Tettigoniidae) in Iowa: two populations which differ in behavior and morphology. Iowa State J. Sci. **44**:193-200.
- SHAW, R. W. AND P. J. WAITE. 1964. The climate of Iowa. Iowa State Univ. of Sci. and Tech. Agr. and Home Econ. Exp. Sta. Special Report No. 38.
- SIMONSON, R. W., GICHEN, F. F. AND G. D. SMITH. 1952. Understanding Iowa soils. W. C. Brown Co., Dubuque, Iowa.
- SMITH, R. W. 1957. An analysis of post-Wisconsin biogeography of the prairie peninsula region based on distributional phenomena among terrestrial vertebrate populations. Ecology **38**(2):205-218.
- SMITH, R. W. 1965. Recent adjustments in animal ranges. In H. E. Wright and D. G. Frey, eds. The Quaternary of the United States, pp. 633-642. Princeton Univ. Press, Princeton, New Jersey.
- THOMAS, E. S. 1951. Distribution of Ohio animals. Ohio J. Sci. **51**:153-167.
- TRANSEAU, E. N. 1941. Prehistoric factors in the development of the vegetation of Ohio. Ohio J. Sci. **41**:207-211.
- WALDEN, B. H. 1911. The Euplexoptera and Orthoptera of Connecticut. Connecticut State Geol. and Nat. Hist. Surv. Bull. No. 16. 169 pp.

COMPARATIVE ANATOMY OF THE VENTRAL REGION
OF ANT LARVAE, AND ITS RELATION TO
FEEDING BEHAVIOR.¹

BY RONALD S. PETRALIA² AND S. B. VINSON

Department of Entomology
Texas A&M University
College Station, Texas 77843

INTRODUCTION

The morphology and systematics of the larvae of ants have been studied in great detail by George C. and Jeanette Wheeler in many articles and is summarized in Wheeler and Wheeler (1976). From the studies of many authors, especially the former and William M. Wheeler (1918, 1920), it is apparent that the mature larvae of many species of ants are fed solid food by the adult worker ants, which place the food on the ventral region of the larvae. Although the Wheelers describe the general morphology of ant larvae, they have not studied the ventral feeding region as a distinct unit, except in larvae where this region is the most specialized (e.g. Pseudomyrmecinae and Camponotini). Consequently, we intend in this study to examine the fine detail of the ventral region of larvae in the hope of clarifying homologies in morphological adaptations for feeding on solid food.

MATERIALS AND METHODS

Mature larvae of 15 species of ants from 6 subfamilies were examined, including:

Dorylinae

Neivamyrmex nigrescens (Cresson). Collected in Portal (Cochise Co.), AZ (July, 1977), and identified by J. Miranda. Three specimens examined with the scanning electron microscope (SEM).

¹Approved as TA 15824 by the Director of the Texas Agricultural Experiment Station in cooperation with ARS, USDA. Supported by the Texas Department of Agriculture interagency agreement IAC-0487 (78-79).

²Current address: Department of Biology, St. Ambrose College, 513 West Locust Street, Davenport, Iowa 52803.

Manuscript received by the editor May 20, 1980.

Ponerinae

Leptogenys elongata (Buckley). Collected from Sonora Research Station (Edwards Co.), TX (July 9–11, 1973), and identified by A. C. F. Hung. Three specimens examined with SEM.

Pachycondyla villosa (Fabricius). Collected from Alamo (Hidalgo Co.), TX, at Santa Ana National Wildlife Refuge (Aug. 15–17, 1973) and identified by A. C. F. Hung. Three specimens examined with SEM.

Odontomachus clarus Roger. Collected from Uvalde (Uvalde Co.), Tx (Aug. 8, 1973), and identified by A. C. F. Hung. Two specimens examined with SEM.

Pseudomyrmecinae

Pseudomyrmex pallidus F. Smith. Collected from Alamo (Hidalgo Co.), TX, at Santa Ana National Wildlife Refuge (Aug. 15–17, 1973) and identified by A. C. F. Hung. Two specimens examined with SEM.

Pseudomyrmex gracilis mexicanus Roger. Collected from Manuel, Tamaulipas, Mex. (Feb. 17, 1973), from *Acacia cornigera* by G. C. Gaumer. Identified by A. C. F. Hung. Five specimens examined with SEM.

Myrmicinae

Pogonomyrmex barbatus (F. Smith). Reared from newly mated queens collected from College Station (Brazos Co.), TX (July 1979) by D. and D. Ball. Identified by J. Mirenda and R. Petralia. One specimen examined with SEM.

Crematogaster laeviuscula Mayr. Reared from colony collected from Port Aransas (Aransas Co.), TX (April 14, 1979), by W. Foerster. Identified by J. Mirenda and R. Petralia. Four specimens examined with SEM.

Monomorium pharaonis (Linnaeus). Reared from colony collected from College Station (Brazos Co.), TX (late winter, 1979), by D. Bogar. Identified by J. Mirenda and R. Petralia. Two specimens examined with SEM.

Solenopsis molesta (Say). Reared from colony collected from colony of *S. invicta* Buren, from Plantersville (Montgomery Co.), TX (April 12, 1979), by R. Petralia. Identified by J. Mirenda and R. Petralia. Final determination was corroborated by the presence of anterior labial spinules on the larvae (Wheeler and Wheeler, 1955). Three specimens examined with SEM.

Trachymyrmex septentrionalis McCook. Collected from College Station (Brazos Co.), TX (May 12, 1964), by P. Adkisson.

Identified by M. R. Smith. Two specimens examined with SEM.

Atta texana (Buckley). Reared from 1 year old colony collected from Ratides Parish, LA (1975 queen), and identified by J. Moser. Five specimens examined with SEM.

Dolichoderinae

Iridomyrmex pruinosum Roger. Reared from Colony collected from College Station (Brazos Co.), TX (April 25, 1979) by R. Petralia. Identified by J. Mirenda and R. Petralia. Three specimens examined with SEM.

Formicinae

Colobopsis pylartes Wheeler. Collected from Davy Crockett National Forest, TX (July 19, 1973), and identified by A. C. F. Hung. Three specimens examined with SEM.

Camponotus rasilis Wheeler. Reared from colony collected from College Station (Brazos Co.), TX (early spring, 1976), by M. R. Barlin. Identified by J. Mirenda and R. Petralia. Four specimens examined with SEM.

All species were identified from adults. Collected material from which specimens were obtained is available in the insect collection of the Department of Entomology, Texas A&M University, College Station, Texas, 77843. Both adults and larvae and/or prepupae are available for all species except *P. barbatus* and *C. laeviuscula* (adults only).

P. barbatus, *C. laeviuscula*, *M. pharaonis*, *S. molesta*, and *I. pruinosum* were collected and reared according to the techniques described for *Solenopsis invicta* Buren (Petralia and Vinson 1978). *C. rasilis* was reared in a large bucket, brood being maintained in Wilson cells and petri dishes covered with a red plastic film. *Atta texana* was reared by Dr. John Moser (USDA Forest Service, Southern Forest Expt. Station, 2500 Shreveport Hwy., Pineville, Louisiana 71360). Larvae of *N. nigrescens* were fixed in 70% ethanol for 2 years. The remaining species were obtained from the insect collection of the Department of Entomology, Texas A&M University, and had been fixed in 80% ethanol for up to 6 years.

Specimens from the insect collection and *N. nigrescens* were subsequently refixed in 3% glutaraldehyde-3% formalin for 3 days or more, post-fixed in osmium tetroxide, dehydrated, critical point dried,

mounted on metal stubs with Tube-Coat™, metal coated, and examined in a JEOL JSM-35 SEM at 20–25 kV.

Specimens of all other species were mounted on metal stubs with Tube-Coat™ and examined alive in a JEOL JSM-35 SEM at 15 kV.

Sectioning of the trophothylax of *P. g. mexicana* and *P. pallidus* was carried out after refixation, but prior to post-fixation. This was accomplished by splitting the larva longitudinally with a hand-held razor blade.

RESULTS

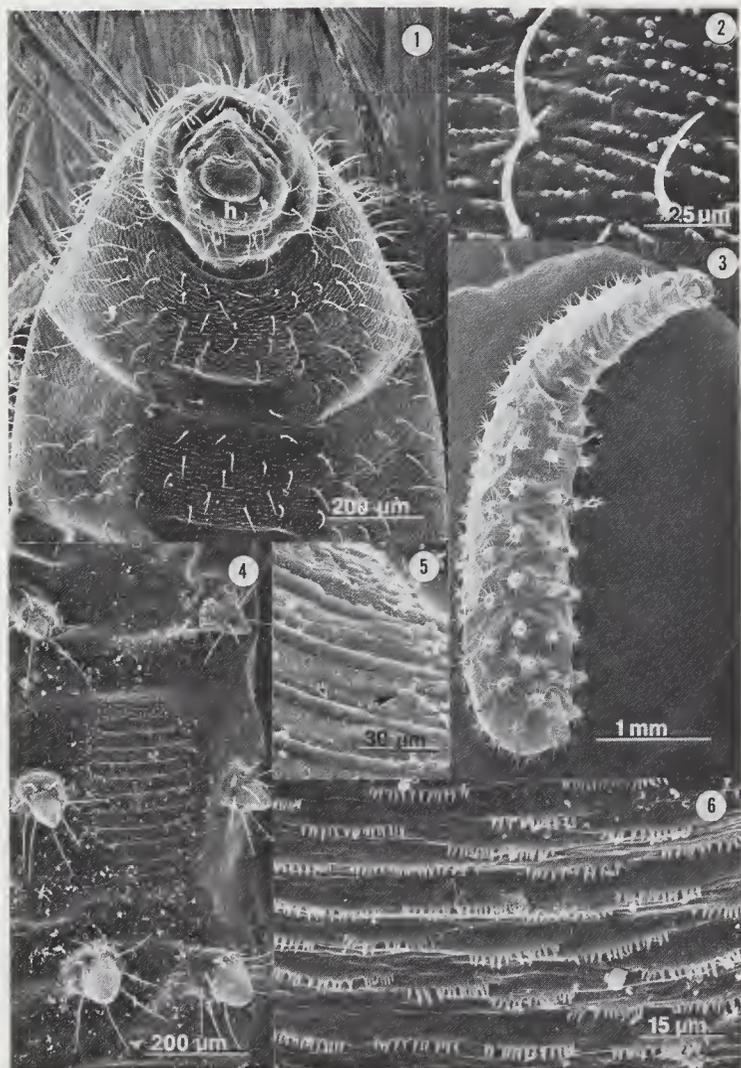
DORYLINAЕ

Neivamyrmex nigrescens— (Figs. 1, 2). There is no distinct attenuation into a neck (Fig. 1). Ventral region of body segments bear similar vestiture, which includes numerous long, simple hairs and rows of blunt spinules, both of which continue to the dorsal surface (Fig. 1). Most spinules point straight outward or slightly posterior (Fig. 2).

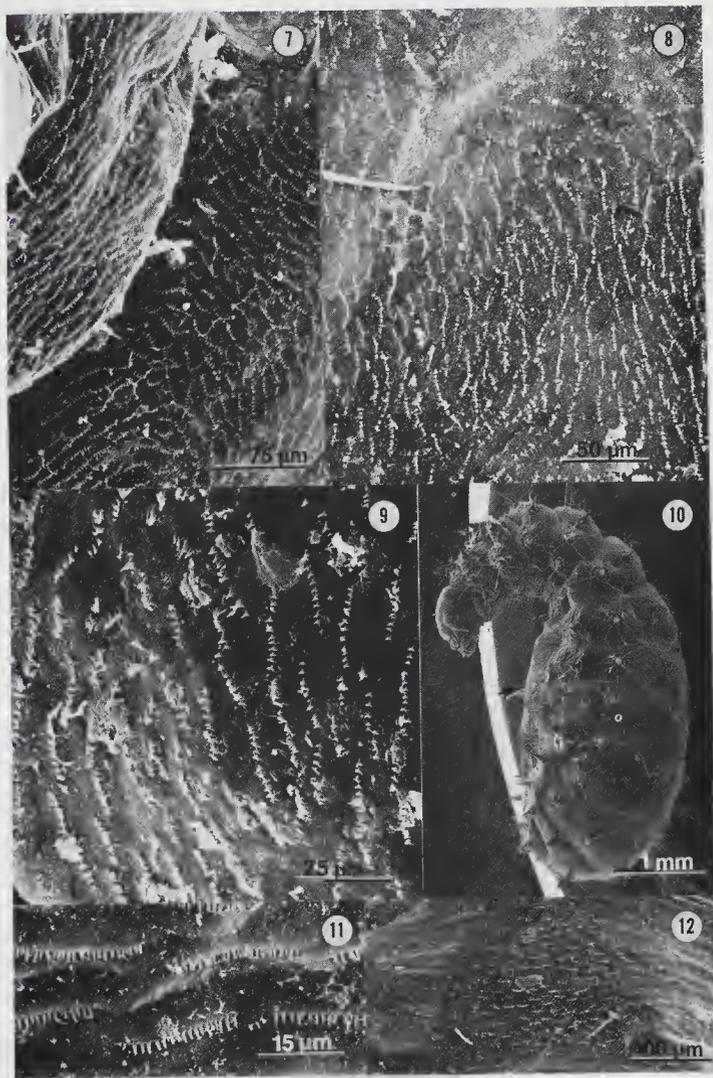
PONERINAЕ, PONERINI

Leptogenys elongata— (Figs. 3–6). Ventral body region bears only a few minute hairs, which are most numerous on the thorax (which attenuates to form the “neck” (Fig. 3)). Large cone-shaped tubercles laterally flank this region, although they become more medial after the 3rd abdominal segment (Figs. 3, 4). Each tubercle bears 6–9 long, simple hairs approximately 1/3 of the distance from the base; this basal 1/3 is distinctly broader than the tapering apex. The apex bears a few blunt spinules or papillae. There are numerous rows of posteriorly projecting spinules on the ventromedial surface of the thorax (Fig. 6) and a few rows on the 1st abdominal segment. A unique cuticular structure is found on the 3rd abdominal segment (Fig. 4). It is roughly ovoid, tapering posteriorly, and consists of 9–10 transverse ridges (Fig. 5) surrounded by small papillose protuberances.

Pachycondyla villosa— (Figs. 7–9). The distinct neck is formed by the thorax and 1st abdominal segment. The ventral body region bears only a few, scattered, minute simple hairs. This region is flanked laterally by elongate, cone-shaped protuberances bearing spinules and a few hairs. These protuberances gradually approach the ventral midline as they near the anus, thus enclosing an elongate, sub-ovoidal region from the neck to the anus. Spinules in short rows are formed in a unique arrangement on the ventral region. Those on the neck form



Figs. 1-6. Fig. 1. Anteroventral body region of *Neivamyrmex nigrescens*. Head (h). Fig. 2. High magnification, from Fig. 1 of *N. nigrescens*, of hairs and rows of spinules. Fig. 3. *Leptogenys elongata* showing ventral ridged structure (large arrow) on 3rd abdominal segment and tubercles (small arrow). Fig. 4. High magnification, from Fig. 3 of *L. elongata*, of ridged structure and tubercles. Fig. 5. High magnification of ridged structure of *L. elongata* showing ridges (small arrow) and papillose protuberances (large arrow). Fig. 6. Posteriorly pointing ventral mesothoracic spinules of *L. elongata*.



Figs. 7-12. Fig. 7. *Pachycondyla villosa*. Note semicircular pattern (lower right) of ventral prothoracic spinules. Portion of the left side of the head is also visible (left portion). Fig. 8. Posteroventral region of *P. villosa* showing circles of spinules of a segment. Fig. 9. High magnification of circles of spinules of posteroventral region of *P. villosa*. Fig. 10. Lateral view of *Odontomachus clarus*. Note posteroventral region (large arrow), and surrounding tubercles (small arrow). Fig. 11. Posteriorly pointing, ventral mesothoracic spinules of *O. clarus*. Fig. 12. Posteriorly pointing spinules of a segment of the posteroventral region of *O. clarus*.

an almost semicircular arrangement on each segment, with anterior spinules pointing posteriorly and lateral spinules pointing medially (Fig. 7). A similar arrangement of spinules is found on the remaining abdominal segments anterior to the anus. However, on these segments the concentric circle of short rows of spinules is complete, including posterior spinules which point anteriorly (Figs. 8, 9).

PONERINAE, ODONTOMACHINI

Odontomachus clarus — (Figs. 10–12). Neck attenuated as in the Ponerini (Fig. 10). Ventral body region bears only a few small, simple hairs. This region is flanked laterally by elongate cone-shaped protuberances (which continue onto the dorsal surface) bearing 4–6 long simple hairs near the apex (Fig. 10). Numerous rows of posteriorly pointing spinules occur medioventrally on at least the first 8 body segments (Figs. 11, 12). The ventral surface of the prothorax also bears a pair of fleshy tubercles anteriorly.

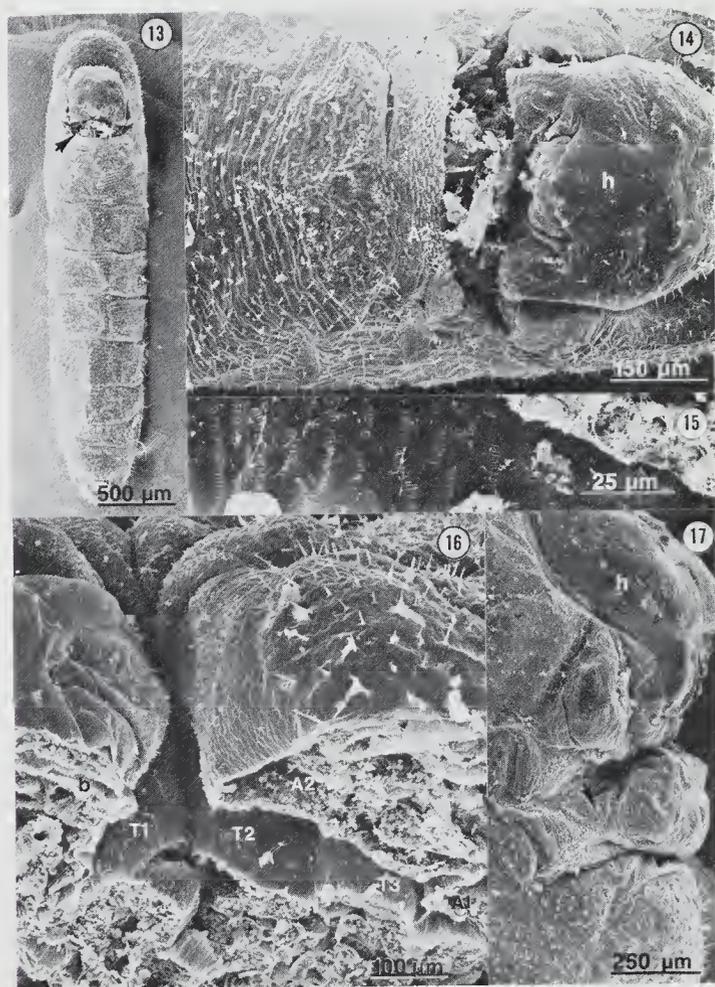
PSEUDOMYRMECINAE

Pseudomyrmex pallidus — (Figs. 13, 14). The structure and vestiture of the trophothylax are similar to those in *P. g. mexicanus* although in the specimen examined, the trophothylax was tear-drop shaped in longitudinal section and the segments were indistinct.

Pseudomyrmex gracilis mexicanus — (Figs. 15–17). The trophothylax is well developed. It is formed from the inverted ventral surfaces of the thorax and 1st 2 abdominal segments. The surface of the trophothylax bears numerous rows of spinules (Figs. 15, 16). Spinules on the thoracic and 1st abdominal segments point towards the posterior boundary of each segment (Fig. 15); those on the 2nd abdominal segment point towards the anterior boundary of this segment. The latter spinules cover the posterior lip of the trophothylax. The posterior portion of the 2nd abdominal segment, as well as the succeeding segments, bears numerous, straight, simple hairs (Fig. 16). In specimens where part of the trophothylax is extruded, the spinules on the extruded region point posteriorly (Fig. 17). The lateral lips of the trophothylax bear spinules pointing medially (Fig. 17).

MYRMICINAE, MYRMICINI

Pogonomyrmex barbatus — (Figs. 18–21). The thorax is attenuated (Fig. 18). Ventral body region bears numerous medially pointed hairs, most of which are denticulate on the distal half. Numerous posteriorly pointing spinules in short rows occur on the ventral region of the thorax and 1st abdominal segment. Numerous short



Figs. 13–17. Fig 13. Ventral view of *Pseudomyrmex pallidus* showing food in trophothylax (arrow). Fig 14. High magnification of food in trophothylax of *P. pallidus*. Note anteriorly pointing spinules on 2nd abdominal segment (A2). Head (h). Fig 15. Posteriorly pointing metathoracic spinules in trophothylax of *Pseudomyrmex gracilis mexicanus*. Fig 16. Section through trophothylax of *P. g. mexicanus*. Note buccal cavity (b), and segments: prothorax (T1); mesothorax (T2); metathorax (T3); 1st abdominal (A1) and 2nd abdominal (A2). Fig 17. Lateral view of extruded trophothylax of *P. g. mexicanus*. Note rows of spinules on metathorax (arrow). Head (h).

rows of posteriorly pointing spinules are on the anteroventral region of abdominal segment 2, while a very few (less than 10) anteriorly pointing spinules are on the posteroventral region of this segment (Fig. 19). Numerous short rows of posteriorly pointing anteroventral spinules and anteriorly pointing posteroventral spinules occur on each of abdominal segments 3-5 (Figs. 20, 21). Abdominal segment 6 bears only a few spinules pointing in each direction, while segment 7 bears very few spinules. Adult queen ants were observed to place solid food on the posteroventral region of larvae, which readily fed upon it.

MYRMICINAE, CREMATOGASTRINI

Crematogaster laeviuscula — (Figs. 22, 23). Head closely appressed to body (Fig. 22). Anteroventral body region bears a few, small, simple hairs, those on prothorax in 2 transverse rows, those on succeeding segments in 1 transverse row (Fig. 22). No evidence of spinules except for groups of a few papillae located laterally near segmentally arranged groups of pleats (Fig. 22, 23).

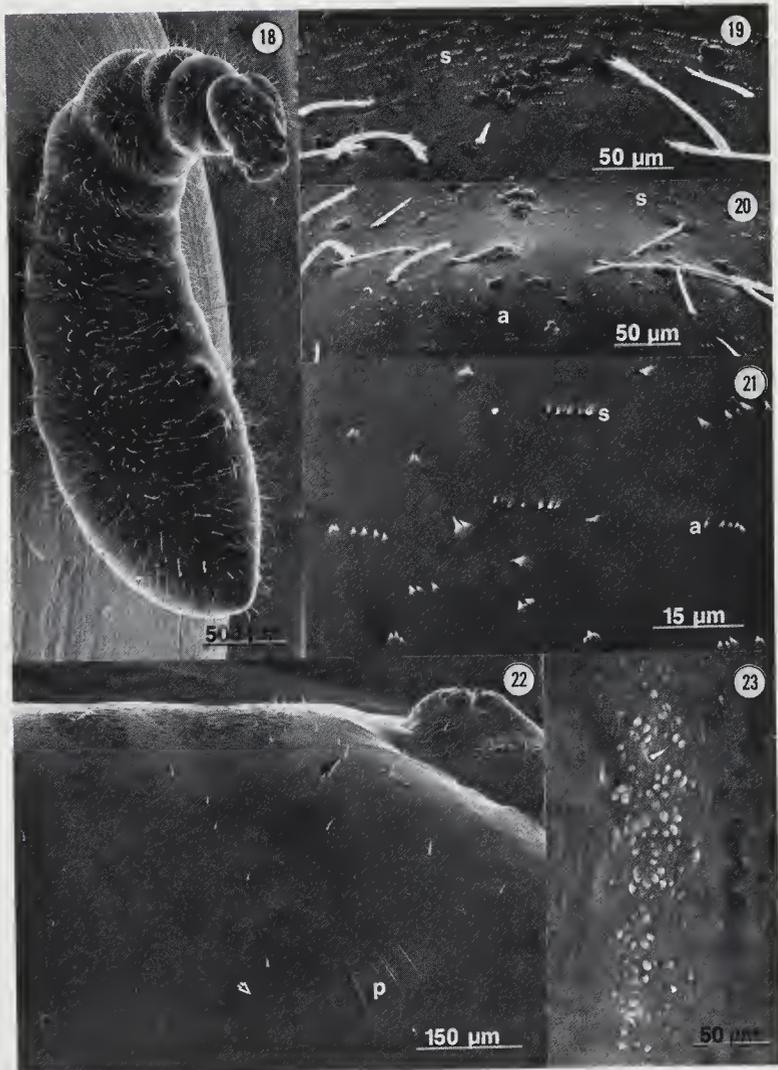
MYRMICINAE, SOLENOPSISIDINI

Monomorium pharaonis — (Figs. 24-26). Head close to body, thorax curved but not forming a distinct "neck" (Fig. 26). Hairs of anteroventral body region all bifid, except for those on prothorax, which bears simple, branched, or bifid hairs. Apices of hairs of ventral region of prothorax and mesothorax (and most of metathorax) straight, whereas most other body hairs with hooked apices (Fig. 25). Spinules of thoracic region mostly point posteriorly (Fig. 24), while those of 2nd and 3rd abdominal segments point anteriorly. First abdominal segment bears only 2-3 indistinct spinules.

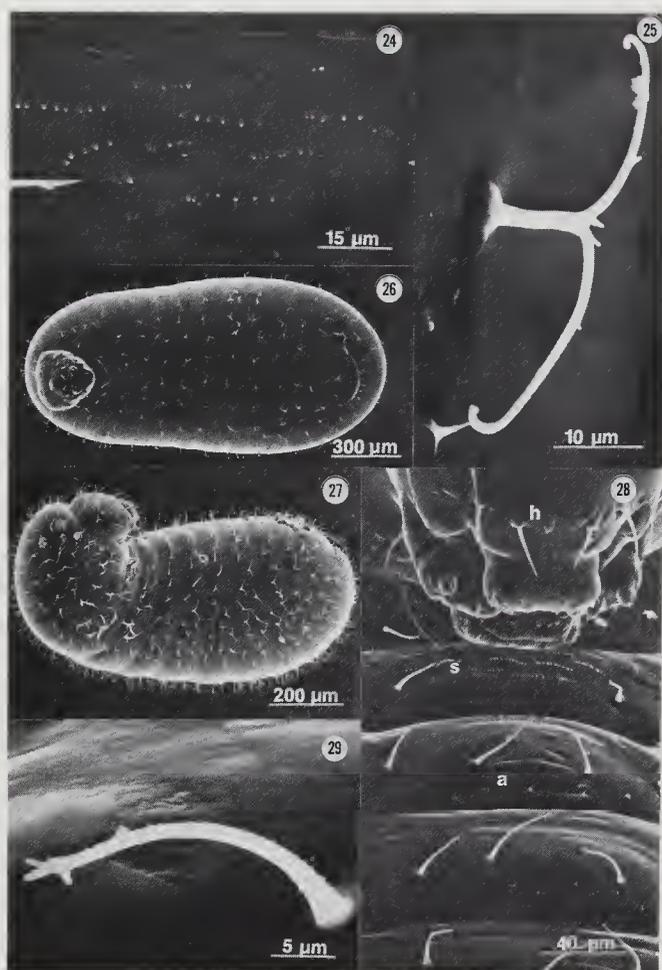
Solenopsis molesta — (Figs. 27-29). Head positioned as in *M. pharaonis* (Fig. 27). Anteroventral region (1st 6 body segments) bears mostly straight, simple hairs (some with branched tips) (Fig. 28). Each segment bears a single transverse row of about 8 simple hairs. The medial bare region between the most medial pair of hairs is especially wide on the thoracic segments. Remaining body hairs are bifid with hooked tips. Hairs papillose (Fig. 29). The rows of spinules on the medial region of each thoracic segment point posteriorly, while those of the 1st 3 abdominal segments point anteriorly.

MYRMICINAE, ATTINI

Trachymyrmex septentrionalis — (Figs. 30-32). Head closely appressed to the body (Figs. 30, 31). Body hairs, which are long, straight, simple (a few with slightly branched apices), are scarce, mostly in ventral region, and weakly papillose (Figs. 30, 31). Ven-



Figs. 18-23. Fig. 18. Lateral view of *Pogonomyrmex barbatus*. Fig. 19. Ventral region of 2nd abdominal segment of *P. barbatus*. Note rows of posteriorly pointing, anterior spinules (s). Fig. 20. Ventral region of 3rd abdominal segment of *P. barbatus*. Note rows of posteriorly pointing, anterior (s) and anteriorly pointing, posterior (a) spinules. Fig. 21. Anteriorly (a) and posteriorly (s) pointing spinules on ventral region of 4th abdominal segment of *P. barbatus*. Fig. 22. Anteroventral region of *Crematogaster laeviuscula*, showing hairs (large arrow), papillae (small arrow), and pleats (p). Fig. 23. High magnification of papillae of *C. laeviuscula*.



Figs. 24-29. Fig. 24. Posteriorly pointing, ventral spinules of metathorax of *Monomorium pharaonis*. Fig. 25. Bifid body hairs of *M. pharaonis*. Fig. 26. Ventral view of *M. pharaonis*. Fig. 27. Ventrolateral view of *Solenopsis molesta*. Note simple hairs of anteroventral region (arrow). Fig. 28. Anteroventral region of *S. molesta*. Note posteriorly pointing, anterior (s) and anteriorly pointing, posterior (a) spinules. Head (h). Fig. 29. Papillose hair from anteroventral region of *S. molesta*.

tromedial hairless area relatively wide on thorax, as in *S. molesta* (Fig. 30). Minute, posteriorly pointing spinules in short rows on ventromedial area of prothorax and mesothorax (Fig. 32).

Atta texana — (Figs. 33–35). Head closely appressed to body (Fig. 33). Leg vestiges prominent (Fig. 33). Body almost hairless. Ventral area of prothorax bears a medial boss bearing numerous spinules pointing straight outward, and 2–6 very short hairs (Figs. 34, 35); other spinules on prothorax point posteriorly (Figs. 34, 35); 2 pairs of very short hairs lateral to boss. Ventromedial area of mesothorax bare of hair and spinules, but flanked laterally by numerous spinules, most pointing straight outward or anteriorly, and 1 pair of very short hairs. Spinules present on succeeding segments.

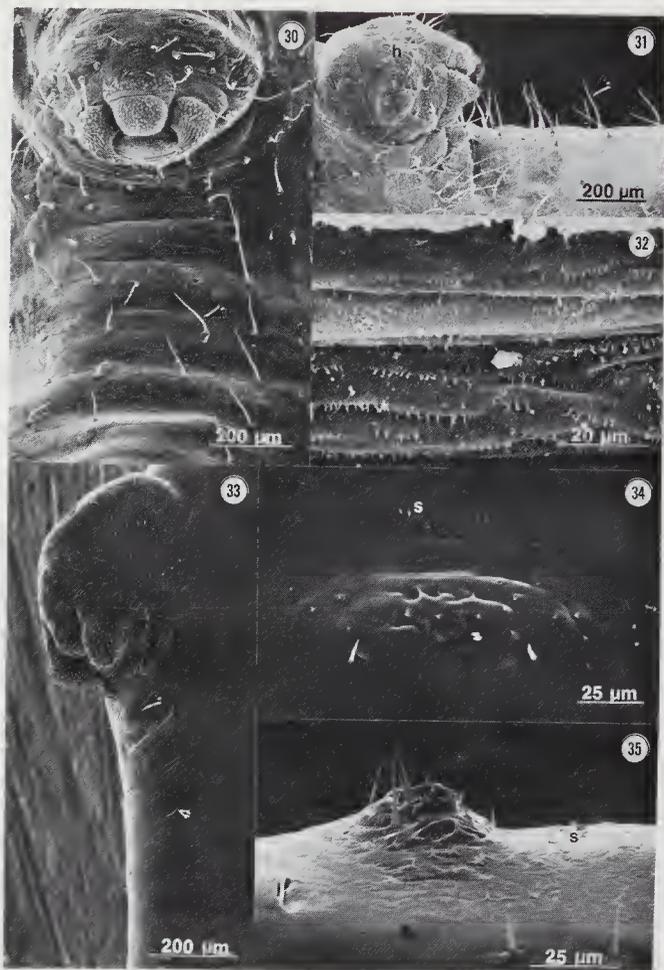
DOLICHODERINAE, TAPINOMINI

Iridomyrmex pruinosum — (Figs. 36–38). Head appressed closely to body (Figs. 36, 37). Anteroventral region with short, simple hairs, numerous only on prothorax. A very few, minute, blunt spinules are located on the ventral surface of the prothorax and mesothorax; spinules become slightly more numerous on posterior segments (Fig. 38).

FORMICINAE, CAMPONOTINI

Colobopsis pylartes — (Figs. 39, 40). Thorax stouter than in *Camponotus rasilis*. Praesaepium on 1st abdominal segment is covered by welt of 2nd abdominal segment (Fig. 39). Medial, hairless area of anteroventral region flanked by long, simple hairs (Fig. 39). Spinules very blunt and point posteriorly, those on lateral flanks of praesaepium (1st 2 abdominal segments) point postero-medially; rows of spinules on meso- and metathoracic segments very well developed and prominent (Fig. 40).

Camponotus rasilis — (Figs. 41–43). Neck developed (Fig. 41). Praesaepium well developed, formed in thorax and 1st 2 abdominal segments (Figs. 41, 42). In some specimens, food, including some brown cuticular material was found in praesaepium. Ventral area of prothorax bears numerous long, simple or bifid hairs. Ventromedial, hairless area of meso- and metathorax and 1st 2 abdominal segments is flanked laterally by a few simple bifid hairs. Most other body hairs are 3–5 branched, interspersed occasionally with a few, very long simple hairs with curled tips. Spinules on anteroventral body region (thorax and 1st 2 abdominal segments) point posteriorly (Fig. 43), except for the most anterior portions of the prothorax where they point anteriorly.



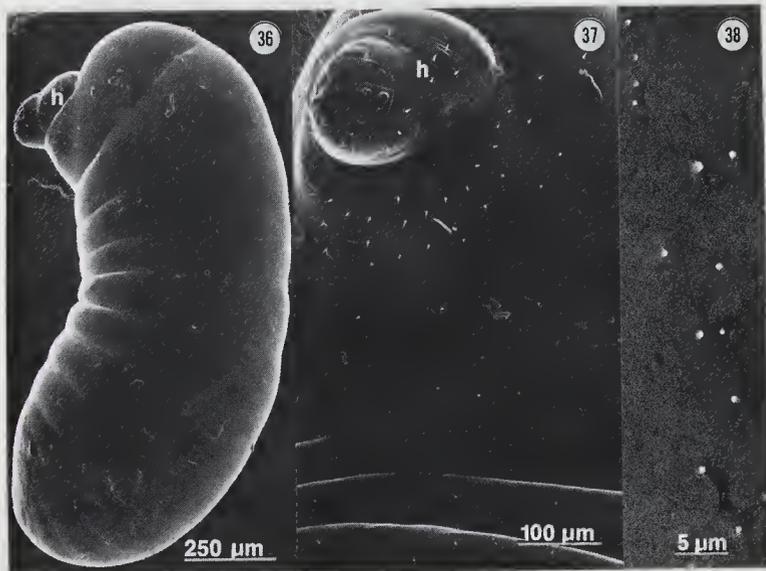
Figs. 30-35. Fig. 30. Ventral view of anteroventral region of *Trachymyrmex septentrionalis*. Note simple hairs (arrow). Fig. 31. Lateral view of anteroventral region of *T. septentrionalis*. Note simple hairs (arrow). Head (h). Fig. 32. Posteriorly pointing ventral prothoracic spinules of *T. septentrionalis*. Fig. 33. Ventrolateral view of anteroventral region of *Atta texana*. Note prothoracic boss (large arrow) and metathoracic leg vestige (small arrow). Fig. 34. Ventral view of prothoracic boss of *A. texana*. Note posteriorly pointing spinules (s) anterior to the boss.

Fig. 35. Lateral view of prothoracic boss of *A. texana*. Note posteriorly pointing spinules (s) anterior to the boss, and left prothoracic leg disc (l).

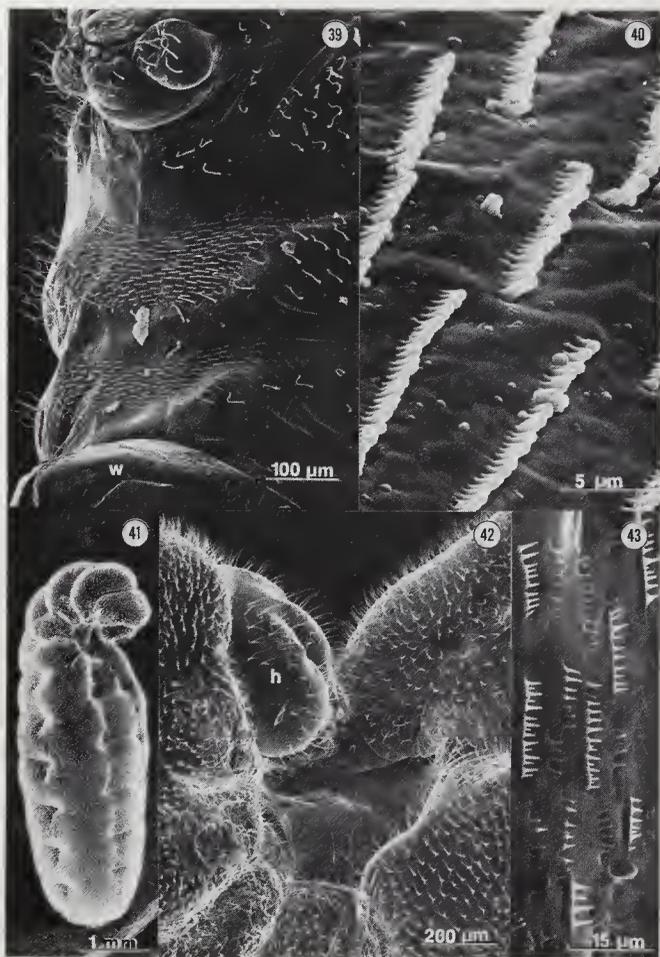
DISCUSSION

The morphology of the ventral body region can be related to feeding behavior. Thus, in larvae which are reported in the literature to be fed only by regurgitation of liquid food from the adult workers, the morphology of this region is relatively unspecialized. In this category can be placed *Crematogaster laeviuscula* and *Iridomyrmex pruinosum*, in which the head is so closely appressed to the body, that it cannot reach the ventral body region with its mouthparts. Larvae of these species bear few or no spinules in this region and the hairs and hair pattern are unspecialized. The papillose regions on *C. laeviuscula* may be vestiges of the rows of spinules found in other ants. Wheeler and Wheeler (1976) state: "... the immobility of a body with a dolichoderoid or crematogastroid shape precludes self-feeding. Hence these larvae must be fed by regurgitation".

The remaining larvae described in this study are reported in the literature to be fed solid food by adult workers.



Figs. 36-38 Fig. 36. Lateral view of *Iridomyrmex pruinosum*. Head (h). Fig. 37. Anteroventral body region of *I. pruinosum*. Note short, simple hairs (arrow). Praesaepium (arrow). Fig. 38. Ventral, metathoracic spinules of *I. pruinosum*.



Figs. 39-43. Fig. 39. Anteroventral region of *Colobopsis pylartes*. Note rows of spinules (arrows) and welt (w). Fig. 40. Posteriorly pointing ventral thoracic spinules of *C. pylartes* magnified from Fig. 39. Fig. 41. Ventrolateral view of *Camponotus rasilis*. Praesaepium (arrow). Fig. 42. High magnification of praesaepium of *C. rasilis*. Head (h). Fig. 43. Posteriorly pointing ventral thoracic spinules of *C. rasilis*.

However, larvae of *Neivamyrmex nigrescens* (Dorylinae) do not show specializations for holding food. In studies based on the laboratory culture methods of Topoff and Miranda (1978a, b), workers placed prey near larvae, which then attached themselves to this food and appeared to suck out the body fluids (Miranda, pers. comm.). Thus, larvae of *N. nigrescens* do not require a specialized ventral feeding region as food is never placed on them. Wheeler and Bailey (1920:270) do not describe how ant larvae in the Dorylinae are fed "pellets made of the flesh of insects".

The simplest arrangement of morphology for holding solid food is found in some Myrmicinae. The 2 species from Solenopsidini described above (*Monomorium pharaonis*, *Solenopsis molesta*) bear similar general patterns of vestiture on the anteroventral region, i.e. with anterior spinules pointing posteriorly and posterior spinules pointing anteriorly, and with hairs mostly simple. Furthermore, the position of the head and curvature of the thorax give them the ability to reach the anteroventral region. Similar morphology was described for *S. invicta* (Petralia and Vinson 1978, 1979). The anteroventral region is least specialized in *M. pharaonis* and it is not known whether this region is used for holding food. Larvae of *S. invicta* and *S. molesta* feed on solid food placed on them (Petralia and Vinson 1978, Wheeler and Wheeler 1955), and in *S. invicta* the hairs and spinules of the anteroventral region are efficient for holding solid food while the larva feeds upon it (Petralia and Vinson 1978). The hairs surrounding the hairless medial area enclose the food particle to form a "food basket", while the medial spinules are arranged to assist attachment of the food. *S. molesta* appears to have a somewhat similar "food basket".

A comparable means of holding food is found on larvae in the Attini. *Trachymyrmex septentrionalis* bears well developed hairs only on the ventral region, with the majority being in the anteroventral region. These hairs appear to be arranged in a similar pattern as in *Solenopsis*. Thus, this may also be a "food basket" since Wheeler and Wheeler (1974, 1976) state: "The ventral hairs of the attine larvae keep the fungal mass [food] firmly in place while the larva is feeding". *Atta texana* is almost bare of hairs but possesses a ventral prothoracic boss with outward pointing spinules and minute hairs. G. C. Wheeler (1948) describes how adult workers place solid food on the mouthparts of these larvae. We speculate that larvae may use this structure

to brace or anchor the food while feeding, because of the close proximity of this boss to the face of the mouthparts, although this is not described in the literature.

The most efficient method for holding solid food, within the Myrmicinae, may be in larvae of *Pogonomyrmex barbatus*. The segments in the posteroventral feeding region (especially abdominal segments 3–5) bear spinules and strongly denticulate hairs, both pointing to the center of each segment. The attenuated thorax allows larvae enough dexterity to feed easily from this region.

This attenuation is even more pronounced in the Ponerinae. The larvae of Ponerinae described here have a long neck which allows them to reach solid food placed on the wide, flattened posteroventral body region which Wheeler and Wheeler (1976) refer to as a food "platter." W. M. Wheeler (1918) describes the feeding behavior of *Odontomachus*: "These larvae are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which food is placed by the workers." This "food platter" is visible in *O. clarus* and *Pachycondyla villosa* where a row of tubercles demarcates this area laterally. It is better developed in *P. villosa* in which a circle of spinules on each segment probably holds food more efficiently than the posteriorly pointing spinules in *O. clarus*. The arrangement of spinules in *P. villosa* may be comparable to that on the posteroventral feeding region of *P. barbatus* (Myrmicinae).

The feeding region on larvae of the ponerine *Leptogenys elongata* may be even more specialized by the development of a unique cuticular process on the ventral surface of the 3rd abdominal segment. The cuticular ridges in this structure seem to be formed from a fusion of the small, blunt papillae or spinules, as is visible in the peripheral parts of the structure. Thus, these ridges are probably homologous to the rows of spinules common on ant larvae. We speculate that this structure may form a "food tray," efficient in holding solid food while the larva feeds upon it.³ Recently, John Mirenda and the authors have made preliminary observations on larval feeding in live colonies of *L. elongata*.⁴ Adult workers place larvae head first into the par-

³Dr. G. C. Wheeler and J. Wheeler suggest that this structure might function as a stridulatory or food-holding structure or both (pers. comm.).

⁴Collected and identified by Dr. J. Mirenda, from College Station (Brazos Co.), TX (March 3, 1980).

tially eaten bodies of isopods, where larvae actively feed. Since Wheeler (1918) states that the larvae of North American Ponerinae feed on food placed on their ventral region, or on insect parts placed near them (observed in *L. elongata*; 1910), it is possible that several methods of feeding are present in the same species. However, an alternative function of the ridged structure is a holdfast. When not feeding, larvae typically curve their "necks" so as to rest the ventral surface of the prothorax or the posteroventral surface of the head against the ridged structure. Perhaps posteriorly pointing spinules hook on the ridges, allowing the larva to maintain the resting position with minimum effort.

The most advanced specializations for holding food are found in the Pseudomyrmecinae and the Camponotini. Many larvae of the Camponotini possess a well developed pocket for holding solid food called a praesaepium (Wheeler and Wheeler 1953). It is best developed in *Colobopsis* as is evident in *C. pylartes*. In both *Camponotus rasilis* and *C. pylartes* the posteriorly pointing spinules on the anteroventral region may function to force the food against the posterior wall of the praesaepium (the posterior wall in *Colobopsis* is the large ventral welt). This is supported by illustrations of a food pellet held in the praesaepium of *C. gasseri* (Forel) (Wheeler and Wheeler 1970).

The "food pocket" is most highly developed in the Pseudomyrmecinae and is called the trophothylax (Wheeler and Bailey 1920; Wheeler and Wheeler 1956). The spinules in the trophothylax are positioned to help hold food in it, although this assistance may be unnecessary.

Specialized feeding regions are also described in larvae of other social Hymenoptera, including the transitory praesaepium of allopodoid bees and some vespids, and the shelf of *Mischocyttarus* (Vespidae: Polybiinae) (Wheeler and Wheeler 1979). We thus assume that morphological adaptations for holding food on the ventral region have evolved independently in numerous taxa within the social Hymenoptera.

In conclusion, the various morphological specializations in the feeding regions of ant larvae are analogous, although not always homologous. Thus, 3 basic types of feeding regions are evident. The first is the "food basket" of larvae of some Myrmicinae, in which the specializations are in the arrangement of homologous groups of

hairs and spinules. The second is the posteroventral "food platter" of larvae of most Ponerinae, in which specializations are in the arrangement of homologous groups of spinules and tubercles. The 3rd is the anteroventral "food pocket" of larvae of Pseudomyrmecinae and Camponotini, in which specializations are in the arrangement of homologous groups of spinules and in the homologous development of the pockets.

ACKNOWLEDGMENTS

Appreciation is extended to Dr. John T. Mirenda for identifying some of the species, Dr. H. R. Burke for his advice and suggestions, and Dr. G. C. Wheeler and J. Wheeler for their critical review. We also thank David Ball, Dr. Margaret R. Barlin, Daniel Bogar, William P. Foerster, Dr. John T. Mirenda, and Dr. John Moser for providing specimens of *P. barbatus*, *C. rasilis*, *M. pharaonis*, *C. laeviuscula*, *N. nigrescens*, and *A. texana*, respectively.

REFERENCES CITED

- PETRALIA, R. S. AND S. B. VINSON
 1978. Feeding in the larvae of the imported fire ant, *Solenopsis invicta*: behavior and morphological adaptations. *Ann. Entomol. Soc. Amer.* **71**: 643-8.
 1979. Developmental morphology of larvae and eggs of the imported fire ant, *Solenopsis invicta* Buren. *Ann. Entomol. Soc. Am.* **72**: 472-84.
- TOPOFF, H. AND J. MIRENDA.
 1978a. Precocial behavior of callow workers of the army ant *Neivamyrmex nigrescens*: importance of stimulation by adults during mass recruitment. *Animal Behavior* **26**(3): 689-706.
 1978b. In search of the precocial ant. *In* *The Development of Behavior: Comparative and Evolutionary Aspects* (M. Bekoff and G. Burghardt, Eds.). New York: Garland.
- WHEELER, G. C.
 1948. The larvae of the fungus-growing ants. *Amer. Midland Natur.* **40**: 664-89.
- WHEELER, G. C. AND J. WHEELER
 1953. The ant larvae of the subfamily Formicinae, part II. *Ann. Entomol. Soc. Amer.* **46**: 175-217.
 1955. The ant larvae of the myrmicine tribe Solenopsidini. *Amer. Midland Natur.* **54**: 119-41.
 1956. The ant larvae of the subfamily Pseudomyrmecinae (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Amer.* **49**: 374-98.

1970. Ant larvae of the subfamily Formicinae: second supplement. *Ann. Entomol. Soc. Amer.* 63:648-56.
1974. Ant larvae of the myrmicine tribe Attini: second supplement (Hymenoptera: Formicidae). *Proc. Entomol. Soc. Wash.* 76:78-81.
1976. Ant Larvae: Review and Synthesis. *Mem. Entomol. Soc. Wash.* 7: 1-108.
1979. Larvae of the social Hymenoptera. *In Social Insects*, Vol. I. (H. R. Hermann, Ed.). New York: Academic Press.
- WHEELER, W. M.
1910. *Ants*. Columbia Univ. Press, New York, 663 pp.
1918. A study on some ant larvae, with a consideration of the origin and meaning of the social habit among insects. *Proc. Amer. Phil. Soc. (Philadelphia)* 57: 293-343.
- WHEELER, W. M. AND I. W. BAILEY.
1920. The feeding habits of pseudomyrmine and other ants. *Trans. Amer. Phil. Soc. (Philadelphia)* (Art. 4): 235-279, 5 pl.

MATING BEHAVIOR OF THREE SPECIES OF CONIOPTERYGIDAE (NEUROPTERA)¹

BY VICTOR JOHNSON²
AND
WILLIAM P. MORRISON³

There have been very few reports of the mating behavior in Coniopterygidae. During the course of studying the biology of 3 species of coniopterygids in California we were fortunate in being able to observe several instances of courtship and mating behavior. These observations were fortuitous and made during field collecting. We were unable to observe mating under laboratory conditions.

Only 3 observations on mating behavior in Coniopterygidae have been reported in the literature. Collyer (1951) described a staggered, parallel, female-above position in *Conwentzia pineticola* Enderlein. He reported that in this species the male holds the hind coxae of the female with his forelegs and mouthparts. A similar staggered, parallel position was observed by Withycombe (1922) in *Parasemidalis annae*. Henry (1976) described a different type of mating behavior in *Aleuropteryx juniperi* Ohm — one in which the male and female mated in a tail-to-tail position.

We have observed courtship and mating in the following 3 species: *Conwentzia californica* Meinander, *Conwentzia barretti* (Banks) and *Semidalis angusta* Banks. Observations were made on newly-collected specimens in Los Angeles County, California.

Specimens were collected by aspirating adults into plastic 10-dram vials. During the course of field collecting, a vial would contain 15–20 adults. All observations on courtship and mating behavior were made in the vials within the first 2 hr following collection. After that time, continued observance of specimens did

¹The investigation reported in this paper (No. 80-7-51) is in connection with a project of the Kentucky Agricultural Experiment Station and is published with approval of the Director.

²Formerly Research Assistant in the Department of Entomology, University of Kentucky, Lexington, Kentucky 40546. Present address: USDA-APHIS-PPQ, Box 22277, Lexington, Kentucky 40522.

³Department of Entomology, Texas Tech University, Lubbock, Texas 79409.
Manuscript received by the editor May 6, 1980.

not reveal additional courtship and/or mating behavior. Mating was observed 3 times in both *C. californica* and *C. barretti* and 4 times in *S. angusta*.

Both sexes were observed to exhibit precopulatory behavior. The female would call by slightly elevating and rotating her abdomen and at the same time, fluttering her wings for 1-2 secs. This behavior was observed while the female was either walking or standing still and would be repeated at various time intervals for up to ca. 1 hr following collection. The male exhibited similar precopulatory behavior. He would elevate his abdomen dorso-anteriorly in a mating position, walk rapidly about and also flutter his wings intermittently for 1-2 secs.

The mating behavior of *C. californica*, *C. barretti* and *S. angusta* was very similar. The male approached the female from the rear and, with his head lowered, would push it up under the abdomen of the female. Simultaneously, the male reached forward with his forelegs and grasped the legs of the female. The male would grasp either 2, 3 or 4 legs of the female, excluding the forelegs which he could not reach. If only a single leg was grasped, the female would extricate herself from the male. The male would approach and grasp a female while she was either still or walking. It was not necessary that the female be quiescent. Males would occasionally approach a female from the side. These males would then quickly move to the posterior of the female and attempt to grasp her legs. Sometimes, the female would avoid the male by flying or walking rapidly away from a male after she had been approached. However, if the male was successful in grasping 2 or more legs, an attempt at copulation ensued.

Following the successful grasping of a female, the male then brought the tip of his abdomen dorso-anteriorly and made contact with the tip of the female abdomen. After aedeagal intromission, the mating pair remained *in copulo* for 10-15 min. The coital stance of the male was such that the abdomen was curved dorso-anteriorly almost to his metathoracic segment. The antennae of the male were extended outward at ca. 90° angle to the body and the wings were spread only slightly. After being successfully grasped, the female spread her wings to a ca. 45° angle to the body, the abdomen was elevated slightly and the antennae were in a porrect position.

During copulation, the female often walked around pulling the male with her. The genitalic grasp is sufficiently strong to maintain

union even when the adults were picked up by the wings with forceps. No postcoital courtship behavior was observed.

While a pair was *in copulo*, additional males sometimes approached. These males would locate the posterior of the mating pair, push under the male, grasp his legs and assume a coital stance. These secondary males would remain in this position for several mins. attempting to mate with the male. In one instance involving *C. barretti*, a third male joined "the chain" and attempted to mate with the second male.

During one collection period, several males and females of *S. angusta* and *C. californica* were in the same vial. Two males and one female of *C. californica* were observed exhibiting precopulatory behavior but no *S. angusta* were observed in this position. A male of *C. californica* then attempted to mate with the much smaller female of *S. angusta*. The male grasped 3 legs of the female and attempted unsuccessfully for ca. 45 min. to mate.

In another instance, 2 different males of *C. californica* grasped and attempted to mate with a male which had just concluded mating with a female. On yet another occasion, while collecting on *Cupressus semperivernus* L. in the Los Angeles State and County Arboretum, ca. 15 males were observed clustered and flying within 0.5 m of a female on a branch.

These observations seem to indicate the presence of a female sex pheromone. No mention of a female sex pheromone has previously been reported in the Coniopterygidae.

Mating has now been observed in 6 species of Coniopterygidae. The 3 species reported herein, in addition to *P. annae* and *C. pineticola*, all exhibit the staggered, parallel, female-above position. These 5 species are all within the subfamily Coniopteryginae. The one species having tail-to-tail mating behavior, *A. juniperis*, is in the subfamily Aleuropteryginae. Perhaps additional observations on other species will indicate that mating behavior is a distinguishing subfamily characteristic.

REFERENCES

COLLYER, E.

1951. The separation of *Conwentzia pineticola* End. from *Conwentzia psociiformis* (Curt.) and notes on their biology. Bull. Entomol. Res. 42:555-564.

HENRY, THOMAS J.

1976. *Aleuropteryx juniperi*: a European scale predator established in North America (Neuroptera: Coniopterygidae). Proc. Entomol. Soc. Washington **78**(2):195-201.

WITHYCOMBE, C. L.

1922. *Parasemidalis annae* Enderlein, A Coniopterygid new to Britain, with notes on other British Coniopterygidae. Entomol. **55**:169-172.

OBSERVATIONS OF SEED-BUG (HEMIPTERA:
LYGAEIDAE)
PARASITISM BY A SPECIES OF
CATHAROSIA (DIPTERA: TACHINIDAE)¹

BY KEVIN W. THORPE² AND B. JANE HARRINGTON
Department of Entomology
University of Wisconsin
Madison, Wisconsin 53706

INTRODUCTION

Tachinids of the genus *Catharosia* Rondani are infrequently collected parasitoids of seed bugs (Hemiptera: Lygaeidae). Sweet (1964) was the first to publish biological information on flies of this genus. He reared *Catharosia* from 15 species of bugs in 11 genera and, after communicating with Dr. Paul H. Arnaud, Jr., concluded that a large complex of *Catharosia* species was probably involved. Later Ashlock and O'Brien (1964) reported rearing 35 *Catharosia lustrans* (Reinhard) from field collected *Thylochromus nitidulus* (Barber) and *Eremocoris opacus* Van Duzee (Lygaeidae: Rhy-parochrominae: Drymini). These authors also reared a single fly through a complete life cycle on a laboratory culture of an undescribed species of *Eremocoris*.

During the summers of 1977 and 1978, we reared 51 adults of a tachinid species from field collected individuals of four closely related lygaeid genera of the rhyparochromine tribe Myodochini. We reared an additional 16 flies through a complete life cycle on laboratory cultured *Ligyrocoris diffusus* (Uhler). Samples from these rearings were identified as a single species of *Catharosia* (P.H. Arnaud, personal communication). Voucher specimens were deposited in the collections of the California Academy of Sciences, San Francisco and the University of Wisconsin, Madison.

¹Research supported by the College of Agricultural and Life Sciences, University of Wisconsin-Madison and by a grant from the University of Wisconsin Graduate School (Project Number 190381). Part of a thesis submitted by K. Thorpe in partial fulfillment of the requirements for the MS degree.

²Present Address: Beneficial Insect Introduction Laboratory, Building 417, BARC-East, Beltsville, Maryland 20705.

Manuscript received by the editor May 6, 1980.

From that rearing effort we present information on the biology of this parasitoid and a description of an interesting structure on the female abdomen that presumably aids in oviposition.

MATERIALS AND METHODS

Lygaeid adults and nymphs were collected from several dry, disturbed habitats in each of three Wisconsin counties. *Ligyrocoris diffusus* and *Perigenes constrictus* (Say) were collected from Dane Co. in southern Wisconsin; *L. diffusus*, *L. sylvestris* (L.), *P. constrictus*, *Sphaerobius insignis* Uhler, and *Zeridonius costalis* (Van Duzee) were collected from Wood Co. in central Wisconsin; and *L. diffusus*, *L. sylvestris*, and *Z. costalis* were collected from Vilas Co. in northern Wisconsin. Field collected bugs were maintained and reared individually or in small conspecific groups at $26 \pm 1^\circ$ C and 16L:8D photoperiod in glass crystalizing dishes (90 × 50 mm) with plastic lids. Each dish was provided with a vial of water stoppered with a dental wick, hulled sunflower seeds, and several thin squares of methyl cellulose. The dishes were checked daily for tachinid pupae, which were transferred to clean vials to prevent fungus infestation. Upon eclosion adult flies were supplied with a dental wick moistened with sugar water. Whenever both sexes of flies became available concurrently they were placed together with laboratory cultured *L. diffusus* nymphs and adults.

Scanning electron photomicrographs of *Catharosia* were obtained from gold-palladium-coated preparations viewed on a Jelco JSM-U3 scanning electron microscope.

RESULTS AND DISCUSSION

Catharosia were reared from all myodochine species collected in Wood Co. and Vilas Co., but none emerged from any bugs collected in Dane Co. *Ligyrocoris sylvestris* is a new host record for the genus *Catharosia*. Sweet (1964) reported rearing *Catharosia* from *L. diffusus* and *L. dipictus* Barber in New England, but not from *L. sylvestris* or *L. caracis* Sweet. Sweet also reported rearing *Catharosia* from the other 3 myodochine species collected in this study.

The rates of parasitism of *L. diffusus*, the myodochine most commonly collected at the Wood Co. site on 19 June and 22 August 1978, were 60% and 16% respectively (Table 1). The difference in

rates of parasitism between the sexes of *L. diffusus* (summed across both collection dates) was not significant at the .05 level.

Table 1. Rates of parasitism by *Catharosia* in *L. diffusus* collected on 2 separate dates in 1978 in Wood Co., Wisconsin.

	19 June		22 August	
	<i>L. diffusus</i> ♂	<i>L. diffusus</i> ♀	<i>L. diffusus</i> ♂	<i>L. diffusus</i> ♀
Number collected	25	40	39	42
Number parasitized	12	27	5	8
% parasitism	48	67.5	12.82	19.05
Total % parasitism	60		16.05	

Laboratory reared flies began mating on the day of eclosion. There was no apparent, regular courtship ritual. However, males appeared to orient visually to females and both sexes frequently flicked their wings upward while running, displaying the white apex of the wing which contrasts sharply with the darker basal portion. This wing flicking behavior may serve in some sort of intraspecific visual communication. Copulating males placed their foretarsi over the females' eyes but no special adaptations of the male foretarsi were discernible. The duration of copulation ranged from a few seconds to several minutes, and copulation was often repeated by single pairs at short intervals.

Examination of female flies revealed an interesting structure located on the fourth abdominal sternum (Fig. 1). It consists of paired plates on either side of the midline covered by a field of spines directed medially and slightly caudad. The presence of this structure was previously noted by Lundbeck (1927) who described the fourth sternum of *Catharosia* as "cleft in the middle and covered with short spinules." Although oviposition was not observed during our rearing efforts, the needle-like nature of the *Catharosia* ovipositor (or larvapositor) suggests subcutaneous deposition of either eggs or larvae into the host. The spined plates probably aid in holding the host during oviposition. A similar structure is found on tachinids of the genus *Celatoria* which parasitize beetles in the family Chrysomelidae, however the structure in this case is located on the apex of a laterally compressed tubercle that extends ventrally from the second abdominal segment and opposes the larvapositor

(Bussart 1937, Walton 1914). Walton suggests that the function of this structure is to hold the host in place as the larvaporator is forced through the beetle's elytra. These ovipositor opposing structures of *Celatoria* and *Catharosia* probably represent convergent evolution of organs serving similar functions but located on different abdominal segments.

Catharosia was found to parasitize both adult and nymphal mydochine bugs, but parasitoids only emerged from adult hosts. One fifth instar *L. diffusus* nymph collected in the field yielded a *Catharosia* after the bug had molted to an adult. All other *Catharosia* obtained from field collected hosts were reared from hosts collected as adults.

In laboratory reared flies total development time from first mating of parent flies until adult progeny eclosed averaged 23.5 days (SE = 1.15, Range = 18-29, N = 15). These data agree with the observed development time of the parasitoids reared from field collected hosts.

The position of *Catharosia* larvae within the host was determined

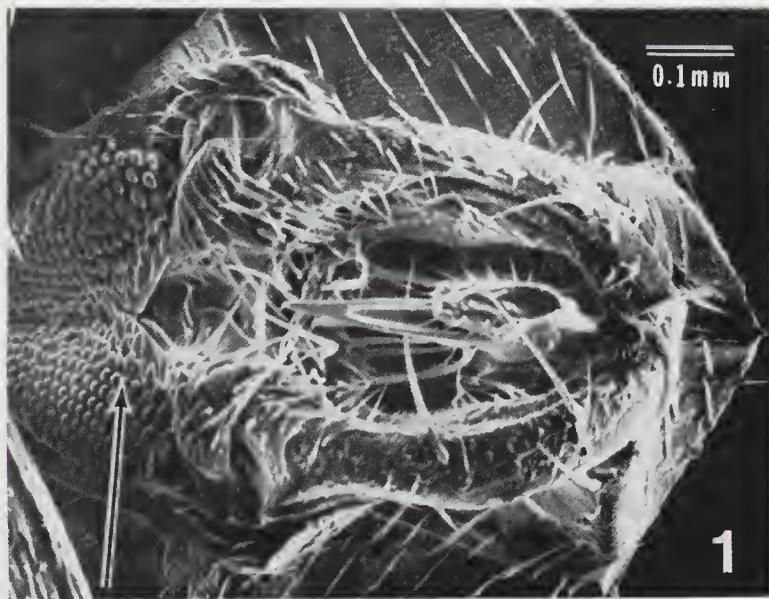


Figure 1. Scanning electron photomicrograph of ventral abdominal surface of a *Catharosia* sp. female showing heavily spined plates on 4th sternum.

from dissections of twenty parasitized *L. diffusus*. Figure 2 depicts the position of a mature third instar larva within an adult *L. diffusus* female. The full grown larva fills the entire abdominal cavity and its posterior spiracle partially protrudes into the bug's thorax where it fits into a respiratory funnel (Clausen (1940) discussed the host tissue origins of such a respiratory funnel). The host-attached, narrow end of the funnel was always found lying very close to either the right (12 examples) or left (8 examples) metathoracic spiracle, and was probably attached to the spiracular stalk not far from the spiracle.

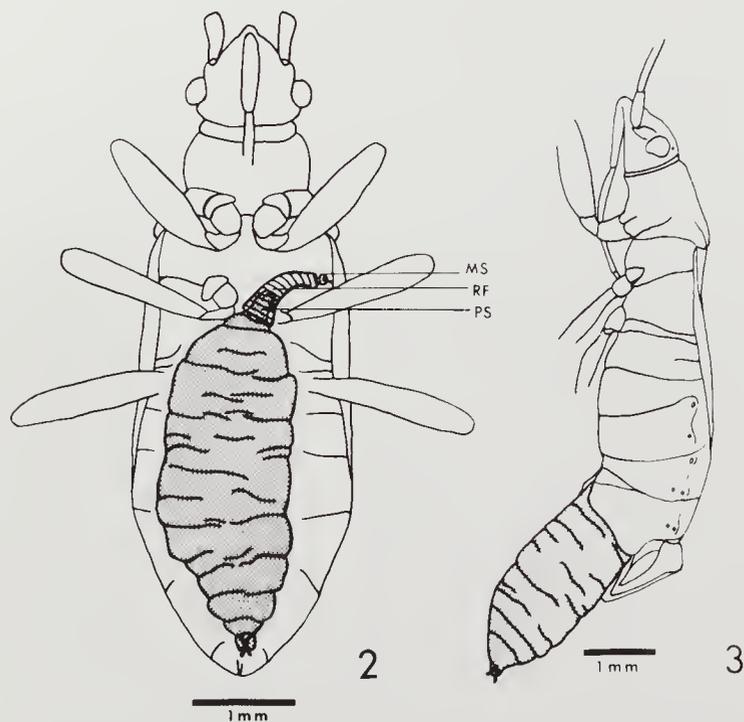


Figure 2. Mature *Catharosia* sp. larva within *L. diffusus* female. Note respiratory funnel attached near host's metathoracic spiracle (MS = metathoracic spiracle of *L. diffusus*; RF = respiratory funnel; PS = posterior spiracle of *Catharosia* larva).

Figure 3. Mature *Catharosia* larva emerging from *L. diffusus* female. Larva is passing beneath ovipositor through cleft in center of host's 7th abdominal sternum.

Mature *Catharosia* larvae emerge by rupturing the intersegmental membrane between the eighth abdominal segment and the pygophore in male hosts, and the seventh sternum and the first valvifers in female hosts. After the larva has passed through, the host's sclerites typically fall back into place, making it difficult to recognize that a parasitoid has emerged. During our study one larva died while emerging from a female *L. diffusus*, providing an opportunity to examine closely how an exit is achieved (Fig. 3). Bugs sometimes lived for several days after the emergence of a fly larva, and Ashlock and O'Brien (1964) reported one female lygaeid (sp?) living for a month after the emergence of a *Catharosia lustrans* larva. This bug produced five eggs, but development of the parasitoid may have been abnormal since the larva died without forming a puparium. Other dissections by these authors and all of our dissections revealed that fully developed gonads are not present in parasitized hosts.

Upon emerging from the host the mature larva moves a short distance away and pupates. Puparia were occasionally found lying in the open on the substrate. However, pupation usually occurred beneath some sort of cover.

The high rate of parasitism found in the Wood Co. *L. diffusus* population when sampled on 19 June 1978 (60%) and the laboratory dissections, which indicate that *Catharosia* sterilizes its host, suggest that this fly may play an important role in controlling seed bug populations.

SUMMARY

Fifty-one adults of *Catharosia* sp. (Diptera: Tachinidae) were reared from *Ligyrocoris diffusus* (Uhler), *L. sylvestris* (L.) (new host record for the genus *Catharosia*), *Perigenes constrictus* (Say), *Sphaerobius insignis* Uhler, and *Zeridonus costalis* (Van Duzee) that were collected in Wisconsin in 1977 and '78. Sixteen flies were reared through a complete life cycle on laboratory cultured *L. diffusus*. Rates of parasitism in field collected *L. diffusus* were 60% on 19 June and 16% on 22 August 1978. The fourth sternum of female flies is modified with spined plates that may help hold the host during oviposition. Both adults and nymphs are parasitized, but parasitoids emerge only from adult hosts. Total parasitoid development time can be as short as 18 days. Mature *Catharosia*

larvae occupy almost the entire host abdomen and extend into the thorax, where a respiratory funnel forms a connection to the host's tracheal system. Parasitized hosts are usually sterile.

ACKNOWLEDGEMENTS

We thank Dr. Paul H. Arnaud, Jr. (Department of Entomology, California Academy of Sciences) for examining and identifying our tachinid specimens and Mr. Martin B. Garment (Scanning Electron Microscope Facility, Department of Entomology, University of Wisconsin-Madison) for his skilled assistance with the SEM photomicrograph.

LITERATURE CITED

- ASHLOCK, P.D. AND C.W. O'BRIEN.
1964. *Catharosia lustrans*, a tachinid parasite of some drymine Lygaeidae (Diptera & Hemiptera-Heteroptera). *Pan-Pacific Ent.* **40**: 98-100.
- BUSSART, J.E.
1937. The bionomics of *Chaetophleps setosa* Coquillett (Diptera: Tachinidae). *Ann. Entomol. Soc. Amer.* **30**: 285-295.
- CLAUSEN, C.P.
1940. *Entomophagous Insects*. McGraw-Hill, New York. 688 pp.
- LUNDBECK, W.
1927. *Diptera Danica. Genera and Species of Flies Hitherto Found in Denmark. Vol. 7: Platypezidae-Tachinidae*, Copenhagen. 517 pp.
- SWEET, M.H.
1964. The biology and ecology of the Rhyarochrominae of New England (Heteroptera: Lygaeidae). Parts I & II. *Entomol. Amer.* **43**: 1-124; **44**: 1-201.
- WALTON, W.R.
1914. A new tachinid parasite of *Diabrotica vittata*. *Entomol. Soc. Wash. Proc.* **16**: 11-14.



ARGYRODES ATTENUATUS (THERIDIIDAE):
A WEB THAT IS NOT A SNARE*

BY WILLIAM G. EBERHARD
Smithsonian Tropical Research Institute
and
Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica

INTRODUCTION

Spiders of the large theridiid genus *Argyrodes*, whose natural history was reviewed by Exline and Levi (1962), seem to have generally abandoned the usual theridiid habit of spinning webs to capture insect prey. A few spin their own webs, but more often they live in the webs of other, larger web-building spiders where they remove prey from the host's web (e.g. Kullmann 1959, Vollrath 1978). The apparently kleptoparasitic species *A. trigonum* (*trigonum* species group) actually preys on its hosts on occasion. *Argyrodes* species in the *Rhomphaea* group have also been found feeding on web spiders, but some in circumstances which suggest a strict predator-prey relationship rather than kleptoparasitism. Exline and Levi (1962) note two observations of *A. (R.) fictilium* preying on web weavers although *fictilium* "often make small theridiid webs of their own". I have found an *A. (R.) projiciens* (O.P. Camb.) feeding on a *Metazygia* sp. which leaves its web up only during the night, thus making kleptoparasitism unlikely; the state of the prey's web indicated that it was attacked as it was building its web early in the evening. I have also seen an unidentified species feeding on an *Araneus* (?) sp., a species which leaves its web up only two to three hours in the early evening and then removes it completely.

Clyne (1979) showed that a species from the *Ariamnes* group, *Argyrodes colubrinus*, uses still another tactic. These spiders also specialize on spider prey, but attack ballooning mature male spiders which walk onto their webs of long, non-sticky threads. Roberts (1952) notes that *A. (A.) flagellum* also spins a web consisting of only a few long, very fine threads; perhaps mistakenly he states that the lines are sticky.

*Manuscript received by the editor February 15, 1980.

This note describes the web and predatory behavior of another species of the *Ariamnes* group, *Argyrodes attenuatus*, which attacks ballooning immature and mature male spiders, and also minute "trapeze" flies which use its web as a resting place. This spider's web serves not as a trap, but rather as a resting site for both types of prey, and as a substrate for the spider's stealthy attacks.

OBSERVATIONS

Argyrodes attenuatus is widely distributed in Central and South America (Exline and Levi 1962). The observations reported here were made on Hacienda Mozambique about 15 km SW of Puerto Lopez, Meta, Colombia (el. approx. 200 m) between June and August 1978 in two patches of periodically flooded forest from which some trees had been cut. The forest at one site was in at least an advanced secondary stage with some relatively large trees, while the other was younger. Voucher specimens have been placed in the Museum of Comparative Zoology, Cambridge, Mass.

Resting Position and Web

More than 40 spiders were seen from 1-3 m above the ground, resting on sparse, irregular, three-dimensional networks of long threads (Fig. 1). The networks ranged from two or three up to seven threads, some of which reached lengths of up to 1-2 m; careful inspection showed that none of the threads were sticky.

During the day the spiders usually rested with all their legs pressed tightly together, with I and II directed forward and III and IV backward, and the abdomen straight or nearly so, giving the animal a stick-like appearance. At night the legs, especially the front ones, were often spread. The spider always rested at a junction of two or more threads. Although the spider could control the form of its long thin abdomen, and sometimes curled it into a tight spiral, I never saw an individual move it in an undulatory or inchworm-like fashion as Göldi (in Exline and Levi 1962) saw *A. (A.) longissimus* do (I did not disturb the spiders as Göldi apparently did, however). The adaptive significance of the extraordinary abdomen of *A. attenuatus* may be at least partly outline camouflage rather than imitation of inch worms as proposed by Exline and Levi (1962).

The spiders replaced the threads they walked along as they moved, and thus probably held one broken end with a leg and spanned the gap with the body as they rested on the web, but they did not tense the lines or sag them suddenly when disturbed as do other spiders with similar reduced webs such as *Miagrammopes* (Akerman 1932, Lubin et al. 1978) and *Ulesanis* (Marples 1955).

Attack Behavior and Prey

Twenty seven spiders were found feeding on or resting near ensnared prey (Table 1). In addition I saw mature females move after but fail to capture a mature male theridiid spider and a small unidentified spiderling on lines in their webs. Some of the spiders' prey were judged to be substantially heavier than the *A. attenuatus* which captured them. In general, small *A. attenuatus* fed on small flies, and larger ones fed mostly on immature non web-building spiders. The ways these prey were secured was determined by direct observation and experiment.

When small spiderlings of several species were placed on webs of mature female *A. attenuatus*, the owners consistently responded by moving toward them and attempting to attack. In a typical capture sequence a spiderling was held dangling from its trail line, and

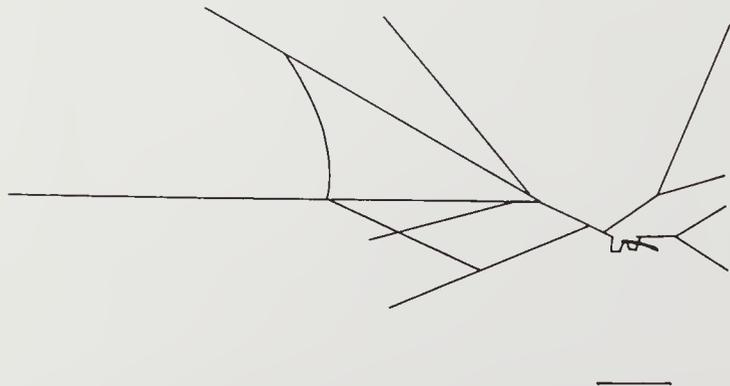


Fig. 1. Web of a mature female *Argyrodes attenuatus*. None of the lines were sticky. (Drawn from a photograph; scale line = 10 cm).

Table 1. Prey found being fed on by *Argyrodes attenuatus* in the field.

Mature and penultimate females	spiderlings
2 small juv. sparassids	18 small flies (5 Cecidomyiidae, 1 Mycetophilidae,
1 imm. salticid	12 ? other Nematocera)
1 imm. ctenid (?)	1 tiny spiderling
1 penult. <i>Theridiosoma</i> (?)	3 (?)

allowed to grab one of the lines of the web of a mature female *A. attenuatus* about 50 cm from where the spider was resting. The spiderling rested immobile after I cut its trail line, while the *A. attenuatus* advanced toward it slowly and smoothly. When the female was about 15 cm away, the spiderling began walking toward her along the line, and she suddenly began approaching more rapidly. Then, before she had reached the advancing spiderling, she quickly turned 180° and pulled a line of wet sticky silk from her spinnerets with her legs IV, apparently contacting the line with the outer surfaces of the tarsi (Figs. 2 and 3). The instant the spiderling came in range, she wrapped it in this thread with a quick movement of the hind legs, then bit it and wrapped it further in apparently dry silk. Finally she carried it dangling from her leg III to the place where she had been resting, and began to feed on it.

Aggressive responses such as these were usually elicited when spiderlings were placed on occupied webs, but *Philoponella* sp. and

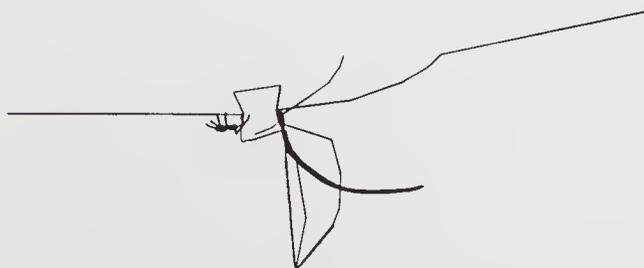


Fig. 2. Mature female *A. attenuatus* attacking an immature ctenid walking on a line in its web. The female has drawn sticky silk (covered with small balls) with both hind legs, and is about to apply it to the spiderling.



Fig. 3. Same as Fig. 2. Note that the sticky line is held on the lateral surface of the spider's right leg IV. The line to the left of the *A. attenuatus* is coated with white powder, while that to the right is uncoated and thus invisible.

Spilasma artifex spiderlings consistently escaped because they did not stay on the *A. attenuatus* lines, but descended on lines of their own, and as the *A. attenuatus* approached them or tried to reel them in, they let out silk faster until the *A. attenuatus* finally turned away.

As noted by Eberhard (1980) and Lahmann and Zuñiga (in prep.), it is common to find small insects, mostly nematocerous flies, hanging at night from spider threads in some forested areas. These "trapeze" flies seem to prefer more or less horizontal lines, but do not discriminate between threads from different spider species, and will even hang on cotton thread (Lahmann and Zuñiga in prep.). Young *A. attenuatus* were frequently found with small flies as prey, and the supposition that these prey had been captured while hanging on the spiders' webs was reinforced when I observed an attack on such a fly. When I first noticed the fly, it was hanging on one of the threads of a spider's web, and the spider was about 5 cm away, facing toward it. As I watched, the spider moved very slowly and smoothly toward the fly, stopping frequently to hang motionless; it took nearly five minutes to cover the 5 cm. There were occasional gentle vibrations of the line, but I could not tell whether they were caused by the spider or a sporadic gentle breeze. As the spider neared the fly, it began waving its front legs slowly; it touched the fly

gently with one of these movements, and immediately withdrew its leg and turned slowly 180° so that its abdomen was toward the prey. Carefully it drew out a strand of sticky silk with first one IV and then the other (as in Figs. 2 and 3) and then suddenly, with the only quick movement of the entire sequence, swung its hind legs upward to bring the sticky thread around the fly, and immediately began wrapping it with dry silk.

Egg Sac

Five different *A. attenuatus* were found with egg sacs. All sacs were elongate and white with a soft papery wall and small yellowish eggs loose inside the central portion. The spider rested either under the sac or adjacent to it with the legs extended in front and behind so that its outline merged with that of the sac.

DISCUSSION

One of the unusual features of *A. attenuatus* is the presence of serrated bristles on the prolateral side of tarsus IV, and the absence of the comb on its inner surface that is usual for theridiids (Exline and Levi 1962). It is thus interesting that, at least in the single case in which leg and thread positions were observed in detail (right leg IV in Fig. 3), the sticky wrapping thread contacted the outer rather than the inner surface of the leg. This association is in accord with the general belief that serrated bristles and combs on the tarsi IV of theridiids serve to manipulate the wet wrapping silk which is apparently peculiar to this family. The advantage of holding the thread on the outer rather than the inner surface of the tarsus is not clear; perhaps it is related to the way in which the spider holds sticky thread poised just before wrapping (Fig. 2), a behavior unique to my knowledge in theridiids.

The web structure, attack behavior, egg sac, and cryptic postures of *A. attenuatus* appear to be very similar to those of *A. colubrinus* (Clyne 1979). *A. flagellum* also apparently assumes the same cryptic posture. *A. attenuatus* differs from what is known of the other two in that it captures small flies and immature spiders as well as mature male spiders, apparently applies less wet silk as it wraps prey, and does not always rest facing up on webs. These spiders appear to be unique in having webs that serve as attractive resting sites and walkways for their prey.

ACKNOWLEDGEMENTS

I am grateful to Mr. Dixon Stroud and Dr. Luis Arango for generously allowing my family and me to stay at Finca Mozambique, and to Dr. H.W. Levi for kindly identifying the spiders. Drs. Levi and F. Vollrath helped with useful references. Financial support was provided by the Comité de Investigaciones of the Universidad del Valle, Cali, Colombia.

REFERENCES

- AKERMAN, C.
1932. On the spider *Miagrammopes* sp. which constructs a single-line snare. *Ann. Natal Mus.* 5:83-88.
- CLYNE, D.
1979. *The Garden Jungle*. Collins, London 184pp.
- EBERHARD, W. G.
1980. Spider and fly play cat and mouse. *Nat. Hist.* 89(1):56-61.
- EXLINE, H. & LEVI, H. W.
1962. American spiders of the genus *Argyrodes* (Araneae Theridiidae). *Bull. Mus. Comp. Zool.* 127(2):75-204.
- KULLMANN, E.
1959. Beobachtungen und Betrachtungen zum Verhalten der Theridiide *Conopistha argyrodes* Walckenaer (Araneae). *Mitt. Zool. Mus. Berlin* 35(2):275-292.
- LUBIN, Y., EBERHARD, W.G., & MONTGOMERY, G.G.
1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the neotropics. *Psyche* 85(1):1-23.
- MARPLES, B.J.
1955. A new type of web spun by the genus *Ulesanis* with the description of two new species. *Proc. Zool. Soc. Lond.* 125:751-760.
- ROBERTS, N.L.
1952. A contrast in snares. pp. 138-141 in McKeown, K.C. *Australian Spiders*. Angus & Robertson, London 287pp.
- VOLLRATH, F.
1978. Behaviour of two kleptoparasitic species of the genus *Argyrodes* Simon (Araneae, Theridiidae). *Symp. Zool. Soc. Lond.* 42:483.

PSYCHE

INDEX TO VOLUME 86, 1979

INDEX TO AUTHORS

- Aiello, Annette.* Life History and Behavior of the Case Bearer, *Phereoeca allutella* (Lepidoptera: Tineidae). 125
- Aiello, Annette.* See *Silberglie, Robert E.*
- Alcock, John.* Selective Mate Choice by Females of *Harpobittacus australis* (Mecoptera: Bittacidae). 213
- Brady, Allen R.* Nearctic Species of the Wolf Spider Genus *Trochosa* (Araneae: Lycosidae). 167
- Brown, William L., Jr.* A Remarkable New Species of *Proceratium*, with Dietary and Other Notes on the Genus (Hymenoptera: Formicidae). 337
- Brown, William L., Jr.* See *Evans, Howard E.*
- Burgess, J. Wesley.* See *Uetz, George W.*
- Carpenter, Frank M.* Lower Permian Insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. 261
- Chadab, Ruth.* Early Warning Cues for Social Wasps Attacked by Army Ants. 115
- Chadab, Ruth* and *Carl W. Rettenmeyer.* Observations on Swarm Emigrations and Dragging Behavior by Social Wasps (Hymenoptera: Vespidae). 347
- Chaffee, Dwight L.* and *Donald C. Tarter.* Life History and Ecology of *Baetisca bajkovi* Neave in Beech Fork of Twelvepole Creek, Wayne County, West Virginia (Ephemeroptera: Baetiscidae). 53
- Christenson, T. E., P. A. Wenzel,* and *Peter Legum.* Seasonal Variation in Egg Hatching and Certain Egg Parameters of the Golden Egg Spider, *Nephila clavipes* (Araneidae). 137
- Dunkle, S. W.* Sexual Competition for Space of the Parasite *Xenos pallidus* Brues in Male *Polistes annularis* (L.) (Strepsiptera, Stylopidae, and Hymenoptera, Vespidae). 327
- Eberhard, William G.* *Argyrodes attenuatus* (Theridiidae): A Web That is Not a Snare. 407
- Evans, Howard E., Charles Kugler,* and *William M. Brown, Jr.* Rediscovery of *Scolecbythus madecassus*, with a Description of the Male and of the Female Sting Apparatus (Hymenoptera: Scolecbythidae). 45
- Evans, Howard E.* See *Rubink, William L.*

- Fowler, Harold G. and Herbert W. Levi. A New Quasisocial *Anelosimus* Spider (Araneae, Theridiidae) from Paraguay. 11
- Harrington, B. Jane. See Thorpe, Kevin W.
- Haskins, Caryl P. and Edna F. Haskins. Worker Compatibilities within and between Populations of *Rhytidoponera metallica*. 301
- Haskins, Edna F. See Haskins, Caryl P.
- Henry, Charles, S. The Courtship Call of *Chrysopa downesi* Banks (Neuroptera: Chrysopidae). 291
- Hook, Allan. See Matthews, Robert W.
- Johnson, Victor and William P. Morrison. Mating Behavior of Three Species of Coniopterygidae (Neuroptera). 395
- Krispyn, Joan. See Matthews, Robert W.
- Kugler, Charles. See Evans, Howard E.
- Lamsas, Gerardo. See Silberglied, Robert E.
- Legum, Peter. See Christenson, T. E.
- Leston, Dennis. Dispersal by Male Doryline Ants in West Africa. 63
- Levi, Herbert W. See Fowler, Harold G.
- Matthews, Robert W., Allan Hook, and Joan Krispyn. Nesting Behavior of *Crabro argusinus* and *C. hilaris* (Hymenoptera: Sphecidae). 149
- McCluskey, Elwood and Siu-Ming A. Soong. Rhythm Variables as Taxonomic Characters in Ants. 91
- Mead, F. W. See Thompson, C. R.
- Morrison, William P. See Johnson, Victor.
- Morse, Roger A. See Seeley, Thomas D.
- Nickerson, J. C. See Thompson, C. R.
- North, Robert C. and Kenneth C. Shaw. Variation in Distribution, Morphology, and Calling Song of Two Populations of *Pterophylla camellifolia* (Orthoptera: Tettingoniidae). 363
- O'Neil, Kevin M. Territorial Behavior in Males of *Philanthus psyche* (Hymenoptera, Sphecidae). 19
- Petralia, Ronald S. and S. B. Vinson. Comparative Anatomy of the Ventral Region of Ant Larvae and Its Relation to Feeding Behavior. 375
- Rettenmeyer, Carl W. See Chadab, Ruth.
- Rubink, William L. and Howard E. Evans. Notes on the Nesting Behavior of the Bethyloid Wasp, *Epyris eriogoni* Kieffer, in Southern Texas. 313
- Seeley, Thomas D., Roger A. Morse, and P. Kirk Visscher. The Natural History of the Flight of Honey Bee Swarms. 103

- Shapiro, Arthur M.* The Phenology of *Pieris napi microstriata* (Lepidoptera; Pieridae) During and After the 1975-77 California drought, and Its Evolutionary Significance. 1
- Shaw, Kenneth W.* See *North, Robert C.*
- Silberglied, Robert E., Annette Aiello, and Gerardo Lamas.* Neotropical Butterflies of the Genus *Anartia*: Systematics, Life Histories, and General Biology (Lepidoptera: Nymphalidae. 219
- Song, Siu-Ming A.* See *McCluskey, Elwood*
- Tarter, Donald C.* See *Chaffee, Dwight L.*
- Taylor, Robert W.* Notes on the Russian Endemic Ant Genus *Aulacopone* Arnoldi (Hymenoptera: Formicidae). 353
- Thompson, C. R., J. C. Nickerson, and F. W. Mead.* Nymphal Habitat of *Oliarus vicarius* (Homoptera: Cixiidae), and Possible Association with *Aphaenogaster* and *Paratrechina* (Hymenoptera: Formicidae). 321
- Thorpe, Kevin W. and B. Jane Harrington.* Observations of Seed-Bug (Hemiptera: Lygaeidae) Parasitism by a Species of *Catharosia* (Diptera: Tachinidae). 399
- Uetz, George W. and J. Wesley Burgess.* Habitat Structure and Colonial Behavior in *Metepeira spinipes* (Araneae: Araneidae), an Orb Weaving Spider from Mexico. 79
- Vinson, S. B.* See *Petralia, Ronald S.*
- Visscher, P. Kirk.* See *Seeley, Thomas D.*
- Wenzl, P. A.* See *Christenson, T. E.*

INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

- | | |
|---|---|
| <i>Anartia</i> , neotropical species, 219 | Calvertiellidae, 284 |
| Anatomy of ant larvae, 375 | <i>Catharosia</i> , 399 |
| <i>Anelosimus</i> , 11 | <i>Chrysopa downesi</i> , 291 |
| Ant larvae, 375 | Comparative anatomy of ant larvae, 375 |
| <i>Aphaenogaster</i> , 321 | Coniopterygidae, 395 |
| <i>Apis mellifera</i> , 103 | <i>Conwentzia barretti</i> , 395 |
| <i>Argyrodes attenuatus</i> , 407 | <i>Conwentzia californica</i> , 395 |
| <i>Aulacopone relictata</i> , 353 | Courtship call of <i>Chrysopa downesi</i> , 291 |
| <i>Baetisca bajkovi</i> , 53 | <i>Crabro argusinus</i> , 149 |
| Bethylid wasp, 313 | <i>Crabro hilaris</i> , 149 |

- Dispersal by male doryline ants, 53
- Doryline ants in West Africa, 63
- Doter minor*, 283
- Dragging behavior by social wasps, 347
- Early warning cues for social wasps attacked by army ants, 115
- Ephemeroptera, 261
- Epyris eriogoni*, 313
- Eudoter delicatulus*, 282
- Feeding behavior of ant larvae, 375
- Habitat structure and colonial behavior in *Metepeira*, 79
- Honey bees, 103
- Life history and behavior of *Pheroeca allutella*, 125
- Lower Permian insects, 261
- Lygaeidae, parasitism, 399
- Mating behavior of Coniopterygidae, 395
- Metepeira spinipes*, 79
- Misthodotes EDMUNDSI*, 280
- Misthodotes obtusus*, 279
- Moravia GRANDIS*, 286
- Natural history of flight of honey bee swarms, 103
- Nearctic species of *Trochosa*, 167
- Neotropical butterflies of the genus *Anartia*, 219
- Nephila clavipes*, 137
- Nesting behavior of *Crabro*, 149
- Nesting behavior of *Epyris eriogoni*, 313
- Notes on Russian endemic ant, *Aulacopone relictata*, 352
- Nymphal habitat of *Oliarus vicarius*, 321
- Observations on swarm emigrations by social wasps, 347
- Oliarus vicarius*, 321
- Palaeodictyoptera, 261
- Palaeoptera, 286
- Paratrechina*, 321
- Phenology of *Pieris napi*, 1
- Phereoeca allutella*, 125
- Philanthus psyche*, 19
- Pieris napi microstriata*, 1
- Polistes annularis*, 321
- Proceratium* DIPLOPYX, 337
- Prottereisma americanum*, 274
- Prottereisma* DIRECTUM, 264
- Prottereisma*, nymphs, 268
- Protopolybia exigua*, 115
- Pterophylla camellifolia*, 363
- Quasisocial *Anelosimus*, 11
- Remarkable new species of *Proceratium*, 337
- Rhythm variables as taxonomic characters in ants, 91
- Rhytidoponera metallica*, 301
- Russian endemic ant, *Aulacopone relictata* 353
- Scolebythus madecassus*, 45
- Seasonal variation in egg hatching of *Nephila clavipes*, 137
- Seed-bug parasitism, 399
- Selective mate choice by *Harpobittacus australis*, 213
- Semidalis angusta*, 395
- Sexual competition for space of *Xenos pallidus*, 327
- Spider genus *Trochosa*, 167
- Swarm emigrations of social wasps, 347
- Territorial behavior of *Philanthus psyche*, 19

Trochosa, Nearctic species, 167

Variation in populations of *Pterophylla*
camellifolia, 363

Web that is not a snare, 407

Worker compatibilities within popula-
tions of *Rhytidiponera*, 301

Xenos pallidus, 327





CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room 154, Biological Laboratories, Divinity Avenue, Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

BACK VOLUMES OF PSYCHE

Requests for information about back volumes of Psyche should be sent directly to the editor.

F. M. CARPENTER
Editorial Office, Psyche
16 Divinity Avenue
Cambridge, Mass. 02138

FOR SALE

REPRINTS OF ARTICLES BY W. M. WHEELER

The Cambridge Entomological Club has for sale numerous reprints of Dr. Wheeler's articles that were filed in his office at Harvard University at the time of his death in 1937. Included are about 12,700 individual reprints of 250 publications. The cost of the reprints has been set at 5¢ a page, including postage; for orders under \$5 there will be an additional handling charge of 50¢. A list of the reprints is available for \$1.00 from the W. M. Wheeler Reprint Committee, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138. Checks should be made payable to the Cambridge Entomological Club.

part
of
the
book
is
lost



Acme

Bookbinding Co., Inc.
100 Cambridge St.
Charlestown, MA 02129

MCZ ERNST MAYR LIBRARY



3 2044 128 503 687

Date Due

Date Due	

2
K
9
11/19

