PSYCHE

A Journal of Entomology

Volume 84

1977

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. 83, no. 3–4, September-December, 1976: August 29, 1977
Vol. 84, no. 1, March, 1977: November 30, 1977
Vol. 84, no. 2, June, 1977: March 28, 1978

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 84 March, 1977 No. 1

CONTENTS

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1976–1977

President	PAUL S. MILIOTIS
Vice-President	GARY D. ALPERT
Secretary	KAREN S. VINSON
Treasurer	FRANK M. CARPENTER
Executive Committee	JOHN A. SHETTERLY JO B. WINTER

EDITORIAL BOARD OF PSYCHE

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: $8.00 for United States and Canada, $9.50 for other countries. Single copies, $2.50.

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 Ave., 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 $22.50 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., 1976, Psyche (Vol. 83, No. 3–4) was mailed August 29, 1977

THE LEXINGTON PRESS, INC. LEXINGTON, MASSACHUSETTS

PSYCHE

Vol. 84 March, 1977 No. 1

ATTACKS ON LARGE OR HEAVILY DEFENDED PREY BY TROPICAL SALTICID SPIDERS

BY MICHAEL H. ROBINSON[1] AND CARLOS E. VALERIO[2]

INTRODUCTION

Spiderlings in the first active instar have severe limitations in prey capture, because of their small size (Valerio, 1975) and particularly in those species that ambush or stalk their prey. The presence of snares or catching webs characteristic of several families expands considerably the range of potential prey items, which is undoubtedly an important pressure in the evolution of such structures. Even web-building spiders have problems with the large heavily-sclerotised prey items (see for instance Robinson & Robinson 1973a, 57–58). Insects with chemical defenses also prove troublesome to spiders (Eisner & Dean, 1976). However, the use of silk in the immobilization wrapping of araneid spiders considerably enhances their ability to subdue large or heavily defended prey (see experimental analyses summarized in Robinson 1975).

Salticids, on the other hand, are among the hunting spiders that subdue their prey without the aid of silk. For this reason, it is widely assumed that they are limited, in general, to prey which is smaller than themselves or to soft-bodied defenseless items (Enders 1975, 745 and references). At first sight this assumption seems perfectly reasonable, since the salticid attacking prey larger than itself must contend with a strength (perhaps) superior to its own. The insect under attack would presumably push against the substrate and exert sufficient pressure either to escape or to injure

---

[1] Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panama Canal Zone.

[2] Escuela de Biologia, Universidad de Costa Rica, Cuidad Universitaria, Costa Rica.

Manuscript received by the editor June 8, 1977.

the spider. We here report on field observations (in Panama and Costa Rica) that show that certain tropical salticids do attack and subdue prey considerably larger than themselves. Among these prey are large araneid spiders that are attacked on the web (but not *across* the web). In making these attacks on large prey the spider may utilize the technique of dropping on its dragline to isolate such prey from the substrate. This action allows the spider to safely attack other types of prey which, although small, are normally protected by social defenses.

OBSERVATIONS

An adult *Phiale* was observed in Panama, preying upon a fully sclerotised adult dragonfly that was at least three times as long as the spider. The spider was on the upper surface of a leaf about 1.5 meters above ground level. At the time of discovery the dragonfly was fluttering spasmodically but the actual capture was not observed. There is little doubt that the dragonfly was attacked after alighting on the leaf. The relative proportions of the spider and its prey are obvious from the photograph (Figure 1.).

Observations in the Central Valley, Costa Rica, provide a clue about how small salticids may subdue large prey. An immature *Menemerus bivittatus* was seen pouncing on a large moth resting on a fence wire. The moth was about half as long again as the spider and perhaps twice as heavy. After the pounce the moth started beating its wings strongly and the spider immediately dropped, on its dragline, until it was well clear of the substrate (figure 2). The spider held the moth with its chelicerae and front legs until the prey was subdued.

Clearly this method of "playing" the prey on the end of a line until envenomation occurs or the prey is exhausted, or both, is a strategy that could be applied to any prey item that tried to escape from the spider by jumping, dropping or flying off the substrate. The tensile strength of the dragline silk, in all probability, greatly exceeds the load exerted by the spider and her prey. The tenacity of the spider's jaw hold may be the critical factor in such attacks.

Dropping below the substrate on a dragline also provides the spider with an effective method of dealing with some species of ants that have social defenses. Thus some species of *Pseudomyrmex* possess a strong alarm pheromone that directs large numbers

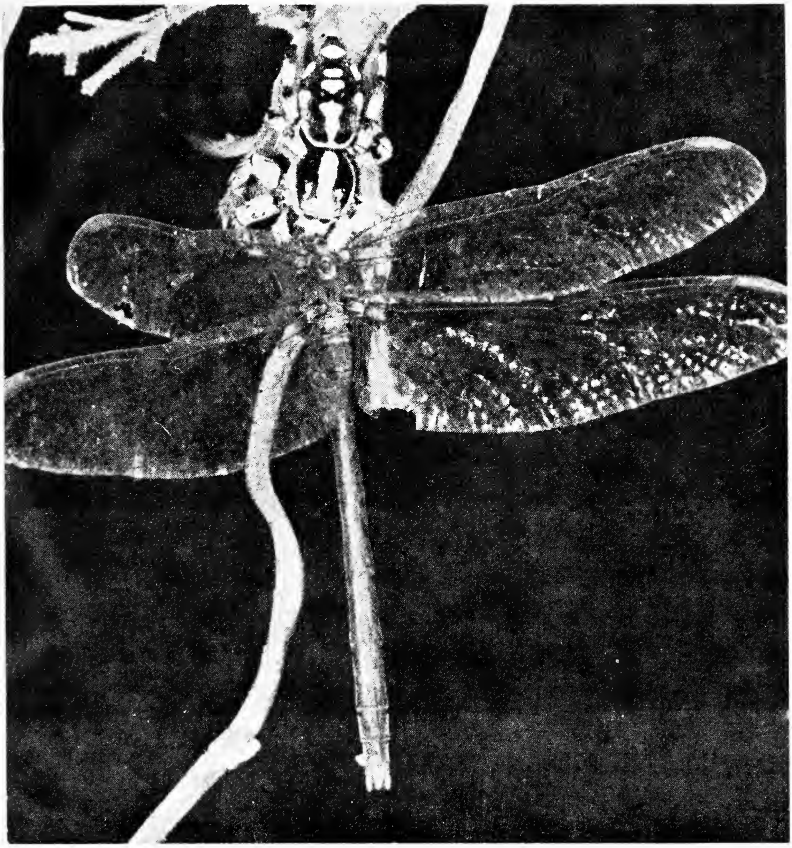


Figure 1. Adult female *Phiale* sp. feeding on anisopteran dragonfly, Navy Pipeline Road, Canal Zone, Panama. June 18th 1976.

of individuals to the exact place where a member of their colony is in danger. The response to the alarm pheromone is very rapid and may occur within seconds (Janzen 1966). This adaptation could effectively deter salticid predation on the ants were it not for the use of the dragline described above. An unidentified salticid (not collected) was observed making effective use of this technique at a lowland site in Guanacaste, Costa Rica. The *Pseudomyrmex* were attacked in an *Acacia* tree. The spider simply pounced on the ant, dropped off the branch and held the ant, suspended on the end of the dragline, and ate it. The ants, attracted by the

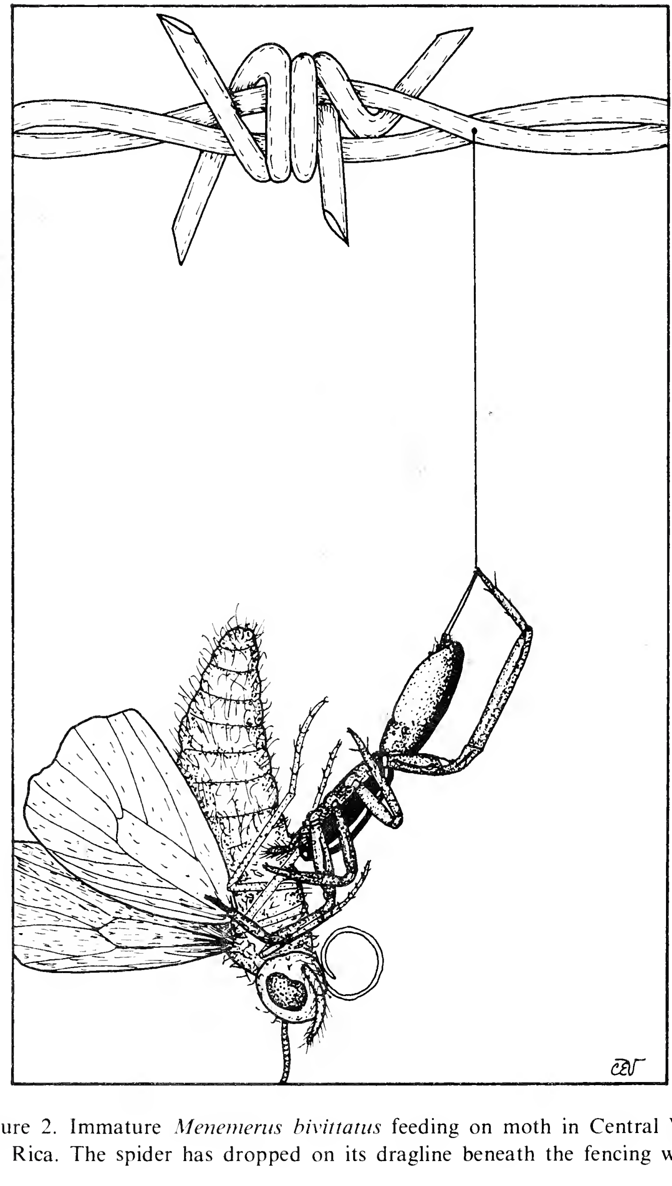


Figure 2. Immature *Menemerus bivittatus* feeding on moth in Central Valley, Costa Rica. The spider has dropped on its dragline beneath the fencing wire.

alarm pheromone, found the end of the dragline, but were unable to descend the thread. The spider returned to the branch and repeated the operation several times during the period of observation. (It is worth noting that at night we frequently find salticids and other diurnal non-web-building spiders suspended on their draglines beneath the vegetation. This may provide the safest way of spending the hours of darkness, since they are virtually isolated from the vegetation on which prowl innumerable predatory arthropods. Should any of these be capable of descending the dragline, the vibrations thereby induced would presumably alert the resting spider.)

Attacks on web-building spiders.

There are indications that web-building spiders are preyed upon by an extensive array of predators although the records are scattered throughout the literature and detailed observations are surprisingly few in number. Bristowe (1941; 331–443) deals comprehensively with the enemies of spiders in general and also describes a wide variety of anti-predator adaptations that spiders possess. The defenses of tropical orb-weavers are reviewed by Robinson & Robinson (1970; 649–653) and these authors describe particular defensive structures or behaviors elsewhere (1973a, 1973b). Tolbert (1975) has reviewed some of the available literature on araneid defensive behaviors in conjunction with an experimental study of the defensive responses of *Argiope aurantia* and *A. trifasciata.*

Records of attacks on orb-weavers by other spiders have been few in number. Bristowe (1941; 377–378) lists a number of attacks on web-building spiders by hunting spiders, and, in particular, by the salticid *Linus fimbiatus.* The spiders attacked included at least one araneid. Bristowe (ibid; 378) implies that the spiders were captured in their webs, "The *Linus* . . . sat in its victim's web to eat the owner". Tolbert (1975) mentions attacks on *Argiope aurantia* and *A. trifasciata* by salticids and states that attacks in the field can be induced by prodding the *Argiope* to move (Tolbert, in litt.). Enders (1974) reports attacks on orb-weavers by orb-weavers and (1975; 970) on the "invasion" of the webs of orb-weavers by errant salticids.

In three months (May–July, 1976) during extensive censusing of webs in a number of forest fringe habitats in the Summit and Gamboa areas of the Panama Canal Zone, 14 adult female *Argiope argentata* were found being consumed by *Phiale* adults. (On one count *Phiale* were found consuming 3 out of 64 spiders censused.) The spiders were, in all cases, off the web and resting on nearby vegetation. The araneid is considerably larger than the salticid (figure 3) and at least twice as heavy. A *Phiale* was also seen feeding on a late instar *Nephila clavipes* (F. Vollrath, pers comm.). No attacks were seen and it was not clear how the salticid had captured the araneid. To settle this problem, salticids were introduced into cages containing adult *A. argentata* (in webs) and watched. The web-builders were not fed and no attacks or "invasions" of the web were seen during intermittent observations over a period of three days. Feeding one spider immediately gave a clue as to the attack method of the salticid. As the *Argiope* moved to attack a grasshopper the salticid became active and moved along the walls of the cage to various positions from which it clearly "looked" at the moving *Argiope.* No attack was made, but when the spider returned to the hub, leaving the wrapped prey at the capture site, the salticid moved to a position on the cage wall almost horizontally opposite the stored prey, and after a number of side to side movements of the cephalothorax, it leapt upon the prey to stand astride it, biting. The *Argiope* immediately started to make *pumping* movements at the hub ('web-flexing', Tolbert 1975). This movement shook the prey item and shortly after its commencement, the salticid jumped off and regained its former position on the cage wall. Feeding the same spider a second time resulted in a similar response on the part of the salticid. This time, after leaping on the completely motionless prey package, it did not provoke the *Argiope* into pumping, and fed undisturbed on the cricket for over five minutes. At this point the host ran to the stored prey and dragged it closer to the hub, and the salticid leapt off to regain the cage wall. The salticid made one more attack on the prey package and then 16½ minutes after the start of the activity, attacked the spider at the hub by leaping on it. The *Argiope* was on the opposite side of the hub to the salticid and immediately dropped to the cage floor. The *Phiale* then walked on the web to the stored prey and fed upon it. Subsequent experimentation showed that the salticids could regularly be induced to attack *Argiope* if the latter were provoked into moving. Attacks on the wrong side of the hub were not successful

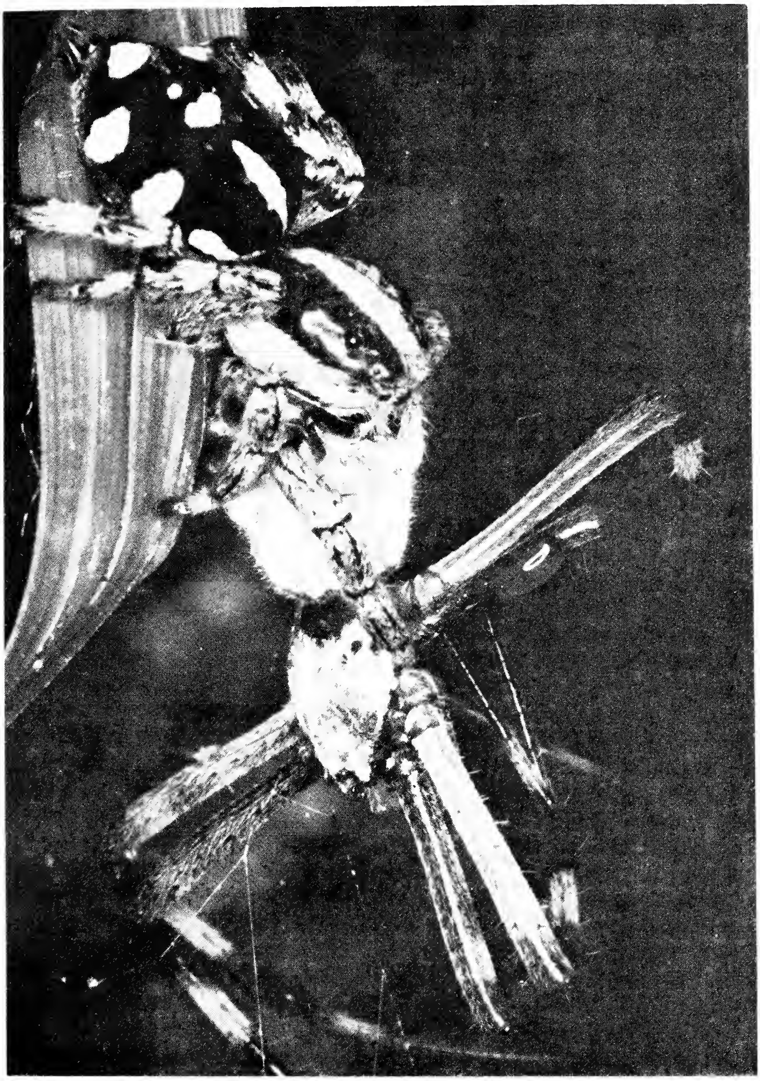


Figure 3. Adult female *Phiale* sp. feeding on adult female *Argiope argentata*. The salticid is perched close to the upper left hand corner of the araneid's web. Old Gamboa Road, Canal Zone, Panama. May 19th 1976.

but attacks from above the dorsal surface of the araneid were successful in all cases. (Eventually, all four *A. argentata* were killed.) In all cases, the araneids jumped off the hub when the *Phiale* contacted them. At the cage floor they moved about but could not displace the salticid and were eventually pulled up the cage wall to a feeding site.

The conditions in the cages probably made the attacks easier than they would be in field conditions. The *Argiope* web was surrounded by a continuous rigid surface on all sides. In the field the salticid must have to rely on discrete vegetation units for originating its attacks and though it can jump from plant to plant until it finds a suitable site, it may not be able to keep the spider in view continuously. In the cages the salticids looked at the *Argiope* from the cage floor, the cage walls and even the cage roof, before eventually lining up on the wall to launch an attack. Where it was possible to gauge the point of origin of attacks with some accuracy, they seemed to occur from a position only slightly above the point horizontally opposite the spider. When launching attacks off the glass sides of cages, the salticid turned around several times before jumping. Subsequent examination showed several silk attachments on the glass in this region. This suggests that the spider may make multiple dragline attachments before long aerial attacks. Take off postures were always head down (i.e. with the cephalothorax lowermost but strongly angled towards the target, and with legs I off the substrate).

These observations made on a small sample in simplified conditions show that an attack on the dorsal surface of a large prey item can be very successful. Movement seems to be necessary for the initiation of hunting behavior, but attacks were made on subsequently motionless prey. The salticids made accurate distance terminations and traversed horizontal distances measured at greater than 12cm. The failure of attacks made from the 'wrong side of the hub' (i.e. with the web between the salticid and the araneid) suggest that the behavior of *shuttling* (= switching sides of the web, Tolbert 1975), may be an effective defense, as argued by Robinson & Robinson (1970). Dropping from the web clearly did not aid the araneid in the experimental situation but could help in defense against salticids in a more natural one. The araneid might be able to brush off its attacker against the vegetation below the web. It can clearly work in other contexts against other predators.

The basic predatory techniques.

Dropping on the dragline to isolate a large prey from the substrate may be partly fortuitous in some cases. Certainly it depends on the prey moving off the substrate as a result of its own escape movements, since the salticid cannot lift it off. However, the case of the attacks on the ants suggests that it may be part of the normal predatory repertoire for dealing with some types of small prey. Attacking large araneids from above their dorsal surface presumably utilizes a technique that is part of normal prey capture but capitalizes on the araneid's inability to make strong scraping movements against its upper surface. It is also probable that such attacks benefit from the fact that the spider is not standing on a rigid substrate when attacked. The peculiar defensive posture adopted by *Nephila* spp. in response to direct tactile stimulation of their dorsal surfaces (Robinson & Robinson 1973a) results in a "barrier" of flexed legs being erected above the spider and could serve to frustrate some dorsal attacks.

SUMMARY

1. Some tropical salticids regularly catch prey larger and heavier than themselves.
2. Such salticids may utilize a dorsal attack on the prey followed by dropping on a dragline to effectively isolate the prey from the substrate.
3. This technique could be much more common than we know and definitely extends the size range for the potential prey of these spiders.
4. The drop and hold technique allows the salticids to attack prey that would normally be protected by social defense.
5. Salticids can make aerial attacks on araneid spiders in their webs and the normal defensive dropping responses of these spiders may, in certain circumstances, facilitate the salticid attack.

REFERENCES

BRISTOWE, W. S.

1941. The Comity of Spiders, Volume II. London, Ray Society.

EISNER, THOMAS AND JEFFREY DEAN

1976. Ploy and counterploy in predator-prey interactions: Orb-weaving spiders versus bombadier beetles. Proc. Nat. Acad. Sci. USA, **73:** 1365–1367.

Enders, F.

1974. Vertical stratification in orb-web spiders and a consideration of other methods of coexistence. Ecology **55:** 317–328.

Enders, F.

1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). Amer. Natur., **109:** 737–763.

Janzen, D. H.

1966. Coevolution of mutualism between ants and acacias in Central America. Evolution, **20:** 249–275.

Robinson, M. H.

1975. The evolution of predatory behaviour in araneid spiders. *In* Baerends, G., Beer, C., & A. Manning, Eds. Function and Evolution in Behaviour, Clarendon Press, Oxford., 293–312.

Robinson, M. H. and B. Robinson

1970. The stabilimentum of the orb web spider, *Argiope argentata:* an improbable defence against predators. Canad. Entomol. **102:** 641–655.

1973a. Ecology and Behaviour of the Giant Wood Spider *Nephila maculata* (Fabricius) in New Guinea. Smithsonian Contr. Zool., **149:**1–76.

1973b. The stabilimenta of *Nephila clavipes* and the origins of stabilimentum-building in araneids. Psyche, **80:** 277–288.

Tolbert, W. W.

1975. Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). Psyche, **82:** 29–52.

Valerio, C. E.

1975. Population structure in the spider *Achaearanea tepidariorum* (Araneae, Theridiidae). J. Arachnol., **3:** 185–190.

THE TAXONOMIC STATUS AND BIOGEOGRAPHIC SIGNIFICANCE OF THE SUMATRAN *FORMICA* (FORMICIDAE, HYMENOPTERA)*

By André Francoeur

Département des Sciences Pures, Université
du Québec à Chicoutimi, Québec, Canada
G7H 2B1

In a paper on the occurrence of *Formica fusca* in Sumatra, W. M. Wheeler (1927) erected the variety *fairchildi* for 12 workers collected above Kota Dah at an altitude of 4,000 feet in a pine forest. It has never been found again as far as I know. The examination of 10 of these specimens located in 3 different U.S. museums revealed a surprising similarity with *Formica glacialis,* a name that I have recently resurrected in a taxonomic revision of the nearctic species belonging to the *Formica fusca* group (Francoeur, 1973). I compared workers of *F. fairchildi* to *F. glacialis* types and topotypes collected by me at South Harpswell, Maine, and no significant difference was noted. All the above specimens meet very well my description of the *F. glacialis* worker. Therefore the formal synonymy is:

Formica glacialis

Formica fusca var. *glacialis* Wheeler, 1908, Bull. Amer. Mus. Nat. History **24:** 624, worker, female, male.

Formica fusca fusca: Wheeler (in part), 1913, Bull. Mus. Comp. Zool. Harvard **53:** 494–497.

Formica fusca: Creighton (in part), 1950, Bull. Mus. Comp. Zool. Harvard **104:** 532.

Formica glacialis: Francoeur, 1973, Mémoire Soc. Ent. Québec **3:** 152–161.

Formica fusca var. *fairchildi* Wheeler, 1927, Psyche **34:** 40–41, worker. Lectotype in MCZ, paratypes in AMNH, MCZ, USNM. NEW SYNONYMY.

This new synonymy eliminates the concept of a distinctive form of *Formica* in the southern half of the Oriental region. The presence of the genus in northern Sumatra perhaps may now be considered as an unexplained introduction rather than a tropical relict as reinterpreted by Gregg (1969) from Wheeler (1927). However,

---

**Manuscript received by the editor August 11, 1977*

the possibility might be considered that the Kota Dah *Formica* sample represents a labelling error, or the misplacement of a vial with North American ants in the Fairchild collecting kit. Such explanation seems much more likely than any introduction of *Formica glacialis* live into Sumatra. Other examples of this sort of mishap are very common in the Wheeler collection. In papers published in 1922 and 1927, Wheeler reported and discussed a similar case for the Philippines.

With this puzzling case once solved, the natural geographic distribution of the genus *Formica* appears to be entirely holarctic. Biogeographic boundaries of course do not follow straight lines; rather, they reflect topography and other factors affecting climate. Mountain ranges carry holarctic elements southward toward and into the tropics in both the Old World and the New. Thus the presence of *Formica* species in the high mountains of Taiwan and Burma is not surprising, since these ranges are nearby outliers or direct continuations of the holarctic uplands of mainland Asia. The range of the genus includes also the high elevations of central Mexico, in North America.

Nevertheless, that *Formica* could at one time have had a much wider or somewhat different distribution can still be supported by its richness, greater than previously recognized, in living species in the southern half of the Holarctic region, and by the presence of fossil *Formica* among numerous other subtropical and warm temperate insects found in the Baltic Amber of Oligocene age.

ACKNOWLEDGEMENTS

I am indebted to Mrs. Favreau, American Museum of Natural History, New York, H. E. Evans, Museum of Comparative Zoology, Harvard University, and D. R. Smith, U.S. National Museum, Washington, for loan of specimens. E. O. Wilson and W. L. Brown have my thanks for critically revising the manuscript. Research supported by National Research Council of Canada Grant A6501.

REFERENCES

GREGG, R. E.

1969. Geographic distribution of the ant genus *Formica* (Hymenoptera: Formicidae). Proc. Ent. Soc. Washington **71**(1): 38–49.

WHEELER, W. M.

1922. Ants of the genus *Formica* in the Tropics. Psyche **29**: 174–177.

AERIAL DISPERSAL BEHAVIOR OF TWO ORB WEAVING SPIDERS

By Wayne W. Tolbert*
Graduate Program in Ecology
University of Tennessee
Knoxville, Tennessee 37916

Introduction

Aerial dispersal, the transport of spiders from place to place by wind and/or convection currents, has been recognized as a feature of spider behavior since the time of Aristotle (Duffey, 1956). Many natural historians and arachnologists have observed and briefly commented on this phenomenon (Emerton, 1908; Bristowe, 1939; Gertsch, 1949; Nishiki, 1966; and Kaston, 1972), and a few studies have been devoted to the environmental conditions associated with the general phenomenon of spider dispersal.

Most studies and observations have been made of mass migrations of several species of spiders, particularly migrations occurring during the winter months (Bristowe, 1939). Duffey (1956) determined that temperature, population density, and stages of the breeding cycle are associated with mass aerial migrations of several species of Linyphiidae. Van Wingerden and Vugts (1974) produced results similar to Duffey's for one lingphiid species, *Erigone artica* (White).

Richter (1970, 1971) has studied in the laboratory some microclimatic factors which influence aerial dispersal in eight species of *Pardosa* wolf spiders. Richter (1970) related the frequency of aeronautic behavior of each species to the abundance and stability and that species' preferred habitat.

The purposes of this study are to describe the aerial dispersal behavior of *Argiope trifasciata* (Forskal), to compare behavioral elements of this species with a sympatric population of the congener, *A. aurantia* (Lucas), and to determine, under actual field conditions, the major physical parameters which influence these behaviors. Factors influencing emergence from the egg sac are discussed elsewhere (Tolbert, 1976, in preparation).

---

*present address — Science Applications, Inc.
P. O. Box 843
Oak Ridge, Tennessee 37830

Manuscript received by the editor May 27, 1977

Methods

This study was conducted in April and May 1975, in a two hectare overgrown pasture in Loudon County, Tennessee; a complete description of the study area is reported elsewhere (Tolbert, 1976). The study area is 3.2 kilometers (2 miles), west of Glendale community. Spiderlings of two orb weaving spider species, *Argiope trifasciata* and *Argiope aurantia,* were observed after emergence from more than 50 egg sacs. The spiderlings from egg sacs were monitored for dispersal and related activities during daylight hours. Spider body temperatures were estimated by the use of a thermocouple junction and associated cylindrical solder model of the same dimensions as a first instar spiderling (0.5 mm × 1.5 mm). Direct readout of model temperatures at dispersal height were recorded on an Esterline-Angus Continuously Recording Potentiometer. Wind speeds at dispersal height were measured with a Rimco miniature cup anemometer, stall speed 0.25 m/sec.

Behavior Prior to Dispersal

Unlike *Argiope aurantia* spiderlings, which emerge from an egg sac over a period of several days or weeks (Tolbert, 1976), *Argiope trifasciata* emerged in mass during the study period of April and May 1975. All spiderlings emerged from any given egg sac within a single day, usually within a period of one to two hours. This was confirmed by cutting open egg sacs from which spiderlings had recently emerged and checking for spiderlings that were left. An ethogram which summarizes the findings of this study on *Argiope* spp. dispersal behavior is depicted in Figure 1. Individuals quickly constructed a communal tangle or communal web, which is a meshwork of interlocking threads, by laying down draglines. Division of labor was not observed; each spiderling simply contributed a small amount of silk to the tangle. Spiderlings observed in 1975 resided on such tangles for several days ($\bar{x} \pm S.\ E. = 3.5 \pm 0.52$ days) before dispersing. Valerio (1975) reports that the common house spider *Achaeranea tepidorium* (C. L. Koch), also spends three to four days in dense clusters on the maternal web before dispersing aerially. Communal tangle formation by *Argiope aurantia* was less common. In the four instances where communal tangles were constructed by *A. aurantia,* the egg sacs had fallen to the substrate. Possibly a differing microclimate near the

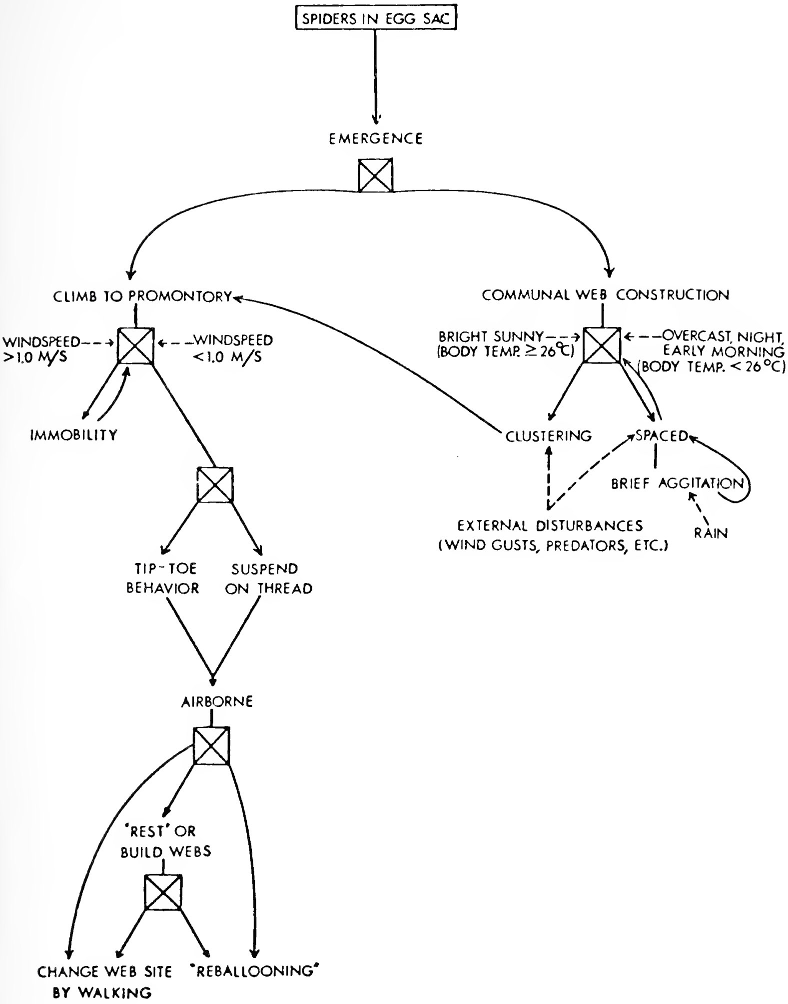


Figure 1. An ethogram of *Argiope* spp. dispersal behavior.

ground as demonstrated by Geiger (1965) influences communal tangle formation. Spiderlings emerging high in the vegetation experience greater exposure to wind which might stimulate ballooning (discussed below). *Argiope aurantia* locate egg sacs higher in the vegetation than *A. trifasciata.* In 1974–1975 and 1975–1976 the means and standard errors of *A. aurantia* egg sac heights were 0.91 ± 0.11 and 1.10 ± 0.13 m, respectively (Tolbert, 1976). *Argiope trifasciata* egg sacs by comparison, were 0.30 ± 0.04 m in 1975–1976 (Tolbert, 1976).

Spiderlings on a communal tangle were tolerant of one another at all times and readily accepted conspecifics from different egg sacs. Several such "transplants" were made during the spring of 1975 with spiderlings from one egg sac transferred to the communal tangle of spiderlings from a different egg sac. After a brief flurry of activity produced by the arrival of the transplants, activity decreased to levels noted before the introductions.

At night, early in the morning, and on overcast days *Argiope trifasciata* spiderlings maintained individual spacing of several times their own body length while on the communal tangle (Figure 2). If disturbed by predators, wind gusts, or rain, spiderlings became agitated but quickly resumed a quiescent attitude if their body temperatures were less than 26° C. On the other hand, if exposed to full sunlight individuals clustered closely together on the communal tangle (Figure 3). If cues were not present for dispersal, the spiderlings remained clustered until after nightfall before spacing out. Though not timed, clustering appeared to take less than a minute. A longer period was required for clustering if the group was partially shaded. The exact cue or clues producing clustering are not known, but clustering occurred only after full exposure to bright sunlight. Air temperatures, spiderling body temperatures, light levels, and perhaps other factors which might provide the required stimuli for clustering all change at this time. More experimentation is needed for elucidation of this problem.

When *Argiope trifasciata* spiderlings are clustered and their body temperatures equalled or exceeded 26° C they were susceptible to dispersal. As indicated in Figure 4, dispersal ceased below 26° C and the preferred temperature range for dispersal was between 33° and 38° C. Ninety-two percent of all *A. trifasciata* spiderlings became airborne or "ballooned" when their estimated body temperatures were between 33° and 38° C. *Argiope aurantia* also dispersed

Figure 2. An emergence of *Argiope trifasciata* with spiderlings exhibiting individual spacing. Arrow in the center of the cluster of spiderlings.

Figure 3. An emergence of *Argiope trifasciata* with spiderlings tightly clustered.

when their body temperatures were above 26° C, and their preferred range was virtually identical to that of *Argiope trifasciata* (Figure 5). Seventy-four percent of *A. aurantia* spiderlings dispersed when their body temperatures were between 33° and 38° C. A disturbance (gust of wind, striking the vegetation to which the communal tangle is attached, striking the tangle itself, and fanning the cluster of spiders directly) resulted in spiderling movement on the tangle. The nature of the disturbance seems to be vibrational and subsequent movement by spiderlings on the interlocking mass of silk threads of the communal tangle appeared to reinforce the initial disturbance. When a sufficient disturbance occurred and spider body temperatures were 26° C or higher, the spiderlings climbed to the top of any available object, usually vegetation. Spiderlings followed one another in mass to the top of a promontory where they prepared to disperse. Neither disturbance nor elevated temperature by itself was sufficient to trigger climbing behavior of *A. trifasciata* (Figure 1). By monitoring spiderling body temperatures on the communal tangle (spiderlings of eight *Argiope trifasciata* egg sacs in 1975), it was apparent that the spiderlings often experienced temperatures within their observed dispersal range (26°–42° C), but did not disperse. This was also evident by the time of residency on communal tangles during sunny periods (Table 1). Striking the vegetation near the tangle or fanning the cluster of spiderlings during times when body temperatures equalled or exceeded 26° C invariably induced climbing. Similar stimulation at body temperatures of less than 26° C failed to produce climbing behavior.

In April 1976, two additional clusters of *A. trifasciata* spiderlings were tested. Even when body temperatures exceeded 26° C and a vibratory stimulus was applied, these spiderlings could not be induced to climb and disperse. While these findings might simply be abberations or due to some genetic differences between populations between the two years, or to some microclimatic variables which were not examined, it seems likely that developmental differences between the spiderlings which emerged in May and those in April may account for the observed difference in behavior.

A. trifasciata overwintered as eggs and the active spiderlings did not develop until April (Tolbert, 1976). A difference of as much as one month to six weeks in the developmental age of spiderlings could influence behavior. It is possible that the older spiderlings would be more prone to dispersal behavior than younger spider-

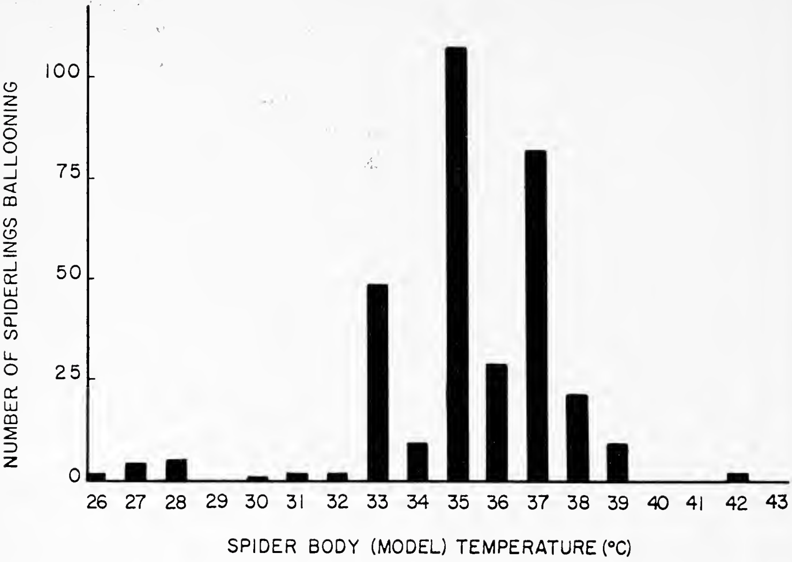


Figure 4. Number of *Argiope trifasciata* ballooning as a function of body (model) temperature.

lings. Residence time by spiderlings on communal tangles was somewhat longer in early May than in late May (Table 1). Computing mean residence time (in days) from the data in Table 1, reveals 7.5 days for the spiderlings emerging on 10 May, 8 days for 11 May, 5 days for 14 May, 2.3 days for 19 May, and 4 days for 22 May.

Richter (1970) has stated that dispersal by spiders normally occurs on days that are unusually warm and calm for the time of year. In the same study, he demonstrated that a wolf spider, *Pardosa purbeckenis* F. O. B. Cambridge exhibited aeronautic behavior when laboratory air temperatures were varied between 18° and 34° C. The percentages of aeronautic behavior for each temperature range he used (which I calculated from his Table 4) were 6.9% (18–19° C), 34.8% (28–29° C) and 36.4% (33–34° C). In 1975, 20 of the 24 *A. trifasciata* spiderling masses dispersed on sunny days (see Table 1). Thus, it appears that dispersal in *Argiope* is influenced by climatogical factors, and in particular temperature. In addition to these findings, Duffey (1966) in monitoring winter

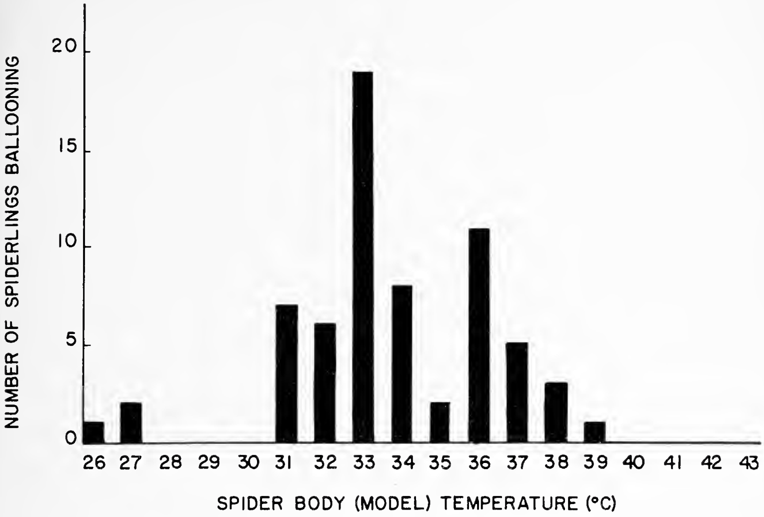


Figure 5. Number of *Argiope aurantia* ballooning as a function of body (model) temperature.

dispersal of linyphiids, indicated that increasing litter temperatures were partially responsible for increased aerial dispersal by members of this litter-dwelling spider family. Gypsy moth (*Porthetria dispar* L.) larvae ascend trees preparatory to aerial dispersal when ambient air temperatures are between 15.6° C (50° F) and 29.4° C (85° F). These larvae, however, have black dorsal surfaces and their body temperatures when exposed to direct sunlight can easily exceed air temperatures (McManus, 1973). Thus, the aerial dispersal of some spider and insect species is influenced by temperature.

Aeronautic Behavior

In preparation for dispersal, individuals may adopt either a "tiptoe" posture, as defined by Richter (1970) or hang suspended from a dragline from which they become airborne (Figure 1). The tiptoe stance, which is widely employed by lycosid spiders (Richter, 1970), results when the spider depresses the cephalothorax toward the substrate and elevates the abdomen. Silk lines are then exuded from the spinnerets. Multiple lines of ballooning silk were often

Table 1. *Argiope trifasciata* residency on communal tangles and associated weather conditions during May, 1975. S = sunny, PC = partly cloudy, C = cloudy, X = presence, Y = dispersal on same day as emergence. Dispersal occurred on last day spiderlings were present.

May	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Weather	S	S	PC	S	S	C	C	C	S	S	S	S	S	PC	PC	S
Egg sac number																
5	X	X	X	X	X	X										
6	X	X	X	X	X	X	X									
11	X	X	X	X	X	X	X	X	X							
12	X	X	X	X	X	X										
13	X	X	X	X	X	X	X	X	X							
14	X	X	X	X	X	X	X	X								
15		X	X	X	X	X	X	X	X							
16		X	X	X	X	X	X	X	X							
17					X	X	X	X	X							
18									X	X						
19									X	X						
20										X	X					
21										Y						
22										X	X	X	X			
23										X	X					
25										X	X					
26										X	X	X	X			
27										Y						
29										X	X	X				
30										X	X	X				
31										X	X	X				
32										X	X	X				
33										X	X					
34													X	X	X	X

observed and there appeared to be four to six lines, but the exact number was not determined. Spiderlings also dispersed directly from silk threads. They dropped on a dragline, cut it and while suspended and holding this thread by leg pairs I and II, let out ballooning silk as before, until they became airborne.

Spiderlings, as a rule, became airborne during relatively calm periods with a preferred windspeed for dispersal of approximately 0.5 m/sec. (Figure 6). During gusty periods spiderlings either did not exhibit tip-toe postures at all or if in that posture, returned to

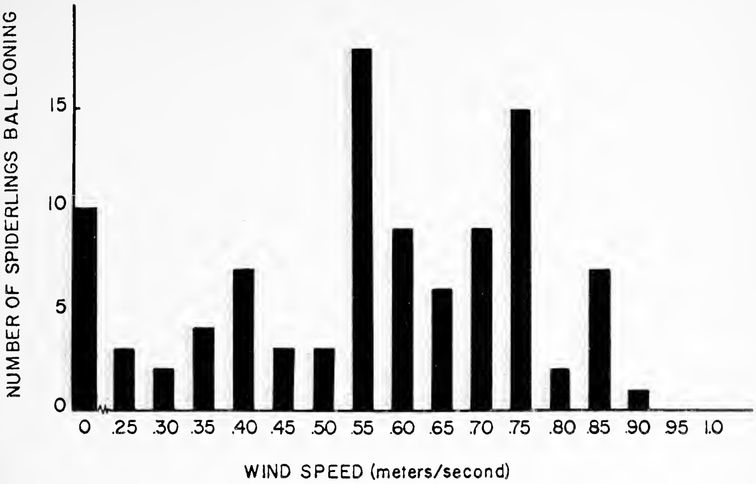


Figure 6. Number of *Argiope trifasciata* ballooning as a function of windspeed.

a normal resting attitude. Spiderlings did not disperse at windspeeds of greater than 0.9 m/sec. (Figure 6). Richter (1971) showed that *Pardosa purbeckensis* had preferred windspeeds for dispersal which were related to their body sizes; larger spiders preferred greater windspeeds. All size classes, however, preferred wind velocities between 0.35 and 1.70 m/sec. These values exceed those observed for *Argiope trifasciata,* which is a slightly larger spider than *Pardosa purbeckensis.* From their study of spiders on Frisian Island (the Netherlands) Van Wingerden and Vugts (1974) concluded that aeronautic behavior ceased when the wind velocity at 2 m above the substrate exceeded 3.0 m/sec. They also found in the same study that unstable air masses near the ground and at dispersal height served as stimuli to aeronautic behaviour. Disturbances (wind gusts) apparently function in a similar fashion for *Argiope trifasciata.*

After a spiderling becomes airborne it will travel on wind currents until deposited at a potential web location. The spiderling may then build a web, or move a short distance from the deposition site (perhaps searching for a site of better potential for web construction), and then build a web (Figure 1). It might also reballoon with or without "searching behavior." Data on the relative frequencies of these behaviors are scarce. Approximately 20 argiopids were observed to reballoon during the course of the study, some as many as six times with the majority (90%) of these observed reballooning bouts occurring when the spiderlings were in close proximity to the egg sac. It is possible that a minimum time or distance requirement must be achieved before the spiderling has satisfied a "ballooning drive." It might also reflect investigator error since spiderlings which drop into dense vegetation are difficult to detect and the probability of finding individuals must decrease with distance from the egg sac (with decreased density of spiderlings). Nevertheless, multiple ballooning bouts probably function to increase emigration from a given area (which would tend to lessen competition for food, web sites or other resources if such resources are in short supply). Since *Argiope* spp. actively select web sites (Enders, 1972, 1973), it is probable that areas judged unsuitable by the spiderlings can be quickly and easily abandoned via reballooning. This finding is consistent with the predictions of Doyle's (1975) habitat selection model. Organisms which encounter coarse-grained (patchy) environments, as *Argiope* do, can improve fitness by selecting habitat types yielding highest survivorship. Riechert (1973) demonstrated that a desert agelenid spider, *Agelenopsis aperta* (Gertsch) improved the quality of its web sites by successive relocation in better web sites. *A. aperta* walked rather than ballooned to new web sites, however. Riechert and Tracy (1975) produced a model of reproductive success that demonstrates a thirteen fold advantage in fecundity of spiders living in good versus poor web sites. Habitat selection and differential survival of *Argiope* spp. is an area worthy of additional research.

One or more days may elapse after the spiderling locates a web site before it actually builds a web there. This is based on two sets of observations. First, spiderlings discovered in the field without webs and checked later the same day had not built webs (N = 5). Only spiderlings found early in the morning and thus not recently dispersed are considered here. Two of these individuals built webs one day later; one built two days later. Second, even during the height of *Argiope trifasciata* aerial dispersal (mid-May) few spiderlings were observed to have webs. Possibly the spiderlings were adjusting from a colonial, passive existence to one of active predation. Whatever the reason(s), considerable mortality is suffered during this period (Tolbert, 1976). Spiderlings would certainly be vulnerable to predation, especially since they do not have the protection a web affords (Tolbert, 1975). Some spiderlings probably starve during this time also (Tolbert, 1976).

Spiderlings underwent a radical change in behavior toward conspecifics after dispersing from the communal tangle. As long as the spiderlings were on the communal tangle they were completely tolerant of one another and during hot sunny periods clustered very closely together. However, after a spiderling constructed an orb web it attacked and ate any prey that contacted the web. Littermates were invariably attacked and treated as prey items when they encountered or were placed on conspecific's orb web. However, it is unnecessary for spiderlings of either *Argiope* species to engage in aerial dispersal before building an orb web. I have successfully reared both species in the laboratory after removing them from egg sacs. After building their first orb web and without the benefit of living on or building a communal tangle or engaging in aerial dispersal, *Argiope* spiderlings still attacked and killed littermates placed on their orb webs.

Although Enders (1972) indicated he has observed unsuccessful ballooning attempts by mid-instar *Argiope aurantia,* my observations indicate that only the emergent (first instar) disperses aerially.

Summary

Although both species are capable of all the behaviors in the ethogram (Figure 1), *Argiope aurantia,* possibly by virtue of their higher, more exposed egg sac locations, generally dispersed shortly after emergence from the egg sac. *Argiope trifasciata* produced communal tangles and engaged in preaeronautic behaviors on these structures before dispersing.

In 1975, both spider species ballooned when their estimated body temperature exceeded 26° C, with most dispersal occurring when body temperatures were between 33° and 38° C. A vibrational stimulus occurring when spider body temperatures are above 26° C resulted in climbing behavior by the mass spiderlings on the communal tangle. Upon reaching the top of a promontory they either became airborne from that point or dropped on a dragline and ballooned from that position. Spiderlings ballooned at relatively low wind speeds (0.5 m/s). Multiple ballooning bouts were observed for some individuals. It is hypothesized that aerial dispersal serves to rapidly space spiderlings over available habitats such that

overcrowding is minimized. Aerial dispersal would also allow successional species such as *A. trifasciata* and *A. aurantia* to colonize newly opened, ephemeral habitats.

ACKNOWLEDGMENTS

I gratefully acknowledge the assistance of James Tanner, Gordon Burghardt, Charles Pless and David Etnier who ably served on my doctoral committee. I am especially grateful to Susan Riechert, my committee chairperson. I acknowledge the financial support of the National Science Foundation, Grant For Doctoral Dissertation Improvement (BMS 74-17602) and the Graduate Program in Ecology of the University of Tennessee.

REFERENCES

BRISTOWE, W. S.
1939. The comity of spiders, Vol. I. Johnson Reprint Corp., New York.
DOYLE, R. W.
1975. Settlement of planktonic larvae: A theory of habitat selection in varying environments. Amer. Natur. **109:** 113-126.
DUFFEY, E.
1956. Aerial dispersal in a known spider population. J. Anim. Ecol. **25:** 85-111.
ENDERS, F.
1972. Web-site selection by *Argiope aurantia* Lucas and other orb weaving spiders (Araneidae). Unpublished Ph.D. dissertation, N. C. State University.
ENDERS, F.
1973. Selection of habitat by the spider *Argiope aurantia* Lucas (Araneidae). Amer. Midl. Natur. **90**(1): 47-55.
EMERTON, J. H.
1908. Autumn flights of spiders. Psyche **15:** 121.
GEIGER, R.
1965. The climate near the ground. Harvard Univ. Press, Cambridge.
GERTSCH, W. J.
1949. American spiders. D. Van Nostrand Co., Inc., Princeton.
KASTON, B. J.
1972. How to know the spiders, 2nd edition. W. C. Brown Co., Dubuque.
MCMANUS, M. L.
1973. The role of behavior in the dispersal of newly hatched Gypsy Moth Larvae. USDA Forest Service Research paper NE-267, 10p.
NISHIKI, S.
1966. On the aerial migration of spiders. Acta Arachnologica **20**(1): 24-34 (Japanese with an English Summary).

RICHTER, C. J. J.

1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa,* Araneae, Lycosidae). Oecologia **5:** 200–214.

RICHTER, C. J. J.

1971. Some aspects of aerial dispersal in different populations of Wolf Spiders, with particular reference to *Pardosa amentata* (Araneae, Lycosidae). Misc. Pap. Landb. Hogesch. Wageningen **8:** 77–88.

RIECHERT, S. E.

1976. Web site selection in a desert spider, *Agelenopsis aperta* (Gertsch). Oikos **27:** 311–315.

RIECHERT, S. E. AND R. TRACY.

1975. A model relating web-site characteristic to spider reproductive success. Ecology **56:** 265–284.

TOLBERT, W. W.

1975. Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). Psyche **82:** 29–52.

TOLBERT, W. W.

1976. Population dynamics of the orb weaving spiders *Argiope trifasciata* and *Argiope aurantia* (Araneae, Araneidae): Density changes associated with mortality, natality and migrations. Unpubl. Ph.D. dissertation, U. of Tennessee.

VALERIO, C. E.

1975. A unique case of mutalism. Amer. Natur. **109:** 235–238.

VAN WINGERDEN, W. K. R. E. AND H. F. VUGTS.

1974. Factors influencing aeronautic behavior of spiders, Bull. Brit. Arach. Soc. **3:** 6–10.

ECOLOGY, ZOOGEOGRAPHY AND TAXONOMY OF THE LOWER RIO GRANDE VALLEY MESOSTENINES (HYMENOPTERA, ICHNEUMONIDAE)

By Charles C. Porter[1]
Department of Biological Sciences, Fordham University
Bronx, N.Y. 10458

Introduction

This study analyzes results of five years' fieldwork with net and Malaise Traps on mesostenine ichneumonids of semiarid subtropical scrub and moist gallery woods habitats in the Lower Río Grande Valley of south Texas. It lists 18 genera and 35 species. The genus *Bicristella* and the species *Trachysphyrus mesorufus, Cryptanura lamentaria,* and *Lymeon leucosoma* are recorded for the first time from the United States. *Cryptanura vallis Mesostenus opuntiae, Bricristella texana, Diapetimorpha sphenos, D. aspila,* and *D. pareia* are described as new. The zoogeographic relationships, phaenology, and habitat preferences of each taxon are recorded and conclusions are adduced as to distributional patterns, annual cycles, habitat selection, and diversity of the entire south Texas mesostenine fauna. The south Texas fauna also is compared with mesostenine communities of other semiarid parts of the Neotropics, such as the Peruvian Coastal Desert and the northwest Argentine Subandino, and all these relict or marginal xerophilic faunas are discussed with regard to their origin in wet forest centers of ichneumonid radiation.

Acknowledgements

Major support for this research was provided in 1976–'77 by a National Science Foundation Grant (DEB 75–22426) and during 1973–'75 by grants from the Committee for Research and Exploration of the National Geographic Society. Mr. David Riskind and Mr. Sim Oefinger, Jr. of the Texas Parks and Wildlife Department issued permits for insect collecting in the Bentsen Río Grande Valley State Park. At Bentsen Park, Mr. Reynaldo Ortíz (Superintendent)

---

[1] Research Associate, Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Gainesville, Florida 32602.

Manuscript received by the editor, May 24, 1977 and Mr. Antonio Salinas (Park Ranger 3) maintained the Malaise Trap used in my 1976 survey and provided cordial assistance on all my visits to the park. Mrs. Vivian Thacker, as trustee of the Valley Botanical Garden, facilitated collecting in that small but important island of natural vegetation. My father, Mr. Carroll B. Porter, also assisted in the Malaise project and in many other ways. Mr. Charles W. Calmbacher of Fordham University prepared and labeled most of the Malaise samples from Bentsen Park. Finally, Dr. Henry K. Townes of the American Entomological Institute loaned several homotypes which helped resolve crucial taxonomic problems.

MATERIALS AND METHODS

Hand collecting with a strong but light net obtained 63% of the 679 specimens captured between May 1973 and March 1977 for use in this study. Sweeping undergrowth yielded numerous mesostenines but many others were netted individually in flight from foliage. Periods annually available for fieldwork included 25 August to 9 September, 18 December to 25 January, 11–21 March (1–8 April in 1975) and 16 May to 10 June. I was in the field 7 days a week and 6–8 hours per day during all visits to south Texas.

To obtain a more comprehensive picture of mesostenine diversity than would have been possible by hand collecting alone, I employed two Malaise Traps during this research. The first was installed at the Valley Botanical Garden in a *Celtis lindheimeri-C. pallida* thicket and functioned from September 1973 until March 1974 but was stolen in April 1974. The second was set up under a large *Pithecellobium flexicaule* in deep woods near a lake at the Bentsen Río Grande Valley State Park and, having already furnished a complete series of samples for 1976, continues to operate during 1977. In both traps, a pint mason jar filled with 70% isopropyl alcohol (commercial rubbing alcohol) was used as the collecting recipient. The trap at the Botanical Garden was changed once a month but I was able to arrange for twice monthly curating of the Bentsen Park trap. Both Malaise Traps were of the "light weight" variety, as perfected by Dr. Henry K. Townes (Townes, 1972, p. 239–247).

THE STUDY AREA

The Lower Río Grande Valley is an alluvial plain that extends along the Río Grande River for about 120 km. in Hidalgo and

Cameron counties of Texas and the Mexican state of Tamaulipas, beginning on the east at the Gulf of México and ending approxmately at the level of Mission, Texas on the west. Nowhere is this Valley much more than 25 or 30 km. wide either north or south of the river. It constitutes an island of fertile soil, relatively high humidity, and comparatively lush vegetation surrounded landward on all sides by desert scrub.

Because of its latitude (26 degrees N.) and proximity to the Gulf, the Valley experiences an extremely mild temperature regimen. The average yearly maximum at Brownsville is 28 degrees C. and the minimum 18.3 degrees C. Summer highs rarely go above 40 degrees C. and the average daily range for July at Brownsville is 33.6 degrees C. to 24.2 degrees C. On the other hand, most winters have only two or three frosts during which the temperature normally does not fall below –3 to –4 degrees C., although the record low for Brownsville is –11 degrees C. (registered in February 1899). The average daily range for January at Brownsville is 21.4 degrees C. to 11.2 degrees C. and such temperatures occur quite consistently throughout the Valley in winter, although from November to March warm periods frequently are interrupted by cold fronts that bring 4–10 day stretches of cloudy weather when the temperature stays between about 4 and 10 degrees C.

Precipitation in the Valley is rather scant, averaging 669 mm. per year at Brownsville. It occurs in winter as protracted fine drizzle, in spring, summer, and fall as occasional thunderstorms, and sometimes in late summer and early fall as torrential inundations that accompany inland-moving hurricanes. September, with an average of 124.8 mm. is the wettest month while March, with 26 mm., is the driest. Although long-term figures suggest fairly even rainfall distribution, there is actually great variation from month to month and from year to year. Protracted droughts are common but some years may have more than 1000 mm. of rain.

Vegetation of the Valley ranges from desert scrub to humid subtropical woodlands best developed along the Río Grande and in the vicinity of water holes. The south Texas flora resembles that which grows in many other semi-arid environments from México to Argentina. Some of the more conspicuous angiosperm genera are *Acacia, Baccharis, Bumelia, Celtis, Cercidium, Condalia, Erythrina, Opuntia, Parkinsonia, Prosopis, Salix, Tillandsia,* and *Xanthoxylum.* This same element occurs also in the ecologically similar Argentine Chaco at the austral extreme of the Neotropics.

Almost all my fieldwork on Valley mesostenines was done in the 500 acre Bentsen Park near Mission and the 20 acre Valley Botanical Garden at McAllen. Otherwise, except for the Santa Ana National Wildlife Refuge near Alamo, most natural vegetation has been extirpated from the Valley and replaced by citrus groves, truck farms, sugar-cane fields and other agricultural systems.

The Valley Botanical Garden is about 16 km. from the Río Grande and thus lacks gallery forest and other really humid associations but offers a sample of scrub communities and moderately humid woods. Here the most abundant or conspicuous larger plants are: *Acacia greggii* (rare), *A. farnesiana* (common), *Baccharis* sp. (common), *Bumelia celastrina* (rare), *Celtis lindheimeri* (common), *C. pallida* (common), *Cercidium floridum* (rare), *Condalia obovata* (common), *C. obtusifolia* (common), *Ehretia anacua* (common), *Forestiera texana* (rare), *Karwinskia humboldtiana* (common), *Leucaena pulverulenta* (scarce), *Morus rubra* (rare), *Opuntia* sp. (common), *Parkinsonia aculeata* (common), *Phaulothamnus spinescens* (rare), *Pithecellobium flexicaule* (rare), *Porlieria angustifolia* (rare), *Prosopis juliflora* (common), *Sabal texana* (rare), *Salix nigra* (common), *Serjania* sp. (common), and *Xanthoxylum fagara* (scarce). Within its 20 acres, the Botanical Garden contains several more or less distinct associations. Dry areas are dominated by *Prosopis juliflora* and *Opuntia* sp. with *Condalia obtusifolia* and *Parkinsonia aculeata* often common also. Moderately dry habitats have at least some of the foregoing species along with *Condalia obovata, Celtis pallida, Baccharis* sp., and *Bumelia celastrina.* Moderately humid sites usually are dominated by *Celtis lindheimeri* in the tree stratum, *C. pallida* in the shrub layer, and by *Serjania* vines at ground level. They also may contain the small tree *Ehretia anacua,* the large shrub *Xanthoxylum fagara,* and the small shrub *Karwinskia humboldtiana.* The large trees *Leucaena pulverulenta* and *Salix nigra* also occur in the Garden but only near ponds and irrigation canals. Finally, some abandoned farmlands near the Garden support open *Acacia farnesiana* woods with a monotonous undergrowth of tall grasses.

The Bentsen Park is much larger and floristically more varied than the Botanical Garden. Only *Sabal texana* occurs in the Garden but not at Bentsen, while *Amyris texana* (common), *Fraxinus berlandieriana* (common), *Mimosa berlandieriana* (moderately common), *Sapindus drummondii* (scarce), *Tillandsia usneoides* (common), and *Ulmus crassifolia* (common) have been found exclusively in the State Park. In addition to all plant associations described for the Botanical Garden, Bentsen Park supports distinctive gallery forest and water hole communities. Lush woods along the Río Grande contain *Salix nigra, Fraxinus berlandieriana, Celtis lindheimeri, Mimosa belandieriana, Acacia farnesiana* and a profligate ground cover of *Serjania* vines. Even more luxuriant is the flora near a permanent water hole, which includes huge examples of *Fraxinus, Ulmus, Leucaena,* and *Ehretia,* some *Pithecellobium* and *Sapindus,* numerous *Xanthoxylum,* some *Mimosa,* abundant *Amyris,* and an impressive epiphyton of *Tillandsia usneoides* on many larger trees. Other dark, damp zones in Bentsen Park are dominated by *Pithecellobium flexicaule.*

Climatically and floristically, the Valley thus emerges as decidedly subtropical and the same is true for most of its fauna, from ichneumonid wasps and diurnal Lepidoptera to reptiles and birds. Indeed, south Texas harbors the richest Neotropic biota of any part of the United States.

THE TRIBE MESOSTENINI

Mesostenines are one of the largest groups in the Family Ichneumonidae and inhabit all continents, having radiated massively in both tropical and temperate regions. They parasitize the pupae of many Lepidoptera as well as of some Coleoptera, Neuroptera, Diptera, and certain Hymenoptera. Most species are taxonomically catholic in host selection, each one being attracted to diverse kinds of pupae in a restricted spatial niche (leaf rolls, ground litter, stems, tunnels in tree trunks, etc.) rather than choosing victims from among one particular genus or even family of insects.

Like most ichneumonids, mesostenines prefer humid forest habitats, so that in the New World they are best represented in the North American Temperate Deciduous Forest and again in various kinds of Latin American subtropical and tropical wet forests. The comparatively dry Lower Río Grande Valley thus has a rather depauperate mesostenine fauna, whose relations are principally but not exclusively Neotropic.

Listed below together with relevant ecological, zoogeographic and taxonomic data are the 18 genera and 35 species of Mesostenini so far recorded from the Lower Río Grande Valley.

1. *Gambrus bituminosus* Cushman

SPECIMENS EXAMINED: 1 female, Bentsen Park, 31 XII '76.

HABITAT: Weeds in sandy area at edge of field not far from Río Grande.

DISTRIBUTION: Mass., N.Y., N.J., Ill., Minn., Ga., La., Cal., new for Texas.

PHAENOLOGY: Summer in north, winter in south.

2. *Gambrus ultimus* (Cresson)

SPECIMENS EXAMINED: 6 females, 2 males: BENTSEN PARK (*Net:* 2 females, 13 I '76; 1 female, 19 I '76; 1 female, 29 XII '76; *Malaise:* 1 male, 16 X '76); BOTANICAL GARDEN (*Net:* 1 female, 12–21 I '76; 1 female, 17–24 III '74; 1 male, 18 III '74).

HABITAT: *Serjania* vine tangles under shade of *Celtis lindheimeri* and other large trees.

DISTRIBUTION: Continental U.S.

PHAENOLOGY: Flies in Valley from October to March with peak in January (4 of 8 collections). Active in north from April to October.

3. *Trychosis subgracilis* (Cresson)

SPECIMENS EXAMINED: 1 female, 2 males: BENTSEN PARK (*Net:* 1 female, 23 I '76; *Malaise:* 2 males, 15–30 IV '76).

HABITAT: *Serjania* vines in gallery woods beneath *Celtis lindheimeri* and *Salix nigra;* entered trap beneath *Pithecellobium flexicaule.*

DISTRIBUTION: Eastern U.S.; first record for Valley.

PHAENOLOGY: January to April in Valley; April to August in northern states.

4. *Trachysphyrus mesorufus* (Cushman)

(Fig. 6)

FEMALE: *Color:* scape black with a broad, nearly percurrent white bar below and brown on dorsal rim; pedicel black; flagellum black with a ventrally incomplete white band on segments 5–11; head and mesosoma black with white markings as follows: basal 2/3 of the otherwise somewhat brownish mandibles; blotch covering most of clypeus; most of face except for a large area between and below antennal sockets and a pair of submedian blotches above clypeus that are narrowly confluent mesad and which connect laterally with a large black area in anterior 1/4 of malar space; very broad orbital ring interrupted only in malar space and ventroposteriorly much expanded and almost reaching hypostomal carina; blotch on apical 1/2 of propleuron; very broad anterior margin of pronotum; very broad humeral margin of pronotum; pair of longitudinal blotches on about median 3/4 of mesoscutum in position of notauli; scutellum; most of postscutellum; tegula; axillary sclerites; subalarum; large anterio-median blotch on mesepisternum just behind prepectal carina; broad stripe in anterior 2/3 of sternaulus; large blotch in lower hind corner of mesepisternum; mesepimeron pure white on dorsal 1/4 and more brownish ventrad; most of dorsal metapleuron; large, dorso-posterior blotch on apical 1/2 of lower metapleuron; and a pair of very broad blotches occupying all but median 1/3 of hind face of propodeum from cristae to apical margin; first gastric tergite red with a broad white band covering apical 1/2 of postpetiole; second tergite black with reddish staining baso-laterally and a broad white subapical band; and following tergites black with broad white apical bands; fore and mid legs ferruginous with tarsus duller and fifth tarsomere dusky, trochanter white with brownish above, and coxa white with a small reddish spot above near apex and more broadly marked with dark red to blackish below; hind leg with coxa red except for a small white blotch above at base, trochanter and trochantellus red, femur more ferruginous, tibia dull ferruginous with a slight dusky tinge on base and blackish on about apical 1/10, first tarsomere brownish black with white briefly throughout on apex and whitish below on apical 1/2, second tarsomere white, third white with a dusky area above subapically, fourth black with a little whitish on base and fifth black; wings hyaline.

Structurally, *mesorufus* much resembles the Floridian *T. weemsi* (Porter, 1974, p. 331–335), from which it may be distinguished by most of the characters listed below:

Length of fore wing: 6.1 mm. *Pronotum:* dorsal margin moderately swollen. *Mesoscutum:* notauli very weak but traceable about 2/3 the length of mesoscutum. *Mesopleuron:* speculum swollen, smooth and shining with only a few large punctures peripherally; surface otherwise almost uniformly with strong, reticulate wrinkling which obscures its punctures. *Wing venation:* radial cell 3.3 as long as wide; second abscissa of radius 0.7 as long as first intercubitus; disco-cubitus broadly angled with a long and conspicuous ramellus at angulation; upper part of nervellus 3.5 as long as lower. *First gastric tergite:* post-petiole 1.7 as wide apically as long from spiracle to apex. *Second tergite:* a little duller and more densely punctate than in *weemsi. Ovipositor:* sheathed portion 0.34 as long as fore wing; nodus distinct, with a very shallow and broad notch; dorsal valve on tip with a gradual, straight taper between notch and apex; tip 0.17 as high at notch as long from notch to apex.

MALE: Unknown.

SPECIMENS EXAMINED: 1 female, Botanical Garden, 2 April 1975.

DISCUSSION: As noted above, *mesorufus* closely resembles the Floridian *T. weemsi* except in color pattern and in some subtle structural characters, whose real value only will be established when more specimens of these elusive ichneumonids are obtained. Townes (1962, p. 256–269) considers all North American representatives of this group as subspecies of *T. planosae.* In view of their allopatry and marked differences, however, I prefer to regard them as species, pending proof of intergradation.

The Texas specimen was swept from a thorny bush (probably *Celtis pallida*) in a dry area of the Botanical Garden dominated by *Prosopis juliflora* with *Condalia obovata* and *Celtis pallida* in the shrub stratum.

The above described female is the third known specimen of *mesorufus* and the first from the United States. Otherwise, this species inhabits México whence it is recorded by Cushman (1930, p. 2) from Cuernavaca in Morelos state and by Townes (1962, p. 259) from "40 km. southwest of Puebla" in Puebla state.

5. *Joppidium brochum* Townes

SPECIMENS EXAMINED: 1 female, Botanical Garden, 5 I '76.

HABITAT: Herbaceous undergrowth on shady side of fence row with *Celtis pallida, C. lindheimeri, Ehretia anacua* and other trees.

DISTRIBUTION: Ky., N.C., Ga., to Okla. and Tex. and into México at least as far as Veracruz and México City.

PHAENOLOGY: Valley record for January; otherwise flies mostly in May and June.

6. *Joppidium rubriceps* Cresson

SPECIMENS EXAMINED: 1 female, Botanical Garden, 1 IV '75.

HABITAT: Herbs, grasses, and pink-flowered verbenas in bright sun.

DISTRIBUTION: N. J. to south Texas.

PHAENOLOGY: Flies from mid March to early November, appearing first and disappearing latest in southern parts of its range.

7. *Lanugo picta* Townes

SPECIMENS EXAMINED: 13 females, 24 males: BOTANICAL GARDEN (*Net:* 4 females, 8 males, 1–15 I '75; 4 females, 8 males, 16–26 I '75; 1 female, 4 IV '75; 1 female, 1 male, 20–31 XII '73; 1 female, 5 males, 24–30 XII '74; *Malaise:* 1 female, III '74; 1 female, 2 males, XII '74).

HABITAT: Open and semi-shaded areas; old fields, hedge rows, woods edges; tall grass at edge of thicket dominated by *Celtis lindheimeri* and *C. pallida;* a few specimens in *Celtis* thicket.

DISTRIBUTION: South Texas to northern Arizona and as far south in México as Chiapas.

PHAENOLOGY: Invernal, Valley records include 3 females and 8 males for December, 8 females and 16 males for January, 1 female for March and 1 female for April. Flies all summer in mountainous parts of west Texas, Arizona and México.

Varies in abundance from year to year: 3 specimens in '73–'74, 34 in '74–'75, none in '75–'76 or so far in '76–'77.

8. *Compsocryptus texensis* Townes

SPECIMENS EXAMINED: 26 females, 6 males: BENTSEN PARK (*Net:* 1 male, 12–20 III '77; 2 females, 29–30 XII '76); BOTANICAL GARDEN (*Net:* 6 females, 5–26 I '75; 2 females, 3 males, 28–30 III '75; 5 females, 1 male, 2–5 IV '75; 1 male, 16–30 V '74; 1 female, 19 XII '76; 8 females, 20–28 XII '74; 2 females, 28–30 XII '73).

HABITAT: Open, dry areas; fields, hedge rows; short grass and low herbs of incipient secondary succession; herbage of poorly tended orange groves; lawns.

DISTRIBUTION: Ka. to Okla. and Tex. south into N. León and Tamaulipas of México.

PHAENOLOGY: Flies from December to May with peak between December and April (13 females in December, 6 males in January, 2 females and 4 males in March, 5 females and 1 male in April, and 1 male in May).

Varies in abundance from year to year: 3 specimens in '73–'74, 25 in '74–'75, none in '75–'76, and 4 so far in '76–'77.

Genus *Cryptanura*

The Valley has three *Cryptanura,* of which one is new and one is here recorded for the first time from the United States.

KEY TO THE U. S. *CRYPTANURA*
(Females only)

1. Second gastric tergite mostly mat; clypeus more or less strongly convex in profile; humeral margin of pronotum not conically produced anteriorly, but often with a carinate elevation above end of epomia; sublateral white stripe of propodeum strongly narrowed basad of crista 2

   Second tergite polished; clypeus nasute; humeral margin of pronotum anteriorly with a prominent subconical to conical expansion; sublateral white stripe of propodeum not narrowed basad of crista 4

2. Epomia not reaching humeral margin of pronotum, the humeral margin not carinate or tuberculate anteriorly; second gastric tergite with a medio-basal white spot .... *C. septentrionalis* Cushman

   Epomia forms a carinate elevation on humeral margin of pronotum anteriorly; second tergite at most narrowly tinged with whitish medio-basally 3

3. Hind coxa white with conspicuous black markings; femora yellowish white with a broad, percurrent dorsal black band; lower metapleuron with coarse oblique wrinkling that becomes irregular only on about dorsal 1/4 and with at most obscure intercalated punctures; propodeal dorsum behind basal trans-carina coarsely and irregularly wrinkled and puncto-reticulate but without discrete punctures .... 11. *C. lamentaria* (Cameron).

Hind coxa mostly fulvous with whitish above; femora uniformly pale fulvous; lower metapleuron coarsely and densely punctate to puncto-reticulate with numerous discrete punctures dorso-anteriad; propodeal dorsum behind basal trans-carina with abundant, mostly discrete coarse punctures, grading into puncto-reticulation only latero-apicad near cristae .... *C. banchiformis* (Megerle).

4. Many segments in apical 1/3 of flagellum up to 1.4 as wide as long; first flagellomere 5.1 as long as deep at apex; malar space 0.88 as long as basal width of mandible; frontal horns on a high common base; mesoscutum with abundant large punctures but with no wrinkling along notauli, except apicad, or on outer margins of lateral lobes; mesoscutum with a large, subcircular median white spot .... 9. *C. compacta* (Cresson).

Segments in apical 1/3 of flagellum averaging about as wide as long; first flagellomere 7.9 as long as deep at apex; malar space 0.46 as long as basal width of mandible; frontal horns on a very low common base, long and sharp; mesoscutum with moderately numerous medium sized punctures that become sparser mesad on lobes and with extensive transverse wrinkling all along notauli and on outer margins of lateral lobes; mesoscutum without a median white spot .... 10. *C. vallis* n. sp.

9. *Cryptanura compacta* (Cresson)

SPECIMENS EXAMINED: 1 female, Bentsen Park, 14 III '77.

HABITAT: Clearing with *Serjania* vines and tall grass on bank of Río Grande in *Salix nigra-Celtis lindheimeri* woods.

DISTRIBUTION: Southern Texas to Honduras.

PHAENOLOGY: Townes (1962, p. 429–'30) records a female of *compacta* from "Cameron County, Texas, 3 August 1928".

10. **Cryptanura vallis** n. sp.
(Fig. 8)

Holotype: female, USA (*Texas:* Hidalgo County, Bentsen Río Grande Valley State Park, 27 XII '76, C. C. Porter). (Townes).

FEMALE: *Color:* antenna black with white annulus on flagellomeres 5–12; palpi whitish; mandible white with black on apical 1/3 and narrowly on dorsal and ventral margins except near base; head white with black as follows: broad, irregular mark extending from a little above anterior tentorial pit ventrad to mandibular condyle; face for a short distance below and between antennal sockets; lower and inner margins of antennal sockets; median half of face and vertex; occiput much more broadly; most of postocciput; about upper 1/4 of temple very broadly, briefly interrupting white orbital ring; and rest of temple very narrowly along occipital carina; propleuron white with black on most of basal 1/4; pronotum black with a broad white band covering most of front margin, except for lower hind corner and a short break dorso-medially, and with white broadly on the swollen humeral margins; thoracic dorsum black with white on prescutellar ridge, broad anterio-lateral margins and most of apical 1/2 of scutellum, most of postscutellum, and on hind margins of meso and metanotal axillary troughs; tegula white; mesopleuron black on most of prepectus and on most of upper 1/3 except for the white subalarum, otherwise wholly white, becoming slightly brownish ventrad, on mesepisternum and mesepimeron; mesosternum black on prepectus but otherwise slightly brownish white; most of dorsal metapleuron white; lower metapleuron white with a pale brownish tinge and briefly stained with darker brown on apex; propodeum white to brownish white with black on a broad, irregular percurrent median longitudinal band which is widest along basal trans-carina and becomes narrower rearward, especially on apical face, as well as at least narrowly blackish throughout along basal carina, blackish around spiracle, and with pale brown staining on much of lateral face between spiracle and crista; first gastric tergite yellowish white with dark brown above on much of apical half of petiole and on most of basal 2/3 of postpetiole as well as a little brownish along ventro-lateral carina; second tergite black with yellowish white on apical 1/3, on very broad lateral margins, and on entire thyridial areas, between which the ground color becomes brownish yellow basad; third tergite black with yellowish white on apical 1/2 and on very broad lateral margins; fourth and fifth similar but even more broadly yellowish with some darker staining in the yellow zones; sixth and seventh yellowish with some darker staining; and eighth dark brown with apex narrowly yellow; fore leg with coxa white, trochanter whitish with

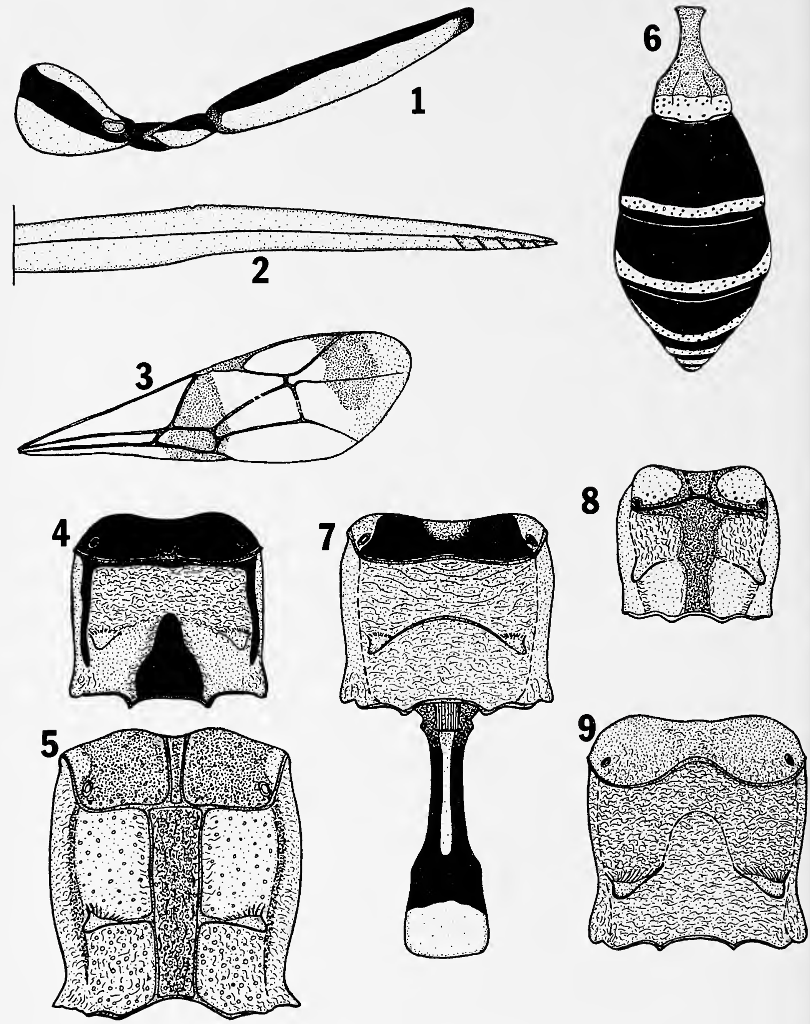


Fig. 1. *Cryptanura lamentaria,* female. Bentsen Park. Side view of hind coxa, trochanters, and femur, showing color pattern. Fig. 2. *Mesostenus opuntiae,* female holotype. Ovipositor tip. Fig. 3. *Lymeon leucosoma,* female. Valley Botanical Garden. Fore wing. Fig. 4. *Diapetimorpha aspila,* male holotype. Dorsal view of propodeum. Fig. 5. *Bicristella taxana,* female holotype. Dorsal view of propodeum. Fig. 6. *Trachysphyrus mesorufus,* female. Valley Botanical Garden. Dorsal view of gaster, showing color pattern. Fig. 7. *Diapetimorpha pareia,* male holotype. Dorsal view of propodeum and first gastric segment. Fig. 8. *Cryptanura vallis,* female holotype. Dorsal view of propodeum. Fig. 9. *Diapetimorpha sphenos,* female paratype. Dorsal view of propodeum.

a brown blotch on basal 2/3 above, trochantellus whitish with some brown staining, femur yellowish white below and mostly brownish above, tibia yellowish white, and tarsus dull yellowish with slight dusky staining toward apex on first segment, more broadly dusky on second and third segments, and blackish almost throughout on fourth and fifth; mid leg similar to fore leg but coxa more dully white with some faint dusky staining, trochanter and trochantellus more broadly brown above, and tarsus mostly dusky to black with yellowish only near base of segments 1–3; hind leg with coxa dull white with a broad but diffuse, nearly percurrent, moderately pale brownish dorsal stripe and with paler brownish staining within and below; trochanter yellowish white with dark brown staining dorso-anteriorly and tinged with paler brown behind; trochantellus similar to trochanter but with darker and more extensive brown areas in front and behind; femur dull brownish yellow, becoming darker brown above and brighter yellow behind; tibia yellow with a little dusky on base; and tarsus yellow with dusky only on apical 1/2 of fifth segment; wings hyaline, stigma yellowish with dark brown on broad peripheries.

Length of fore wing: 8.7 mm. *Flagellum:* scarcely flattened below on apical 1/3, segments between white annulus and apex averaging as wide as long; first segment 7.9 as long as deep at apex. *Temple:* 0.3 as long as eye at upper 1/3; very strongly and directly receding. *Front:* horns on a very low common base, large and sharply conical; surface practically without wrinkles between level of horns and anterior ocellus. *Clypeus:* nasute; apical margin truncate. *Pronotum:* epomia sharp in scrobe but ending above in a large tubercle, so that the otherwise gently swollen dorsal margin of pronotum has a moderately prominent subconical projection at this point. *Mesoscutum:* shining with numerous medium sized punctures that become sparser centrad on lobes and rather broadly, more or less transversely wrinkled interiorly and exteriorly along notauli and on outer margins of lateral lobes as well as with an area of coarse, irregular wrinkling between notauli toward their terminus; notauli moderately impressed, reaching about 4/5 the length of mesoscutum. *Scutellum:* weakly convex. *Mesopleuron:* prepectus with a very short ridge opposite lower hind corner of pronotum; surface between prepectal carina and speculum mostly with strong, nearly regular longitudinal wrinkling which becomes weaker, and mingled with large, obscure punctures, on lower half, where there are also some smooth areas. *Lower metapleuron:* with uniform, coarsely reticulate wrinkling; juxta-coxal carina not defined. *Front tibia:* moderately inflated. *Hind trochantellus:* 0.57 as long as its trochanter in dorsal view. *Third hind tarsomere:* ventrally with about 8–9 strong spines (in addition to the apical group) which are not arranged in regular longitudinal rows. *Propodeum:* spiracle 1.5 as long as wide; cristae large and strongly projecting short ligulate, about 1.1 as long as wide at base, apical carina weakly defined and gently arched forward between them; dorsal face behind basal trans-carina with rather coarse, irregular but not much reticulate wrinkling; the apical face centrally with strong longitudinal wrinkling, becoming smooth sublaterally and then transversely wrinkled laterad. *First gastric tergite:* postpetiole 1.4 as wide at apex as long from spiracle to apex; gently arched in profile. *Second gastric tergite:* smooth and highly polished with a few tiny, very sparse punctures. *Ovipositor:* sheathed portion 0.43 as long as fore wing; tip 0.20 as high at nodus as long from nodus to apex, weakly sagittate with a direct taper between nodus and apex.

MALE: Unknown.

TYPE: In collection of Dr. Henry K. Townes, 5950 Warren Rd., Ann Arbor, Michigan, 48105.

RELATIONSHIPS: The polished second gastric tergite, nasute clypeus, and rather strong subconic projection anteriorly on the humeral margin of the pronotum suggest affinity with *C. compacta,* to which *vallis* runs in Townes' key to the North American *Cryptanura* (1962, p. 427). However, *compacta* differs from *vallis* in many chromatic and structural features of which those not already mentioned in my foregoing key are summarized below:

Mesopleuron black on lower 2/3 except for a broad, oblique white area extending from prepectal carina to lower hind corner but not invading speculum or approaching mesopleural suture except far below; propodeum black with a very broad white stripe on each side reaching rearward from basal trans-carina across crista to hind margin; fore and mid femora broadly black above; hind coxa pure white with an almost percurrent broad black stripe dorsally and with other black markings; hind femur black with yellow anteriorly and posteriorly; dorsal margin of pronotum very strongly swollen and produced anteriorly into an exceptionally prominent broadly conical projection; prepectus opposite lower hind corner of pronotum with a strong ridge that extends ventrad about 3/4 the distance to prepectal carina; mesopleuron behind prepectal carina with coarser and more oblique wrinkling than in *vallis;* front tibia a little more strongly inflated than in *vallis;* propodeal spiracle 2.0 as long as wide; propodeal cristae a little more narrowly ligulate than in *vallis,* 1.4 as long as wide at base; apical trans-carina completely absent between cristae; dorsal face of propodeum behind trans-carina with more regularly reticulate wrinkling than in *vallis;* apical face of propodeum with coarse reticulate wrinkling that becomes transversely biased laterad; first gastric tergite more strongly arched in profile than in *vallis;* postpetiole 1.6 as wide at apex as long from spiracle to apex.

FIELD NOTES: Swept from *Serjania* vines near Río Grande in shade of *Celtis lindheimeri, Salix nigra, Fraxinus berlandieriana* and other trees.

SPECIFIC NAME: *Vallis* is the genitive of the Latin noun *valles* or "valley".

11. *Cryptanura lamentaria* (Cameron)
(Fig. 1)

FEMALE: *Color:* antenna black with a broad white stripe below on scape and a white annulus on flagellomeres 6–11; palpi white with apical segment of each blackish; mandible mostly black with a large white blotch on base; clypeus white with black on median 2/3 and pale brown on lateral 1/3 of apical margin as well as broadly black on lateral and dorso-lateral margins around and mesad of anterior tentorial pits; white on most of face, cheek, and a broad orbital ring which is narrowed and briefly interrupted on upper 1/4 of temple; head otherwise with black on median half of front and vertex and more broadly on occiput and postocciput as well as increasingly narrowly black ventrad along occipital carina to about dorsal 1/2 of temple; mesosoma black with profuse white markings as follows: about apical 3/4 of propleuron; broad front margin of pronotum, ending about 4/5 the distance ventrad to lower hind corner and also enclosing a pair of small, dorso-lateral black spots; all but about median 1/6 of dorsal margin of pronotum very broadly; large median spot on mesoscutum between apices of notauli; prescutellar ridge; most of scutellum except for an anterio-median black spot; most of post-scutellum; hind rims of meso and metanotal axillary troughs; tegula; subalarum; very broad oblique band across mesopleuron from mid-height of front margin to lower hind corner; about upper 1/3 of mesepimeron; a pair of very large blotches covering much of mesosternum on each side of median groove and confluent posterio-dorsad with white mesopleural band; most of dorsal metapleuron; about dorso-posterior 3/4 of lower metapleuron; and a pair of broad propodeal stripes which extend dorsad from hind margin to include cristae and then reach forward, a little more narrowly, almost to basal trans-carina; first gastric tergite black with yellowish white dorsally on much of petiole and on about apical 1/2 of postpetiole as well as laterally toward apex of petiole and on most of postpetiole; second tergite black with a brown tinged yellowish white band on base, abruptly widened sublaterally to cover thyridia, as well as broadly yellowish white laterally and on apical 1/3; third and fourth tergites black with very broad apical and lateral yellowish white bands; fifth and sixth mostly yellowish white grading into black dorsad; seventh similar to preceding but more broadly black dorsally; eighth and ninth black with yellowish white laterally and on apical rims; fore and mid coxae white with black on most of apical 1/2 posteriorly; hind coxa yellowish white with a broad, percurrent anterio-dorsal black band and a similar but premedially interrupted posterio-dorsal band as well as blackish on extreme base ventrally; trochanters and trochantelli whitish with considerable black above; femora yellowish white with a broad, percurrent dorsal black band; tibiae yellow with some dusky staining posterio-basally on front and mid tibiae and a little more broadly blackish on base of hind tibia; fore and mid tarsi with first segment yellow with a little dusky staining apicad and succeeding segments blackish except narrowly yellow on base of second; hind tarsus with segments 1–4 yellow and 5 mostly black except grading into brownish on base; and wings hyaline with stigma black.

Length of fore wing: 10.7 mm. *Flagellum:* definitely flattened below on apical 1/3, its widest segments 1.5 as wide as long, the first segment 5.7 as long as deep at apex. *Malar space:* 0.71 as long as basal width of mandible. *Temple:* 0.4 as long as eye at upper 1/3; strongly and directly receding. *Front:* horns stout and broad, not on a common base; strongly wrinkled between level of horns and anterior ocellus. *Clypeus:* strongly and a little asymmetrically convex in profile; apical margin slightly convex. *Pro-*

notum: epomia strong in scrobe and reaching far dorsad onto the moderately swollen humeral margin of pronotum, where it forms a carinate elevation. *Mesoscutum:* shining with abundant coarse, medium-sized punctures which are mostly subadjacent to a little sparser; notauli sharp and narrow, reaching about 2/3 the length of mesoscutum. *Scutellum:* gently convex. *Mesopleuron:* prepectus opposite lower hind corner of pronotum with a long ridge that extends 2/3 or more the distance ventrad to prepectal carina; surface between prepectal carina and speculum with strong oblique wrinkling that on lower 1/2 becomes only gradually a little weaker and mingled with large but mostly obscure punctures; mesopleural suture grossly foveolate on lower 1/2. *Lower metapleuron:* with coarse oblique wrinkling that becomes more irregular dorsad and has only obscure intercalated punctures; juxta-coxal carina traceable for about basal 0.5 of metapleuron. *Front tibia:* moderately inflated. *Hind trochantellus:* 0.36 as long as trochanter in dorsal view. *Third hind tarsomere:* in addition to apical spines with four longitudinal rows of strong spines numbering about 15 in all. *Propodeum:* spiracle 1.9 as long as wide; cristae strongly projecting ligulate, about 2.0 as long as wide at base, the apical trans-carina absent between them; dorsal face behind basal trans-carina with strong irregular wrinkling and puncto-reticulation but without discrete punctures; apical face almost uniformly with strong and quite regular transverse wrinkling. *First gastric tergite:* postpetiole 1.5 as wide at apex as long from spiracle to apex; in profile pyramidally elevated above spiracle. *Second gastric tergite:* mostly mat with fine micro-reticulation and on about basal 2/3 with numerous shallow, medium-sized punctures separated in general by about 1.0–2.0 their diameters. *Ovipositor:* sheathed portion 0.46 as long as fore wing; tip 0.2 as high at nodus as long from nodus to apex, its profile between nodus and apex only slightly convex.

MALE: Unknown.

SPECIMENS EXAMINED: 2 females, USA (*Texas:* Hidalgo County, Bentsen Río Grande Valley State Park, 29 XII '76, C. C. Porter); PANAMÁ (*Chiriquí:* Valley of the Clouds, 17 III '60, K. W. Brown). (Porter, Townes).

DISCUSSION: This is the first record of *lamentaria* for the United States. The species has been cited previously only from Costa Rica, Guatemala, and Panamá.

A homotype from Panamá, loaned by H. K. Townes, is undoubtedly conspecific with the Texas specimen, differing only as follows:

No white on scape; apical segments of palpi only slightly dusky; white band on anterior margin of pronotum briefly interrupted medially; all of lower metapleuron white; gastric tergites 4–9 more broadly white; posterio-dorsal black band of hind coxa percurrent; first flagellomere 6.3 as long as deep at apex; malar space 0.83 as long as basal width of mandible; ridge on lower prepectus extending about 2/3 the distance ventrad to prepectal carina; hind trochantellus 0.47 as long as its trochanter in dorsal view; punctures of second gastric tergite sparser, mostly separated by more than 2.0 their diameters.

Among its relatives, *lamentaria* most resembles *C. banchiformis* of the eastern United States and the two nearly replace one another geographically since *banchiformis* ranges down to San Antonio, Texas within less than 500 km. of the Valley. *Lamentaria* differs from *banchiformis* mainly in its black and white (instead of mostly fulvous) femora and in having the lower metapleuron and propodeal dorsum strongly wrinkled but with at most obscure intercalated punctures (instead of with numerous discrete punctures). The two species probably stem from a common ancestor which, during warmer and wetter Tertiary times, ranged uniformly from México up along the Gulf arc into eastern United States but then was fragmented by Pleistocene glacial maxima into southeastern (Florida) and southwestern (México) isolates, which have practically reestablished contact during the present moderately warm interglacial.

The unique Texas female was netted as it flew about a tangle of *Serjania* vines in gallery woods along the Río Grande. This is the same habitat and same general area where *C. compacta* and *C. vallis* also were collected.

Genus *Mesostenus*

12. *Mesostenus gracilis* Cresson

SPECIMENS EXAMINED: 6 females, BENTSEN PARK (*Malaise:* 1 female, 1–15 V '76); BOTANICAL GARDEN (*Net:* 1 female, 16–30 V '74; *Malaise:* 4 females, III '74).

HABITAT: Herbaceous undergrowth in *Celtis lindheimeri-C. pallida* woods.

DISTRIBUTION: U.S. and northern México.

PHAENOLOGY: March to May in Valley; flies from March to November elsewhere in southern part of its range and from late May to mid-October farther north.

13. **Mesostenus opuntiae** n. sp.
(Fig. 2)

Holotype: female, USA (*Texas:* Hidalgo County, Valley Botanical Garden at McAllen, 10 I '76, C. C. Porter). (Townes).

FEMALE: *Color:* scape black with a little dull brown below; pedicel black with dull brown on apex; flagellum black with a little pale brown on base of first segment and a ventrally interrupted white band on segments 6–11; palpi brownish white; mandible white on basal half with apical half grading through pale brown into black on teeth; head mostly white on clypeus, cheek, face, and on a broad, uninterrupted orbital band, which progressively widens rearward and below to cover much of temple, as well as with pale brownish on mandibular condyles, hypostomal carina, medio-dorsal margin of clypeus, slightly on apical face and apical margin of clypeus, and on antennal sockets, and with black broadly and irregularly along lateral and dorso-lateral margin of clypeus, irregularly around antennal sockets below, on about median half of front and vertex, more broadly on occiput and post-occiput, and then increasingly more narrowly ventrad on temple along occipital carina to about its lower 1/5; pronotum black basally with fulvous on apical half that grades into dull white on apical margin; pronotum black with a broad white band on most of front margin and on all but about median 1/5 of dorsal margin; mesoscutum black with a median white blotch located between apices of notauli and with white on pre-scutellar ridge; scutellum black, broadly margined with white laterally and behind; postscutellum mostly white; meso and metanotal axillary troughs black with hind rims narrowly whitish; mesosoma otherwise fulvous with white on tegula, subalarum, broadly on about upper 4/5 of front margin of mesepisternum, toward dorsum of mesepimeron, dully in lower hind corner of mesepisternum, and dully on apex of lower metapleuron, as well as with black above, below and behind subalarum, on most of prepectus, on most of apex of metasternum in front of mid coxae, in most of groove at base of propodeum, irregularly ventrad on front margin of lower metapleuron, rather irregularly on submetapleural carina and on most of metasternum; gaster fulvous with some faint and diffuse dusky staining; legs fulvous with tibiae and tarsi duller and fifth tarsomeres dusky, front coxa extensively white above and in front with a large dark brown dorsal blotch enclosed by the white, front trochanter white tinged dorso-anteriorly and with slight dusky staining above; mid coxa with a large white blotch on basal half anterio-dorsally, mid trochanter brownish stained above; and with a little dusky on apex of hind trochantellus; wings hyaline with stigma pale brown.

Length of fore wing: 6.3 mm. *First flagellomere:* 5.0 as long as deep at apex. *Clypeus:* small, in profile rather strongly and a little asymmetrically convex, its apical margin slightly convex. *Malar space:* 0.85 as long as basal width of mandible. *Temple:* at its upper 1/3 about 0.34 as long as eye in lateral view; strongly receding and gently convex. *Mesoscutum:* smooth and shining with abundant, moderately small, sharp punctures (coarser and denser in *thoracicus*). *Mesopleuron:* prepectal carina sharp to about lower 0.2 of hind margin of pronotum and then becoming obsolete in a vertically elliptic, slightly raised white callus. *Wing venation:* areolet 1.3 as wide as high at apex; nervulus interstitial. *Hind trochantellus:* 0.20 as long as hind trochanter in dorsal view. *Propodeum:* elongate and rather strongly sloping rearward with little discontinuity between basal and apical face, apical face 0.7 as long as basal; apical trans-carina absent medially, laterally forming very low, broad, weakly oblique subcrescentic cristae; surface strongly and densely punctate with some intercalated wrinkling, especially rearward and a little more finely and sparsely punctate basad of basal trans-carina. *First gastric segment:* postpetiole 0.81 as wide apically as long from spiracle to apex. *Second gastric tergite:* mat with very fine but well developed micro-reticulation and abundant small, shallow punctures separated mostly by a little more or a little less than their diameters. *Ovipositor:* sheathed portion 0.83 as long as fore wing; tip 0.7 as long from nodus to apex as deep at nodus.

MALE: Unknown.

TYPE: In collection of Henry K. Townes, 5950 Warren Rd., Ann Arbor, Michigan, 48105.

RELATIONSHIPS: This species resembles *M. sicarius* Townes (1962, p. 448–450), especially because of its short prepectal carina which ends dorsally in a white callus, but may be distinguished by the characters summarized in the following key:

1. Ovipositor tip 0.7 as long from nodus to apex as deep at nodus; propodeal cristae weakly oblique; first flagellomere 5.0 as long as deep at apex; postpetiole 0.83 as wide apically as long from spiracle to apex; propodeal punctation definitely sparser basad of basal trans-carina; second gastric tergite mat with small punctures separated in general by a little more to somewhat less than their diameters .... *M. opuntiae* n. sp.

   Ovipositor tip 11.5 as long from nodus to apex as deep at nodus; propodeal cristae strongly oblique; first flagellomere 4.2 as long as deep at apex; postpetiole 0.95 as wide apically as long from spiracle to apex; propodeal punctation hardly sparser basad of basal trans-carina; second gastric tergite more shining with small punctures separated mostly by about 1.5 their diameters .... *M. sicarius* Townes.

FIELD NOTES: Netted in arid *Prosopis-Opuntia* association.
SPECIFIC NAME: from the genitive singular of *Opuntia.*

14. *Mesostenus longicaudis* Cresson

SPECIMENS EXAMINED: 5 females, 7 males: BENTSEN PARK (*Net:* 1 female, 12–20 III '77; *Malaise:* 1 male, 16–31 V '76); BOTANICAL GARDEN (*Net:* 1 male, 12–20 III '77; 2 females, 15 III '76; 1 female, 1 IV '75; 2 males, 27 VIII '76; 1 female, 3 males, 3–9 IX '76).

HABITAT: Herbaceous growth in abandoned orange groves; amid pink verbenas on an otherwise well-cut lawn; weedy areas at edge of woods; rarely strays into deep woods; flies in full sunlight.

PHAENOLOGY: Peaks in spring and late summer. Seems absent in winter and June-July. Valley records include 4 specimens for March, 1 for April, 1 for May, 2 for August, and 4 for September. Flies from mid-spring to mid-fall in most of south but does not appear before early July in north.

DISTRIBUTION: Most of U.S. and México.

Genus *Bicristella*

This is the first record of *Bicristella* from the United States.

15. *Bicristella texana* n. sp.
(Fig. 5)

Holotype: female, USA (*Texas:* Hidalgo County, Bentsen Río Grande Valley State Park, 29 XII '76, C. C. Porter). (Townes).

FEMALE: *Color:* antenna black with a white annulus on flagellomeres 5–11 and a little brownish toward apex below; maxillary palpus white with a little brownish on apical segment; labial palpus white with dusky toward apex of penultimate and on all of apical segment; mandible white with apical 1/4 dark brown; head white with black or blackish markings as follows: narrow apical margin of clypeus; rather broad ventral margin of anterior 1/2 of malar space; weak staining on mandibular condyle; some staining around anterior tentorial pit; narrow median line on about upper 1/3 of face; antennal sockets largely; a little more than median 1/2 of front and vertex; occiput more broadly; most of post-occiput; and temple, increasingly more narrowly, ventrad along occipital carina to about its upper 0.4; propleuron white; pronotum black with front margin very broadly white, except for a narrow dorso-median interruption, and all but about apical 1/4 of humeral margin broadly white; thoracic dorsum black with white on a large callus-like area on lateral lobe of mesoscutum above tegula, on prescutellar ridges and broad lateral and very broad apical margins of scutellum, on post-scutellum, and on apical rims of meso and metanotal axillary troughs; tegula white internally grading marginally into blackish; mesosternum and mesopleuron white with weak testaceous suffusion on all but about upper 1/3 of mesopleuron, as well as with black above subalarm, obliquely between apex of subalarum and dorsal margin of speculum and in subspecular depression; upper metapleuron almost wholly white; lower metapleuron white with a faint testaceous tinge; part of propodeum basad of basal trans-carina black with slightly testaceous white on much of lateral 1/5, except for black margining spiracle behind, as well as more narrowly white all along basal trans-carina and finely whitish on median longitudinal carinae; part of propodeum behind basal trans-carina also slightly testaceous white with an almost percurrent black stripe between median longitudinal carinae and a black stripe along all of pleural carina except near apex; first gastric segment white with a large black area on apex of petiole and about basal 2/3 of postpetiole, narrowly black on apex of post-petiole, and with a broad, almost percurrent black stripe ventro-laterally; second tergite black with a broad subapical white band, even more broadly white laterally, and with a transverse white blotch medially at about basal 1/5; third tergite like second but without a sub-basal white blotch; following tergites similar to third but with the subapical white band increasingly narrower mesad and broadly interrupted medially on sixth and following; fore leg pale testaceous with coxa white, except for a brownish streak dorso-basally, and tarsomeres 2–5 mostly dusky; mid leg similar to fore leg except for weak testaceous staining on coxa; hind leg pale testaceous with coxa grading into white near base and with a broad, percurrent, weakly contrasting pale brownish stripe on its dorsum and with tarsus yellow except for blackish on the last segment; wings hyaline with stigma whitish grading marginally into pale brown.

Length of fore wing: 7.4 mm. *Flagellum:* scarcely flattened below toward apex; first segment 6.4 as long as deep at apex. *Front:* horn large, stout and conical, situated a little below center of front. *Clypeus:* bluntly nasute; apical margin convex. *Malar space:* 0.75 as long as basal width of mandible. *Occipital carina:* fine and sharp, joining the moderately raised hypostomal carina below in a weak depression at a distance above base of mandible equal to about 1/2 basal width of mandible. *Temple:* strongly and directly receding; 0.21 as long as eye at upper 1/3. *Pronotum:* humeral margin strongly swollen, evenly rounded and not especially prominent at anterior end; epomia strong throughout in scrobe but not prolonged dorsad or ventrad; anterior margin bluntly angulate below middle. *Mesoscutum:* smooth and polished with a few sparse punctures; notauli sharply impressed and reaching about 2/3 the length of mesoscutum; lateral lobe opposite tegula with a large, gently raised, nearly circular white callus which is set off internally by a longitudinal impression. *Mesopleuron:* subalarum swollen; prepectal carina reaches dorsad about to upper 0.5 of hind margin of pronotum; prepectus opposite lower hind corner of pronotum with a rather high ridge that extends about 1/3 the distance ventrad to prepectal carina; surface shining with strong longitudinal wrinkling that becomes weaker and partially interrupted on upper 1/2, where there are some scattered large punctures, as well as ventro-posteriorly, where there are more numerous large punctures. *Lower metapleuron:* with strong oblique wrinkling that grades anterio-dorsad into puncto-reticulation and finally becoming smooth for a short distance near front margin. *Wing venation:* areolet 1.6 as wide as high at apex; second recurrent a little basad of second intercubitus; nervulus slightly antefurcal; postnervulus broken at lower 0.4. *Fore tibia:* moderately inflated. *Hind femur:* 1.6 as deep at middle as at apex. *Hind tibia:* inner spur 0.41 as long as basitarsus. *Propo-*

deum: spiracle 1.4 as long as wide; basal trans-carina almost straight medially; apical trans-carina represented sublaterally by strong, broadly cuneate cristae but interrupted on median 1/3 of propodeum; median longitudinal carinae well defined throughout and enclosing a very narrow, parallel-sided area-basalis and a broader but also long and parallel-sided combined areola and median apical area; pleural carina obsolete; surface shining, apicad of basal trans-carina with more numerous very large puntures that are moderately sparse on area dentipara but which become denser and mingled with longitudinally biased to reticulate wrinkling on areola, median apical area, and latero-apical area. *First gastric segment:* petiole with a sharply triangular lateral expansion at base; postpetiole 0.6 as wide at apex as long from spiracle to apex. *Second gastric tergite:* smooth and highly polished with scattered tiny punctures emitting short, sparse setae. *Succeeding tergites:* with denser tiny punctures and setae which in part equal or exceed the length of their interspaces. *Ovipositor:* sheathed portion 0.51 as long as fore wing; tip 0.15 as high at nodus as long from nodus to apex, dorsal valve with a very long and slightly concave taper between nodus and apex.

TYPE: In collection of Henry K. Townes, 5950 Warren Rd., Ann Arbor, Michigan, 48105.

RELATIONSHIPS: *Texana* resembles the Mexican and Guatemalan *B. humerosa* (Cushman, 1931, p. 51–52, fig. 4 on p. 4) but differs in that the occipital carina reaches the hypostomal carina below (becomes obsolete below in *humerosa*), because the propodeum anteriad of the apical trans-carina is punctured on the area dentipara and longitudinally rugose medially (polished before the apical trans-carina in *humerosa*), in the well-defined, elongately rectangular areola (in *humerosa* the apical trans-carina is acutely angled forward medially and a single median longitudinal carina reaches forward from the vertex of the angulation to the basal trans-carina), and in having the apical margins of gastric tergites 2 and 3 narrowly black (no black on apical margins in *humerosa*).

From the other Mexican *Bicristella, B. univittata* (Cresson), *texana* differs because the occipital and hypostomal carinae join in a weak declivity (instead of being separated by a broad, deep depression), by its shorter temple (0.21 as long as eye at upper 1/3 vs. 0.38 in *univittata*), and by its longer epomia, medially longitudinally wrinkled (instead of mostly smooth and polished) mesopleuron, narrow and well-defined area-basalis (broadly and poorly developed in *univittata*), and black and white (instead of uniformly testaceous) gaster.

B. bicarinata (Cushman) from Panamá may be separated from *texana* by its color (ferruginous with head black) and by many structural features (clypeus not prominent in profile, occipital carina separated by a deep groove from hypostomal carina, temple concave in dorsal view, mesopleuron finely and sparsely punctate, subalarum reduced to a carina, and propodeum sparsely punctate with its apical trans-carina forming medially an acute angle from which a single carina extends forward to the basal trans-carina).

Cameron's (1885, p. 236) original diagnosis of *B. chontalensis,* the only other described Middle American *Bicristella,* shows that his species has a short frontal horn (horn is long in *texana*) and that it deviates chromatically from *texana* in numerous aspects (mandible black at base, mesoscutum with a yellow line along outer edge of central lobe and without a white callus opposite tegula, lower metapleuron with a black mark over hind coxa, petiole black at base, and fore and mid coxae with a black line at base and a larger black spot at apex, and hind coxa marked with yellow).

The Cuban *B. tricolor* (Brullé) resembles *texana* because its occipital carina is complete ventrad to the hypostomal carina and the mesopleuron is discally striate but may be distinguished because it has two deep pits at the base of the frontal horn, the anterio-lateral margin of the pronotum sharply angulate below the middle, the scape below and apex of the frontal horn white, the mesoscutum with discal white lines that extend nearly the length of the inner margins of the lateral lobes, and the legs mostly ferruginous.

Finally, *B. testacea* (Taschenberg), the only other described *Bicristella,* ranges over most of South America and differs strikingly from the black, white and testaceous *texana* in being uniformly ferruginous to testaceous with only the head black.

FIELD NOTES: Swept near R. Grande from *Serjania* vines in *Salix-Celtis-Fraxinus* gallery woods.

SPECIFIC NAME: for the state of Texas.

Genus *Diapetimorpha*

The Valley has seven *Diapetimorpha,* of which three are described as new.

KEY TO THE U.S. *DIAPETIMORPHA*

Females

(Females of *pareia* and *aspila* unknown)

1. Propodeum black with conspicuous white markings, including at least a broad band on each side that reaches from somewhat in front of crista to or nearly to hind margin 2
   Propodeum black or ferruginous to fulvous, its pale markings, if any, confined to cristae and often area immediately around cristae 3

2. Malar space 0.50 as long as basal width of mandible; propodeal cristae low, about 0.37 as long as their basal width; propodeum basad of basal trans-carina with a pair of large white lateral blotches; gastric tergites 2–6 blackish basally with broad fulvous and whitish apical bands .... 18. *D. picta* Townes.
   Malar space 0.70 as long as basal width of mandible; propodeal cristae longer, about 0.9 as long as their basal width; propodeum wholly black basad of basal trans-carina; gastric tergites 2–6 wholly fulvo-ferruginous ....*D. rufigaster* Cushman

3. Pronotum and mesoscutum black, with or without white markings 4
   Pronotum and mesoscutum fulvous or ferruginous, with or without white markings 6

4. Malar space 0.80 as long as basal width of mandible; head and mesosoma almost uniformly black and white at most only on propodeal cristae and sometimes very slightly on scutellum; gaster wholly feruginous .... 21. *D. introita* (Cresson).
   Malar space 0.60–0.70 as long as basal width of mandible; head, pronotum, and mesoscutum black with white markings; mesopleuron, metapleuron and propodeum extensively fulvous to ferruginous; always a large median white blotch on gastric tergite 7 5

5. First flagellomere 6.6–7.1 as long as deep at apex; lower metapleuron with coarse, mostly longitudinally biased wrinkling that becomes somewhat reticulate only on dorsal 1/4 or less; dorsal face of propodeum between trans-carinae with strong, more or less longitudinally biased wrinkling; propodeal cristae

strongly projecting subligulate to ligulate, 0.7–1.2 as long as wide at base; broad white orbital ring interrupted only at bottom of eye; humeral margin of pronotum white throughout; scutellum pure white; first gastric tergite with a white apical band (except in S. Florida populations) .... 16. *D. macula* (Cameron).

First flagellomere 5.5–6.0 as long as deep at apex; lower metapleuron with strong longitudinal wrinkling that becomes reticulate on dorso-posterior half; dorsal face of propodeum between trans-carinae with strong, complexly reticulate wrinkling; propodeal cristae prominent, broadly cuneate, 0.4–0.5 as long as wide at base; white only on frontal orbit; humeral margin of pronotum more than half black; scutellum yellowish ferruginous; no white on apex of first gastric tergite ....17. *D. sphenos* n. sp.

6. Lower metapleuron with strong longitudinal wrinkling; whitish at least on pronotal collar and propodeal cristae 7

Lower metapleuron either only punctate or punctate and obliquely wrinkled; no white on mesosoma 8

7. Malar space 0.80 as long as basal width of mandible; mesosoma brownish ferruginous, except for whitish pronotal collar and propodeal cristae; fourth gastric tergite dusky .... *D. brunnea* Townes

Malar space 0.63–0.73 as long as basal width of mandible; mesosoma fulvous with profuse yellowish white markings including scutellum, humeral margin of pronotum, and a pair of median stripes on mesoscutum; fourth gastric tergite fulvous. .... *D. alabama* Cushman

8. Malar space 0.65–0.75 as long as basal width of mandible ....22. *D. acadia* Cushman

Malar space 1.05 as long as basal width of mandible .... *D. rugosa* Townes

Males

1. Gastric tergites 2–7 black or brownish black with broad white apical bands...2

Gastric tergites 2–7 ranging from yellowish fulvous to ferruginous, sometimes with blackish basal bands but never with white apical bands 5

2. Tyloides sharp longitudinal carinae on flagellomeres 11 or 12 to 19, those of 12 or 13 to 17 or 18 extending more or less the length of their segments; mesopleuron and lower metapleuron largely with medium-sized coarse punctures that mostly are separated by less than 2.0 their diameters or sometimes in part on metapleuron and on mesopleuron in front of speculum with puncto-reticulation to more or less regular longitudinal wrinkling; mesopleuron black with white on subalarum and sometimes one or two whitish blotches on lower 1/4 above sternaulus ...... 21. *D. introita* (Cresson)

Tyloids often very faint and not extending nearly the length of their segments, at most flagellomeres 12 to 15 with sharp, carinate tyloids reaching 0.4–0.6 their length; mesopleuron and lower metapleuron with small to tiny rather weak punctures separated in general by 2.0 or more their diameters and without wrinkling or puncto-reticulation, except sometimes above speculum or just along pleural carina; 2/3 or more of mesopleuron white 3

3. Malar space 0.80–0.85 as long as basal width of mandible; scape entirely black; propodeum apicad of basal trans-carina uniformly pale fulvous .... 20. *D. pareia* n. sp.

Malar space 0.48–0.58 as long as basal width of mandible; scape largely white below; propodeum apicad of basal trans-carina white with black markings 4

4. Temple 0.38 as long as eye at upper 1/3; pronotal scrobe without wrinkles except for the short epomia; juxta-coxal carina absent; propodeal cristae large, strongly projecting, bluntly triangular; propodeum entirely black basad of basal trans-carina .... 19. *D. aspila* n. sp.

Temple 0.50–0.60 as long as eye at upper 1/3; pronotal scrobe with numerous wrinkles in addition to the scarcely differentiated epomia; juxta-coxal carina almost complete but irregular at least on apical 1/2; propodeal cristae weakly cuneate, low, broad, and scarcely projecting; propodeum basad of basal trans-carina black with a large white sublateral blotch .... 18. *D. picta* Townes

5. Tyloids sharp carinae extending full length of several segments; lower metapleuron with moderately coarse punctures 6

Tyloids carinate but either obsolescent and almost impossible to see or, if fine and sharp, generally shorter than the length of their segments; lower metapleuron with fine, weak punctures 7

6\. Malar space 0.75 as long as basal width of mandible; clypeus moderately convex in profile; mesosternum usually entirely fulvous, sometimes partly black and rarely entirely black; epomia rather weak . . . . 22. *D. acadia* Cushman

Malar space 0.83 as long as basal width of mandible; clypeus weakly convex in profile; mesosternum largely or entirely black; epomia moderately strong . . . . *D. rugosa* Townes

7\. Mesoscutum black with a pair of median white lines or with a median white blotch 8

Mesoscutum mostly or entirely fulvous, with or without a pair of median whitish dashes 10

8\. Tyloids sharp longitudinal carinae on 4 segments but in most cases shorter than their segments; flagellum with a white band on about 5 segments; pronotum apicad of basal trans-carina white with a broad black stripe along pleural carina almost to apex and black narrowly along basal trans-carina . . . . *D. rufigaster* Cushman

Tyloids hard to see, low, indistinct ridges extending about 0.3 the length of several segments; flagellum at most with a poorly defined postmedian brown section; propodeum apicad of basal trans-carina dull fulvous to yellowish or whitish and without black or with black only along basal trans-carina 9

9\. White orbital ring interrupted on vertex and upper half of temple; pronotum white with a very large black apico-lateral area; mesopleuron black with white on subalarum and speculum and with more or less whitish stained fulvous on most of lower 1/3 of mesepisternum behind prepectal carina as well as throughout on mesepimeron . 17. *D. sphenos* n. sp.

White orbital ring complete; pronotum wholly white; mesopleuron mostly whitish or stramineous to weakly brownish white, in some specimens with black on as much as anterior 1/3–1/2 below sub-alarum . . . . . 16. *D. macula* (Cameron)

10. Eye about 75% surrounded with yellowish white, the whitish orbit being interrupted on upper part of temple; mesoscutum without a median pair of whitish dashes .... *D. brunnea* Townes

Eye completely surrounded with yellowish white; mesoscutum with a median pair of whitish dashes .... *D. alabama* Cushman

16. *Diapetimorpha macula* (Cameron)

SPECIMENS EXAMINED: 17 females, 4 males: BENTSEN PARK (*Net:* 1 female, 19 III '76; 1 male, 9 VI '76; 12 females, 1 male, 2–10 IX '76; 1 female, 29 XII '76); BOTANICAL GARDEN (*Net:* 1 female, 16 III '74; 1 female, 19 XII '76; *Malaise:* 2 males, 10–31 X '73; 1 female, XII '73).

HABITAT: Dark, damp woods; herbaceous undergrowth beneath *Pithecellobium flexicaule; Celtis lindheimeri-C. pallida* association.

DISTRIBUTION: Va. to Fla. west to Tex. and south to Veracruz state in México.

GEOGRAPHIC VARIATION: Townes (1962, p. 384–387) divides *macula* into several subspecies, among which my Valley material agrees most closely with *D. m. macula,* heretofore not recorded north of México.

PHAENOLOGY: Flies almost throughout the year with peak in September. Valley records include 2 females for March, 1 male for June, 12 females and 1 male for September, 2 males for October, and 3 females for December. North of the Valley *macula* is active between March and November.

17. **Diapetimorpha sphenos** n. sp.
(Fig. 9)

Holotype: female, USA (*Texas:* Hidalgo County, Bentsen Río Grande Valley State Park, 1–15 XI '76, Malaise Trap, C. C. Porter). (Townes). *Paratypes:* 1 female, 2 males, USA *(Texas:* Hidalgo County, Bentsen Río Grande Valley State Park, 1–15 V '76, Malaise Trap, C. C. Porter; Valley Botanical Garden at McAllen, X '73, Malaise Trap, C. C. Porter). (Gainesville, Porter).

FEMALE: *Color:* antenna black with much dull to pale brown on scape, and sometimes pedicel and base of first flagellomere, and with a ventrally interrupted white band on flagellomeres 4 (apically) to 9 and sometimes slightly onto base of 10; head black with palpi brownish white, mandible brownish white with dark brown on apical 1/4, brownish white on mandibular condyle, dull brown on apical 1/3 of clypeus, at times with a brownish median spot on face somewhat below antennal sockets, and with white broadly on most of frontal orbit; propleuron black; pronotum black with a broad white band on most of front margin except for hind corners, a large, broadly triangular white mark on median 1/3 of dorsal margin which is contiguous medially with white band on front margin and which encloses a more or less well developed central brown area, and with a little pale brown on upper hind corner; thoracic dorsum black with tegula white, a pair of short median white stripes on mesoscutum in apical 1/3 of notauli, scutellum shining ferruginous with a yellowish tinge, postscutellum yellowish to ferruginous white, and hind rim of meso and metanotal axillary troughs narrowly whitish to ferruginous; mesopleuron and mesosternum black with ferruginous on about ventro-posterior 2/3 of mesepisternum, narrowly on adjacent mesosternum, and on most of mesepimeron as well as with white on much of subalarum and toward dorsum of mesepimeron; mesosoma otherwise uniformly ferruginous; gaster ferruginous with a trace of faint dusky staining on the more apical tergites and with a very large medio-apical white blotch on tergite 7 and a similar but smaller white area on 8; legs ferruginous to stramineous with blackish anterior and posterior staining on hind trochanter and with 5th tarsomeres dusky; wings hyaline with fore wing faintly brown tinged and stigma rather pale brown.

Length of fore wing: 4.6–4.8 mm. *First flagellomere:* 5.5–6.0 as long as deep at apex. *Clypeus:* moderately convex in profile. *Malar space:* 0.62–0.64 as long as basal width of mandible. *Temple:* 0.19–0.22 as long as eye at upper 1/3. *Pronotum:* scrobe extensively wrinkled. *Mesoscutum:* finely and densely punctate with a broad band of delicate transverse wrinkling along anterior 2/3 of notauli, mostly internally, and with stronger longitudinal wrinkling between notauli on about their apical 1/3. *Mesopleuron:* in large part with strong wrinkling that is more or less regularly longitudinal above and more irregular below or which sometimes is longitudinally biased throughout. *Lower metapleuron:* with strong longitudinal wrinkling that becomes very irregular on dorso-posterior 1/2; juxta-coxal carina obsolete, weakly suggested only near base. *Propodeum:* basal trans-carina rather strongly curved forward medially; apical trans-carina curved far forward and slightly to markedly irregular medially, its cristae broadly and strongly projecting cuneate; surface with strong reticulate wrinkling that is finer basad of basal trans-carina. *First gastric segment:* postpetiole 1.1–1.3 as wide apically as long from spiracle to apex. *Ovipositor:* sheathed portion 0.42–0.48 as long as fore wing; tip 0.23–0.24 as high at nodus as long from nodus to apex.

MALE: *Color:* scape pale brownish to whitish with a little dusky staining dorsad; pedicel dark brown with apex paler; flagellum dark brown, becoming gradually a little paler apicad; palpi white; mandible white with dark brown on apical 1/3; head black with white on clypeus, face, broad frontal orbits, very broad hind orbit of about 1/2 of eye, and throughout from malar space to hypostomal carina; propleuron white; pronotum white with a very large black area apico-laterally; thoracic dorsum black with tegula white and with a large, transverse, anteriorly emarginate postmedian white blotch on mesoscutum, and with white on scutellum, postscutellum, and narrow hind margins of meso and metanotal axillary troughs; mesopleuron black with white on subalarum and speculum and with more or less whitish stained fulvous on most of lower 1/3 of mesepisternum behind prepectal carina as well as throughout on mesepimeron; mesosternum testaceous-stained white except black anteriad of prepectal carina; upper metapleuron white; mesosoma otherwise pale fulvous to yellowish with hind face of propodeum more whitish; gaster pale fulvous with dark brown to black on extreme base of petiole, on basal half of segment 2, and on basal 1/3 of 3, as well as with paler brown to equally dark brown or black on basal 1/4 of 4–6 and dusky on much of 7; fore leg with coxa, trochanter, and trochantellus white, femur and tibia pallid fulvous, and tarsus whitish with fifth segment dusky and a little dusky above on third and fourth segments; mid leg similar to fore leg but with light fulvous staining dorsad on coxa, trochanter, and trochantellus and with tarsus largely dusky except for whitish narrowly on tips and bases of segments 2–4 and with segment 1 dull fulvous grading into dusky on apical 1/2 with tip whitish; and hind leg pale fulvous with considerable blackish on trochanter, sometimes slightly dusky on apex of trochantellus and base of femur, tibia a little dusky at base and dusky stained on most of apical 2/3 except below, and with tarsus blackish with dull white on base of first segment and pure white on apical 1/3 of first segment and on all of segments 2–4; wings hyaline with stigma brownish.

Length of fore wing: 3.5–3.6 mm. *Flagellum:* tyloids not clearly defined; first flagellomere 4.1–4.5 as long as deep at apex. *Clypeus:* moderately convex. *Malar space:* 0.55–0.65 as long as basal width of mandible. *Temple:* 0.47–0.52 as long as eye at upper 1/3. *Pronotum:* scrobe smooth, without wrinkles except for short epomia or sometimes with several oblique wrinkles in addition to epomia. *Mesoscutum:* smooth and polished with numerous, well spaced small punctures that become somewhat larger and denser anteriad. *Mesopleuron:* smooth and polished with small, scattered punctures and only a little longitudinal wrinkling limited to dorsal region behind subalarum. *Lower metapleuron:* smooth and polished with scattered small, weak punctures that become only a little larger and denser dorsad toward pleural carina; juxta-coxal carina defined for a short distance near base. *Propodeum:* basal trans-carina only weakly curved forward medially; apical trans-carina complete, advanced far forward medially, its cristae scarcely raised; surface smooth and polished basad of basal trans-carina, moderately wrinkled apicad of apical trans-carina. *First gastric segment:* postpetiole 0.84 as wide apically as long from spiracle to apex.

TYPES: The holotype is in the collection of Henry K. Townes, 5950 Warren Rd., Ann Arbor, Michigan. One male paratype has been donated to the Florida State Arthropod Collection (Division of Plant Industry, Entomology Bureau, Florida Department of Agriculture, Gainesville, Florida, 32602) and a male and female paratype are retained in the author's personal collection (301 N. 39th Street, McAllen, Texas, 78501).

RELATIONSHIPS: This species is close to *D. macula* but may be easily distinguished by the structural and chromatic characters given in the key.

FIELD NOTES: *Sphenos* has been collected only by Malaise Trap and appeared at both the Bentsen Park and Botanical Garden collecting stations. It is thus a species of shady woods, associated with large trees such as *Pithecellobium flexicaule* and *Celtis lindheimeri.*

Sphenos may have separate fall and spring generations, as there are records for October and November and again for May.

SPECIFIC NAME: From the genitive of the Greek noun *sphen* (*sphenos*) or “wedge”, in reference to the shape of the propodeal cristae.

18. *Diapetimorpha picta* Townes

SPECIMENS EXAMINED: 2 males, BENTSEN PARK (*Net:* 1 female, 17 III ’76; 1 male, 17 III ’77).

HABITAT: *Serjania* vines in *Salix nigra* woods along Río Grande.

DISTRIBUTION: Previously recorded only from Florida and south Georgia (Townes, 1962, p. 387). Among material loaned by Townes is a male from Kansas (Clark County, 12 VI ’60, R. L. Fischer). *Picta* thus probably ranges over the southeastern U.S. and into México.

19. **Diapetimorpha aspila** n. sp.

(Fig. 4)

Holotype: female, USA (*Texas:* Hidalgo County, Valley Botanical Garden at McAllen, XII ’73, Malaise Trap, C. C. Porter).

FEMALE: unknown.

MALE: *Color:* antenna black with scape broadly white below, a little brown on apex of pedicel and base of first flagellomere, and a white annulus on flagellomeres 9–15; palpi white with a pale brownish tinge; mandible white with apical 1/3 dark brown; head white with black on median 1/2 of front and vertex, more broadly on occiput, on postocciput, and ventrad increasingly more narrowly along occipital carina to about its lower 0.1; propleuron white; pronotum black with a very broad white band throughout on anterior margin, a much narrower and apically attenuate white band on most of humeral margin, and a little white on upper hind corner; thoracic dorsum black with a large, more or less rectangular, anteriorly deeply emarginate postmedian white blotch on mesoscutum, and with white on scutellum, postscutellum, and hind rims of meso and metanotal axillary troughs; tegula white; mesopleuron black with white on subalarum and on most of its lower 3/4 apicad of prepectal carina, except for a large, irregular black blotch below speculum and for black in about upper 0.7 of pleural suture; mesosternum black on prepectus and otherwise white with a little brownish staining in front of mid coxae; upper metapleuron white except for black on its narrow lower 1/3; lower metapleuron white with black irregularly along its anterior margin; propodeum basad of basal trans-carina entirely black and apicad of basal trans-carina white with a broad anteriorly gradually narrowed black blotch that reaches forward from gastric insertion about 2/3 the distance to basal trans-carina as well as with a broad black stripe along about basal 7/9 of pleural carina; first gastric segment with white on basal 1/2 of petiole above and laterally and on apical 1/2 of postpetiole as well as with brownish yellow on most of petiole ventrally; gastric tergites 2–7 black with very broad white apical bands and tergite 8 and claspers brownish yellow; fore leg with coxa, trochanter, and trochantellus white, femur and tibia dull pale fulvous, and tarsus pale brownish with segments 3–5 blackish; mid leg with coxa white with a yellowish brown tint, trochanter yellowish white with considerable brown staining, trochantellus yellowish white, femur and tibia pale fulvous and tarsus blackish grading irregularly into dull fulvous on basal 1/2 and with a little pale brownish on tips of segments 1–4; hind leg bright, deep fulvous on coxa, trochanter, trochantellus, femur and tibia and with considerable dark brown on trochanter, a little blackish on base of tibia, and slight dusky staining toward apex of tibia, and tarsus with segment 1 black on basal half and white on apical half, segments 2–4 white, and 5 black; wings hyaline with stigma dark brown.

Length of fore wing: 5.0 mm. *Flagellum:* first segment 4.25 as long as deep at apex; segments 12–15 with tyloides in the form of fine but sharp carinae that extend about 0.4–0.6 the length of each. *Malar space:* 0.58 as long as basal width of mandible. *Clypeus:* moderately strongly and asymmetrically convex, weakly nasute in lateral view. *Temple:* at upper 1/3 about 0.38 as long as eye in lateral view. *Pronotum:* scrobe smooth and polished, without wrinkles except for the short epomia. *Mesoscutum:* smooth and polished with numerous tiny, well spaced punctures. *Mesopleuron:* mostly smooth and polished with small, scattered punctures. *Lower metapleuron:* smooth and polished with small, very well spaced punctures that are scarcely denser dorsad; juxta-coxal carina absent. *Wing venation:* intercubitus about 3.0 as long as width of radial vein. *Hind femur:* 5.1 as long as deep at middle. *Propodeum:* basad of basal trans-carina smooth and shining with numerous medium-sized punctures, laterad and behind basal trans-carina rather strongly and irregularly wrinkled; basal trans-carina almost straight; apical trans-carina forming broad and strongly projecting bluntly triangular cristae, between the cristae advanced far forward but, except for a short median segment, practically effaced. *First gastric segment:* postpetiole 0.91 as wide at apex as long from spiracle to apex; tergite smooth and shining with a few tiny, scattered punctures.

TYPE: The holotype is in the collection of Henry K. Townes, 5950 Warren Rd., Ann Arbor, Michigan, 48501.

RELATIONSHIPS: *Aspila* closely resembles *D. picta* but may be distinguished by the characters summarized in the key.

FIELD NOTES: Collected by Malaise Trap in a partially shaded *Celtis lindheimeri-C. pallida* thicket.

SPECIFIC NAME: from the Greek adjective *aspilos* or "unspotted", in reference to the uniformly black propodeal base of this species.

20. **Diapetimorpha pareia** n. sp.
(Fig. 7)

Holotype: male, USA (*Texas:* Hidalgo County, Valley Botanical Garden at McAllen, 1 I '76, C. C. Porter). (Townes). *Paratype:* male, USA (*Texas:* Hidalgo County, Bentsen Río Grande Valley State Park, 15–30 IV '76, Malaise Trap, C. C. Porter). (Porter).

FEMALE: unknown.

MALE: *Color:* antenna black with a pale yellow annulus on flagellomeres 9–18 or 19; palpi white; head white with black, preceded by a narrow brownish zone, on apical 1/3 of mandible, a small dusky spot just above dorsal corner of clypeus, a little dusky around anterior tentorial pits, and black on median 1/2 of front and vertex, more broadly on occiput, on all but ventral corner of postocciput, and ventrad, increasingly more narrowly, on temple along occipital carina to about its upper 0.5; propleuron white; pronotum black with a broad white band on all but extreme hind corner of front margin, a narrow white band on anterior 2/3 of humeral margin, and with white on upper hind corner, or sometimes white narrowly throughout on humeral margin; thoracic dorsum black with a large more or less rectangular postmedian white spot on mesoscutum, and with white on scutellum, postscutellum, and hind rims of meso and metanotal axillary troughs as well as with some yellowish staining anteriorly in metanotal axillary trough on each side of postscutellum; tegula white; mesosternum and mesopleuron pale yellow, becoming more nearly white anterio-dorsally on mesopleuron, as well as sometimes with a little brownish staining above subalarum, a large black area above speculum, and more or less black on dorsal 1/2 of prepectus; dorsal metapleuron and groove at base of propodeum yellow and sometimes with a little brownish staining on dorsal metapleuron anteriorly at about upper 1/3; lower metapleuron pale yellow testaceous; propodeum pale fulvous with black basad of basal trans-carina in most of region between spiracle and area-basalis, which is dull testaceous or yellow grading into black apically and laterally; first gastric segment yellow with black above on petiole and basal 2/3 of postpetiole, except for a broad median yellow stripe on basal 4/5 of petiole; second gastric tergite black with a broad yellow apical band and pale fulvous on thyridia; succeeding tergites similar to second except that the apical yellow bands reach farther forward laterally; fore leg with coxa, trochanter, and trochantellus yellow with a little brown staining above on trochanter, femur and tibia pale testaceous, and tarsus testaceous grading into dusky or black on last three segments; mid leg similar to fore leg except that the coxa, trochanter, and trochantellus have a faint testaceous suffusion, the tibia sometimes becomes dusky above on apical 1/4, and the tarsus varies from mostly blackish to dusky on segments 2–5 and somewhat paler on 1; hind coxa, trochanter, trochantellus and femur rather intense shining testaceous with a brown streak ventro-anteriorly on base of coxa (absent in paratype) and some brown staining above toward base of trochanter, on apex of trochantellus, and on base of femur; hind tibia yellowish testaceous with a little dusky on base and blackish on apical 1/3 or a little more, and hind tarsus white with black on basal 1/8 of first segment, at least laterally, and on apical 1/4 of last segment; wings hyaline with stigma dull brownish white.

Length of fore wing: 7.1–7.5 mm. *Flagellum:* first segment 3.9–4.3 as long as deep at apex; tyloids very weak, sometimes faintly detectable as longitudinal discontinuities on segments 10–16 which extend about 0.5–0.8 the length of each segment. *Malar space:* 0.80–0.85 as long as basal width of mandible. *Clypeus:* weakly convex in profile. *Temple:* 0.60 as long as eye at upper 1/3. *Pronotum:* scrobe smooth and polished and without wrinkles except for the short epomia. *Mesoscutum:* smooth and polished with abundant tiny punctures separated by 4–5× their diameters. *Mesopleuron:* smooth and polished with numerous well spaced, tiny punctures and with a little longitudinal wrinkling above speculum.

Lower metapleuron: mostly smooth and shining with many tiny, sparse punctures that become larger and denser, with a little intercalated wrinkling, only dorsad near the obsolete pleural carina; without juxta-coxal or, in paratype, with juxta-coxal carina defined only on basal 1/3. *Propodeum:* smooth and polished basad of basal trans-carina, otherwise rather coarsely and irregularly wrinkled; basal trans-carina almost straight; apical trans-carina in holotype irregularly traceable between the broad and moderately projecting triangular cristae and in paratype sharp but only slightly curved forward between the lower, more cuneate cristae. *First gastric segment:* postpetiole 0.87 as wide at apex as long from spiracle to apex; its surface smooth and polished with a few tiny, scattered punctures.

TYPE: The holotype is in the collection of Henry K. Townes, 5950 Warren Rd., Ann Arbor, Michigan, 48105 and the paratype in the collection of Charles C. Porter, 301 N. 39th St., McAllen, Texas, 78501.

RELATIONSHIPS: In habitus and color this species resembles *D. picta* and *D. aspila* but may be separated from both by its much longer malar space and by chromatic features such as its entirely black scape and uniformly pale fulvous propodeal base.

FIELD NOTES: Taken by sweeping *Serjania* vines in a partial clearing near the edge of a *Celtis lindheimeri-C. pallida* thicket and in a Malaise Trap located in deep shade beneath a large *Pithecellobium flexicaule.*

SPECIFIC NAME: From the Greek noun *pareia* or "cheek," in reference to the long malar space.

21. *Diapetimorpha introita* (Cresson)

SPECIMENS EXAMINED: 15 females, 12 males: BENTSEN PARK (*Net:* 3 females, 1 male, 12–20 III '77; 1 male, 7 IX '76); BOTANICAL GARDEN (*Net:* 1 female, 17 I '75; 6 females, 4 males, 12–20 III '77; 1 male, 5 IV '74; 1 male, 16–30 V '74; 1 male, 30 VIII '76; 1 male, 1 IX '73; 1 female, 9 IX '76; 4 females, 20–31 XII '74; *Malaise:* 1 male, IX '73; 1 male, X '73).

HABITAT: Open, sunny places; tall grass at edge of fields and thickets; herbaceous growth in abandoned orange groves; occasionally enters dense woods.

DISTRIBUTION: N.C. to Tex. and into Nuevo León, México.

PHAENOLOGY: Peaks in spring and fall; possibly absent in summer. Valley records include 1 female for January, 9 females and 5 males for March, 1 male for April, 1 male for May, 1 male for August, 1 female and 3 males for September, 1 male for October, and 4 females for December. North of the Valley *introita* flies from mid-spring to early fall but disappears by July in most of Texas.

22. *Diapetimorpha acadia* Cushman

SPECIMENS EXAMINED: 1 female, 4 males: BOTANICAL GARDEN (*Net:* 1 female, 1 male, 12 III '77; 1 male, XII '73; *Malaise:* 2 females, III '74).

HABITAT: Exposed areas to dense woods; weeds in bright sun; partially shaded hedge row; *Celtis lindheimeri-C. pallida* thicket.

DISTRIBUTION: Va. to Tex. and Mexican state of Coahuila.

PHAENOLOGY: Valley records are for December and March. North of the Valley it flies from late spring to early fall and peaks between 15 August and 15 September.

Genus *Listrognathus*

23. *Listrognathus glomerata* Townes

Townes (1962, p. 424–425) gives one undated record of this species from "Cameron County, Texas". I have not collected *glomerata* personally.

Glomerata ranges from New Jersey to south Texas and flies mostly from early spring to late fall.

24. *Listrognathus rufitibialis* Cushman

SPECIMENS EXAMINED: 19 females, 3 males: BENTSEN PARK (*Net:* 2 females, 12–20 III '77; 2 females, 23–30 XII '76); BOTANICAL GARDEN (*Net:* 6 females, 9–11 I '76; 1 female, 16 I '75; 1 female, 24 I '76; 1 male, 12–20 III '77; 1 male, 16–30 V '74; 1 female, 19 XII '76; 4 females, 22–28 XII '75; 2 females, 1 male, 20–31 XII '73).

HABITAT: Exposed to shaded areas; fields at edge of woods; *Serjania* vines in woodland clearings; in bright sun among small herbaceous plants on paths through open brushland.

DISTRIBUTION: Eastern U.S. from N. J., Ind., and Okla. southward.

PHAENOLOGY: Valley populations peak in winter, my data including 8 females for January, 2 females and 1 male for March, 1 male for May, and 9 females and 1 male for December. North of the Valley it flies mostly from June to September.

Genus *Mallochia*

25. *Mallochia agenioides* Viereck

SPECIMENS EXAMINED: 10 males: BENTSEN PARK (*Net:* 1, 23 I '76; *Malaise:* 1, 16–31 I '76; 1, 1–15 II '76; 2, 16–28 II '76; 2, 1–15 V '76; 1, 16–31 VIII '76; 2, 1–15 IX '76).

HABITAT: Most Valley specimens were collected by a Malaise Trap installed in deep woods under a large *Pithecellobium flexicaule.* Farther north, *agenioides* often is found in grassy, overgrown meadows.

DISTRIBUTION: R.I. to Ks. and south to Florida. These are the first records for Texas.

PHAENOLOGY: Valley records are for January, February, May, August, and September. Elsewhere *agenioides* flies mostly from mid-spring to mid-summer.

26. *Mallochia frontalis* Townes

SPECIMEN EXAMINED: 1 male, Bentsen Park, 1–15 IX '76.

HABITAT: Caught by Malaise Trap in dense woods under shade of a large *Pithecellobium flexicaule.*

DISTRIBUTION: N.J., Md., Va., N.C., Ks., Tex.

PHAENOLOGY: North of the Valley *frontalis* flies between March and August.

Genus *Lymeon*

The Valley has three *Lymeon,* of which one here is recorded for the first time from the United States.

KEY TO THE U.S. *LYMEON*
(Females only)

1. Mesoma black with profuse white markings 2
   Mesosoma fulvous or ferruginous, with or without white markings 3

2. Mesoscutum with a single median white spot; lateral lobe of mesoscutum throughout with medium-sized, sharp, moderately dense punctures .... 27. *L. cinctiventris* (Cushman)

   Mesoscutum with a pair of submedian white stripes; lateral lobe of mesoscutum, except on about basal 1/3, sparsely punctate .... 28. *L. orbus* (Say).

3. Discoidella completely absent; lateral lobe of mesoscutum polished; second gastric tergite black with a broad white apical band; fore wing without dark cross bands .... *L. bicinctus* (Cresson).

   Discoidella well developed; lateral lobe of mesoscutum mat; second gastric tergite wholly fulvous; fore wing with a median and subapical dark cross band 4

4. Clypeus prolonged ventrally as a conical point; malar space 1.5 as long as basal width of mandible; head mostly fulvous and without black areas; no white on pronotum, subalarum, and propodeal cristae .... *L. nasutus* (Pratt).

   Clypeus strongly convex but not pointed ventrally, the apical margin almost truncate; malar space 0.66 as long as basal width of mandible; head mostly black, sometimes with clypeus and face fulvous; white on broad anterior margin of pronotum, subalarum, and propodeal cristae .... 29. *L. leucosoma* (Cameron).

27. *Lymeon cinctiventris* (Cushman)

SPECIMENS EXAMINED: 1 female, 4 males: BENTSEN PARK (*Net:* 1 female, 29 XII '76); BOTANICAL GARDEN (*Net:* 2 males, 16 I '75; 1 male, 1 IV '75; 1 male, 24 XII '74).

HABITAT: Damp area in tall grass beneath *Salix nigra* and *Acacia farnesiana* near irrigation canal.

DISTRIBUTION: Md. to Fla. and west to Tex.

PHAENOLOGY: Valley records are for December, January and April. Farther north, *cinctiventris* flies between April and September.

28. *Lymeon orbus* (Say)

SPECIMENS EXAMINED: 3 females: BENTSEN PARK (1, 19 I '76); BOTANICAL GARDEN (1, 1 IV '75; 1, 30 XII '74).

HABITAT: Herbaceous undergrowth in dense woods.

DISTRIBUTION: N.Y. to Fla. west to Wis., Ks., Tex., and Nuevo León state of México.

GEOGRAPHIC VARIATION: Specimens from México and the Valley have the female hind coxa white with a black area above, black narrowly throughout on base, and with a large black blotch on basal half anterio-ventrally. In material from eastern North America the female hind coxa is fulvous with a more or less well developed whitish dorsal blotch.

PHAENOLOGY: Valley records are for December, January and April. Elsewhere it flies mainly from spring to fall.

29. *Lymeon leucosoma* (Cameron)

(Fig. 3)

FEMALE: *Color:* scape pale fulvous; pedicel pale fulvous to dusky; flagellum with first segment pale fulvous to dull brownish grading into blackish on apical 1/2, second and third segments black with a little brownish below, fourth black with a little white on apical 1/3, fifth through eighth white with some pale brownish below, ninth black with white on basal 1/3 above and brownish below, and succeeding segments dull brownish with some dusky staining on the more basal ones and paler apicad; head black with pale brown on mandibular condyles and face and clypeus sometimes largely stained with pale fulvous and with mandible mostly white on basal 2/3 but on apical 1/3 grading through pale brown into black; palpi whitish brown; mesosoma rather opaquely pale fulvous with some black basad in mesonotal axillary trough, a little dusky staining in some other areas, and with white broadly on all but about lateral 1/5 of front margin of pronotum, dully anteriad on tegula, on most of subalarum, vaguely toward top of mesepimeron, sometimes weakly on sides of scutellum and on postscutellum, and on propodeal cristae; gaster rather opaquely pale fulvous with slight dusky tinging; legs pale fulvous, duller on tibiae and tarsi, and dusky on fifth tarsomeres; wings hyaline, the fore wing with a median brown crossband occupying basal 1/2 of discocubital cell, extreme base of second discoidal cell, about apical 3/4 of first brachial cell and extending briefly into base of second brachial cell, as well as with a subapical brown cross band that covers apical 1/4 of radial cell, almost median 1/2 of third cubital cell, and about dorso-median 1/3 of third discoidal cell; stigma brownish white.

Length of fore wing: 4.5–5.8 mm. *First flagellomere:* 6.1–7.5 as long as deep at apex. *Clypeus:* strongly and asymmetrically convex with apical face distinctly shorter and more strongly declivous than basal. *Malar space:* 0.66 as long as basal width of mandible. *Temple:* 0.36 as long as eye at upper 1/3; moderately and directly to a little convexly receding; dully to rather strongly shining with variably developed fine micro-reticulation and more or less numerous small, obscure punctures. *Pronotum:* humeral margin scarcely swollen; epomia more or less well defined in scrobe among some other variably developed irregular wrinkles. *Mesoscutum:* notauli weakly defined on about basal 1/3 of mesoscutum and traceable almost to apex as a wide band of oblique rugosities; surface mat with fine micro-reticulation and stronger wrinkling along notauli and rearward on central lobe as well as with numerous, medium sized, shallow and obscure, mostly subadjacent or sparser punctures. *Mesopleuron:* mostly mat and rather finely reticulately wrinkled but with some discrete punctures on prepectus and on dorsal 1/3; speculum smooth and polished. *Lower metapleuron:* with rather strong reticulate wrinkling that sometimes becomes more regularly oblique ventro-posteriad. *Wing venation:* areolet 0.68–0.76 as high as part of second recurrent above bulla, first intercubitus reclivous; discoidella well developed, upper part of nervellus 1.5–1.8 as long as lower; brachiella well developed. *Fore tibia:* only slightly swollen. *Propodeum:* median part of basal groove with some sharp longitudinal ridges; spiracle 1.2 as long as wide; cristae small but strongly projecting subligulate tubercles, apical carina otherwise lacking. *First gastric segment:* postpetiole 1.3 as wide apically as long from spiracle to apex, its surface a little dully shining with well defined micro-reticulation; dorso-lateral carina traceable throughout and mostly sharp. *Second gastric tergite:* thyridium transverse; surface mat and finely reticulate with small, sparse, obscure punctures emitting short, widely spaced setae. *Ovipositor:* sheathed portion 0.34 as long as fore wing; tip 0.26 as high at nodus as long from nodus to apex and directly tapering between nodus and apex.

MALE: Unknown.

SPECIMENS EXAMINED: 4 females, USA (*Texas:* Hidalgo County, Valley Botanical Garden at McAllen, 12–27 I '74, C. C. Porter; Bentsen Río Grande Valley State Park, 19 I '76, C. C. Porter); MEXICO (*Jalisco:* Guadalajara, 17 VII '51, H. E. Evans). (Porter, Townes).

DISCUSSION: These are the first records of *leucosoma* from the United States and México, the species having been cited previously only from Guatemala (Cameron, 1886, p. 259).

A homotype from Guadalajara, México loaned by H. K. Townes differs from my Texas material only in having the tegula a little more broadly white, the sides of the scutellum white, and the postscutellum white.

One of the Valley specimens was collected in the humid "Sunken Garden" at the Valley Botanical Garden, where it was swept from weeds at the edge of a thicket dominated by *Ehretia anacua.* The other was taken at Bentsen Park along the banks of the Río Grande in *Serjania* vines beneath *Salix nigra* and *Celtis lindheimeri.*

Genus *Acerastes*

30. *Acerastes pertinax* (Cresson)

SPECIMENS EXAMINED: 87 females, 92 males: BENTSEN PARK (*Net:* 3 females, 12–13 I '76; 3 females, 19 I '76; 3 females, 18–19 III '76; 1 male, 17 VI '73; 2 females, 1–13 VI '76; 1 female, 30 VIII '76; 1 female, 7 IX '76; 2 females, 27 XII '75; 6 females, 29–30 XII '76; *Malaise* (1976): 4 males, 15–30 IV; 5 females, 10 males, 1–15 V; 1 female, 20 males, 16–31 V; 1 male, 1–15 VI; 1 female, 16–30 VI; 1 male, 1–15 VII; 1 male, 16–31 VII; 2 males, 16–31 VIII; 5 males, 1–15 IX; 1 female, 2 males, 1–15 X; 6 males, 16–31 X; 1 female, 1 male, 1–15 XI; 1 female, 1 male, 16–30 XI; 1 male, 16–31 XII); BOTANICAL GARDEN (*Net:* 1 female, 5 I '75; 1 female, 18 I '75; 1 female, 26 I '76; 2 females, 1 male, 12–21 I '76; 4 females, 1 male, 17–24 III '74; 1 female, 5 IV '75; 1 male, 16–30 V '74; 1 male, 1 VI '75; 5 males, 1 IX '76; 1 female, 18 XII '76; 9 females, 1 male, 20–31 XII '74; *Malaise* (1973): 3 females, 18 males, X; 26 females, 8 males, XI; 9 females, XII).

HABITAT: Open to dense scrub or woods with abundant ground cover of grasses, forbs, or vines; gallery woods; *Celtis lindheimeri-C. pallida* association; etc. Townes (1962, p. 405) gives the "usual habitat" of *pertinax* as "weedy fields or meadows" but it rarely enters such areas in south Texas.

DISTRIBUTION: Md. to Fla. and Tex. south to Brasil; Cuba, Jamaica.

PHAENOLOGY: Valley populations fly almost throughout the year with a spring peak in March-May and a fall maximum from September to January. Monthy totals include 11 females and 1 male for January, 7 females and 1 male for March, 1 female and 4 males for April, 6 females and 31 males for May, 3 females and 3 males for June, 2 males for July, 1 female and 2 males for August, 5 females and 6 males for September, 4 females and 26 males for October, 28 females and 10 males for November, and 25 females and 2 males for December. All but 50 of the 179 specimens were collected by Malaise Traps. *Pertinax* shows some fluctuation in abundance from year to year. Malaise Trap surveys in the '73–'74 season and in 1976 have obtained 64 and 65 specimens respectively, while hand collecting accounted for 18 specimens in '73–'74, 7 in '74–'75, 20 in '75–'76, and 5 so far in '76–'77.

In the eastern U. S. *pertinax* flies mainly during August and September but in subtropical latitudes is more or less active all year.

Genus *Polycyrtidea*

31. *Polycyrtidea limitis* Cushman

SPECIMENS EXAMINED: 17 females, 17 males: BENTSEN PARK (*Net:* 1 male, 3 I '76; 1 female, 2 males, 12–13 I '76; 3 females, 2 males, 19 I '76; *Malaise:* 1 male, 1–15 IV '76; 1 male, 1–15 V '76; BOTANICAL GARDEN (*Net:* 1 male, 7 I '75; 1 female, 2 males, 10–11 I '76; 1 male, 18 I '76; 1 female, 1 male, 18–22 I '76; 2 females, 12–21 I '74; 1 male, 16–30 V '74; 2 females, 26 XII '75; *Malaise:* 1 female, I '74; 4 females, 4 males, III '74; 1 male, XII '73); SANTA ANA NATIONAL WILDLIFE REFUGE (*Net:* 1 male, 24 XII '75).

HABITAT: Shaded, weedy places; *Serjania* vines in gallery woods; in tall grass beneath large *Celtis lindheimeri.*

DISTRIBUTION: Lower Río Grande Valley to Costa Rica.

PHAENOLOGY: Most abundant in January but flies almost throughout the year. My records include 10 females and 9 males for January, 4 females and 4 males for March, 1 male for April, 2 males for May, and 3 females and 1 male for December. Townes (1962, p. 407) gives two additional Valley records: 1 female, 30 July, Hidalgo County and 1 male and 1 female, September, Brownsville.

Limitis may vary in numbers from year to year, since 4 specimens were taken in '73–'74, 10 in '74–'75, 18 in '75–'76, and 2 in '76–'77.

Genus *Pachysomoides*

32. *Pachysomoides stupidus* (Cresson)

SPECIMEN EXAMINED: 1 female, Bentsen Park, 24 XII '75.

HABITAT: Netted from *Ulmus crassifolia* at edge of forest trail.

DISTRIBUTION: N.C. to Fla., Tex., and south to Brasil.

PHAENOLOGY: North of the Valley *stupidus* flies mostly between between August and October.

33. *Pachysomoides fulvus* (Cresson)

SPECIMENS EXAMINED: 5 females: BENTSEN PARK (*Net:* 1, 12–20 III '77; 1, 29 XII '76); BOTANICAL GARDEN (*Net:* 26 I '75; 1, 12–20 III '77; 1, 20–31 XII '73).

HABITAT: Undergrowth of well shaded woods; dense weeds in untended orange grove.

DISTRIBUTION: U.S. and southern Canada to México and Cuba.

PHAENOLOGY: North of the Valley *fulvus* is active mainly from early summer to mid-fall but, in mild years, still may be flying up to December and January as far north as Maryland, Nebraska, and British Columbia.

Genus *Messatoporus*

34. *Messatoporus discoidaloides* (Cresson)

SPECIMENS EXAMINED: 4 females, 5 males: BENTSEN PARK (*Net:* 2 females, 13–19 I '76; 1 male, 27 XII '75; 1 female, 29 XII '76; *Malaise:* 1 male, 1–15 IX '76); BOTANICAL GARDEN (*Net:* 2 males, 12–20 III '77; 1 female, 1 IV '75; 1 female, 19 XII '76).

HABITAT: Shaded places; *Serjania* vines in *Celtis-Salix* gallery woods; *Celtis lindheimeri-C. pallida* association.

DISTRIBUTION: Quebec and Minn. south to S.C. and Tex.

PHAENOLOGY: Most common in the Valley from December to early April. Farther north it flies between May and November.

Valley populations vary in abundance from year to year, as my data include no specimens for '73–'74, 1 for '74–'75, 3 for '75–'76, and 5 for '76–'77.

Genus *Agonocryptus*

35. *Agonocryptus discoidaloides* (Viereck)

SPECIMENS EXAMINED: 97 females, 133 males: BENTSEN PARK (*Net:* 1 female, 12 I '76; 3 males, 17–19 III '76; 2 males, 12–20 III '77; 2 males, 8–10 IX '76; 3 males, 29 XII '76; *Malaise* (1976): 1 male, 1–15 II; 1 female, 4 males, 15–30 IV; 1 male, 16–31 V; 5 males, 16–31 VII; 7 males, 1–15 VIII; 1 male, 16–31 VIII; 3 males, 1–15 IX; 8 males, 16–30 IX; 7 males, 1–15 X; 9 males, 16–31 X; 1 male, 1–15 XI; 1 female, 2 males, 16–30 XI; 1 female, 1 male, 1–15 XII); BOTANICAL GARDEN (*Net:* 10 females, 7 males, 12–21 I '74; 2 females, 1–15 I '75; 6 females, 16–21 I '75; 13 females, 2 males, 1–15 I '76; 10 females, 2 males, 15–24 III '74; 2 females, 28 III '75; 1 male, 15 III '76; 15 females, 16 males, 12–20 III '77; 2 females, 1 male, 2–5 IV '75; 1 female, 1 male, 17–24 V '74; 1 female, 23 VIII '73; 1 male, 30 VIII '75; 1 male, 7 IX '76; 13 females, 13 males, 20–31 XII '73; 5 females, 3 males, 20–31 XII '74; 3 females, 2 males, 23–23 XII '75; 1 female, 18 XII '76; *Malaise* (1973): 3 males, X; 3 females, 15 males, XI; 2 females, 1 male, XII '73).

HABITAT: In or at edges of moderately to deeply shaded woods, especially where there are dead trees, shrubs, or vines; sometimes abundant around fallen *Celtis lindheimeri;* in winter visits *Condalia obovata* shrubs in bright sun; on *Serjania* vines or herbaceous undergrowth in woods; often in orange groves on dead branches of frost-damaged citrus trees. Flies in open during winter and keeps to deep shade in hotter months. Males fly much more actively than females.

DISTRIBUTION: N.H. and Wis. to Fla. and south Texas.

PHAENOLOGY: Valley populations peak between December and March but show some adult activity throughout the year. Monthly totals include 36 females and 11 males for January, 1 male for February, 27 females and 24 males for March, 3 females and 5 males for April, 5 males for July, 1 female and 9 males for August, 14 males for September, 19 males for October, 3 females and 19 males for November, and 26 females and 24 males for December. Of the 230 specimens, 76 (8 females and 68 males) were obtained by Malaise Traps. *Discoidaloides* fluctuates in numbers from year to year. Malaise Trap surveys in the '73–'74 season and in 1976 have obtained 24 and 52 specimens respectively, while hand collecting yielded 66 specimens in '73–'74, 19 in '74–'75, 21 in '75–'76, and 40 in '76–'77.

North of the Valley, *discoidaloides* flies mainly between April and October.

CONCLUSIONS

Zoogeography

The 18 Valley mesostenine genera fall into three zoogeographic categories: Neotropic, Sonoran, and Holarctic. Neotropic genera are Latin American taxa with centers in the Brasilian Highlands, the Andean Cloud Forests, and the mountains of Middle America. The Sonoran group includes genera which originated along the Madro-Tertiary geoflora in the southwestern U.S. and northern México. The Holarctic element is circumpolar with maximum development in Temperate Deciduous Forests. Ten Valley genera are Neotropic: *Cryptanura, Bicristella, Diapetimorpha, Mallochia, Lymeon, Acerastes, Polycyrtidea, Pachysomoides, Messatoporus,* and *Agonocryptus;* four genera are Sonoran: *Joppidium, Lanugo, Compsocryptus,* and the *Longicaudis* group of *Mesostenus;* and five are Holarctic: *Gambrus, Trychosis,* the *Transfuga* group of *Mesostenus, Listrognathus,* and *Trachysphyrus.*

The Neotropic group requires special comment. This fauna predominates at the generic level, includes 22 of the 35 species reported, and accounts for 543 of the 679 specimens collected. Although the modern Neotropic radiation is centered in Latin American humid forests, only one of the genera cited, *Bicristella,* reaches its northern limit in the Valley; all others range farther into North America, where they inhabit principally the southeast. This northeastern group seems descended from a larger and more pervasive Middle and North American Tertiary fauna that was pushed south by Pleistocene glaciations. During glacial maxima, a few of these Neotropic elements survived in the southeastern U.S., while many retreated southwest into the more hospitable lower latitudes of Middle America. Interglacials allowed some expansion from Pleistocene refugia but the accompanying aridity in subtropic latitudes has slowed movement of moisture-loving ichneumonids. Thus, southeastern isolates have expanded with the Temperate Deciduous Forest and Southern Pine-Oak Forest as far north as Maryland or New Jersey and southwest into Texas, while some Mexican species have followed subtropical deciduous woods into Texas. However, the semiarid scrub now covering much of south Texas and northeast México has prevented massive interchange between the present-day Middle American and southeast North American Neotropic faunas.

The Valley is a comparatively humid refugium surrounded by more arid habitats and located near the southwest limit of interglacial expansion for North American Neotropic species and close to the northeast limit for most Middle American species. Its Neotropic mesostenines are thus of complex distributional affinities. Four species, *Cryptanura compacta, C. lamentaria, Lymeon leucosoma,* and *Polycyrtidea limitis,* are Middle American and range from the tip of Texas to Central America. *Cryptanura vallis, Bicristella texana, Diapetimorpha sphenos, D. aspila,* and *D. pareia* are apparently endemic to the Valley but almost certainly will be found also in México when that poorly known fauna has been better collected. *Acerastes pertinax* and *Pachysomoides stupidus* extend all the way from Brasil to the southeastern U.S. On the other hand, *Diapetimorpha picta, Mallochia agenioides, M. frontalis, Lymeon cinctiventris, Messatoporus discoidalis,* and *Agonocryptus discoidaloides* are mainly eastern North American and reach their southern limit in the Valley. *Diapetimorpha macula, D. introita, D. acadia,* and *Lymeon orbus* likewise are centered in the Atlantic and Gulf states but range south a variable distance into México and *Pachysomoides fulvus* extends over the entire U.S. and well into México. Obviously, Pleistocene alteration of glacials and interglacials, as well as wetter and drier epochs within interglacials, have produced in the Valley a multiple overlap of northern and southern Neotropic mesostenines.

Valley mesostenine genera show extremely wide affinities. *Cryptanura, Diapetimorpha, Mallochia, Lymeon, Acerastes, Pachysomoides, Messatoporus,* and *Agonocryptus* range from the northeastern U.S. to subtropical Argentina, *Polycyrtidea* from Texas and Florida to Argentina, and *Bicristella* from Texas to Argentina. The 11 Neotropic mesostenine genera represented in the eastern U.S. *all* reach Argentina. Of the 34 genera found in Middle America, 33 cover at least a large part of South America also, while only one is endemic. About 20 more Neotropic mesostenine genera are endemic to South America. The Neotropic mesostenines thus seem to have evolved in South America during the Tertiary and to have spread northward massively in those warmer and wetter times. The modern Middle American fauna, generically, is a vast sample of the South American and the North American fauna a decimated vestige of the same stock. In the Tertiary, when humid forests covered much of North America below 40 degrees N. Lat. and when temperatures there, if scarcely tropical, were milder than at present, most of the Middle American mesostenine genera probably ranged far up the Gulf and Atlantic coasts. All of these moisture rather than temperature-controlled taxa tolerate winters with repeated frosts (as shown by their present-day altitudinal and latitudinal distribution in México) and, in fact, there are few, if any, Neotropic mesostenines which are "tropical" in the sense of requiring frost-free winters. This is why a fair number of Neotropic mesostenines survived glaciation in the southeastern U.S. This is also why the Valley should be viewed not only as a present-day northern outpost of the main Neotropic fauna but also in historical perspective as an area once situated deep within the vaster Tertiary Neotropics.

Comparison with other Neotropic Deserts

Recent hand collecting surveys in the Peruvian Coastal Desert (Porter, 1975b) and net and Malaise sampling in the northeast Argentine Subandino (Porter, 1975a) allow comparison of Valley mesostenines with those of two ecologically somewhat similar areas in remote parts of the Neotropics.

The Peruvian Desert reaches from south Ecuador to north Chile on the Pacific Coastal Plain and adjacent Andean foothills of western South America. Its rainfall varies from 80 mm. per year in northern Perú to 0.5 mm. at Arica, Chile but, near the coast, massive fogs supply additional humidity. This desert is frost-free, at least on the Coastal Plain, but the cold Humboldt Current running just off shore keeps temperatures moderate (at Arica, Chile the summer day-night range is about 20–30 degrees C. and the winter range approximately 10–22 degrees C.). Thus we confront the paradox of a humid but almost rainless, cool but frost-free tropical desert.

Hand collecting during June-July of 1974–'76, mainly around Chiclayo, Trujillo, and Lima, Perú and Arica, Chile, has obtained from this desert in fertile valleys between sealevel and 2000 m. a mesostenine fauna of 12 genera and 31 species. There are nine Neotropic genera (*Biconus, Cyclaulus, Diapetimorpha, Basileucus, Lymeon, Acerastes, Polycyrtidea, Messatoporus* and *Agonocryptus*), one Pantropic genus (*Baltazaria*), two Sonoran genera (*Compsocryptus, Mesostenus* of the *Longicaudis* group), and two Holarctic genera (*Trachysphyrus, Mesostenus* of the *Transfuga* group).

Note that all these genera except *Biconus, Cyclaulus, Basileucus,* and *Baltazaria* are shared with the Valley. A simple index of affinity (Odum, 1971, p. 144) thus gives 0.606 (out of a possible 1.000) as the degree of similarity between the Valley and Coastal Desert mesostenine faunas. Actually, the real value probably approaches 0.777, since four more Valley genera (*Cryptanura, Bicristella, Mallochia,* and *Pachysomoides*) occur also in the Ecuadorian rainforests and Andean cloud forests, so that they very likely penetrate the northern fringes of the desert.

The northwest Argentine Subandino of Salta, Tucumán, Catamarca, and La Rioja provinces resembles the Valley because it is in subtropical latitudes where many Neotropic taxa approach their distributional limits. However, the Subandino differs from the Valley by its inland location and relatively high altitude (study sites between 900 and 2000 m.). Thus it has a much cooler temperature regimen that includes frequent winter frosts (annual average temperature 13–15.5 degrees C. vs. 23.4 degrees C. for the Valley). Moreover, the Subandino is a genuine semidesert with only 80–250 mm. of rain per year (vs. 669 mm. for the Valley).

Three years' use of 10 Malaise Traps and frequent collecting trips at all seasons between 1966 and 1972 obtained from the northwest Subandino a mesostenine fauna of 10 genera and 33 species, including seven Neotropic taxa (*Dotocryptus, Diapetimorpha, Basileucus, Polycyrtidea, Polycyrtus, Messatoporus,* and *Agonocryptus*), two Sonoran genera (*Compsocryptus* and *Mesostenus* of the *Longicaudis* group), and two Holarctic genera (*Trachysphyrus* and *Mesostenus* of the *Transfuga* group). Considering *Polycyrtus* almost certainly present in the Valley (it is in the eastern U.S. and northeast México), we get for the Valley and the Subandino a similarity index of 0.580, one surprisingly high for two localities separated by about 42 degrees of latitude. In fact, since the Valley genera *Cryptanura, Bicristella, Mallochia, Pachysomoides,* and *Joppidium* reach at least the borders of the Subandino in northwest Argentina, the index of similarity eventually could prove as high as 0.8000.

With regard to the Neotropic element, the above comparison of south Texas, coastal Peruvian, and Subandean mesostenines, only reemphasizes the vast South and Middle American distributions of so many of these genera. Species, of course, differ widely from place to place but at the generic level we find remarkable similarity between faunas as distant as the south Texan and the northwest Argentine. This correspondence between Texan, Peruvian, and Argentine arid-adapted mesostenine communities also shows that the same versatile genera tend to survive anyplace in Middle and South America where local conditions become dry enough to eliminate the wet forests which are the optimum habitat for most Neotropic mesostenines. Almost equally, it suggests a correlation between dry and cold tolerance, since nine of the ten Neotropic genera that reach well north in the eastern U.S. also occur in one or more of the dry areas studied (*Cryptanura, Polycyrtus, Diapetimorpha, Lymeon, Mallochia, Acerastes, Pachysomoides, Messatoporus,* and *Agonocryptus*).

Sonoran mesostenines also show much affinity among the three study areas. These genera are centered in México and the southwestern U.S. and evolved there in response to increased aridity and orogeny which affected that region in the latter half of the Tertiary. The Valley has four Sonoran taxa (*Joppidium, Lanugo, Compsocryptus,* and *Mesostenus* of the *Longicaudis* group) and two of these, *Compsocryptus* and the *Longicaudis* group of *Mesostenus,* are the only Sonoran mesostenines known from the Peruvian Desert and the Subandino. However, *Lanugo* reaches the Peruvian Andes and so might be found on the coast and *Joppidium* possibly enters both deserts, since it is known from Ecuador and turns up again in the Argentine Chaco. Most of these genera favor semiarid habitats, from thorn scrub to subtropical deciduous forests, and doubtless extended their distributions in the driest parts of the Tertiary and during interglacial xerothermic episodes. The present moderately wet interglacial has produced some notable Sonoran disjunctions, such as the above-mentioned case of *Joppidium* and that of *Compsocryptus,* which has many species in the western U.S. and México, a single representative in Florida and Cuba, an isolated species in the Peruvian Coastal Desert, and another disjunct species in northern Argentina.

The Holarctic element, consisting mainly of genera adapted to temperate forests, shows more discontinuities among Middle and South American arid zones than do the Sonoran and Neotropic faunas. *Gambrus, Trychosis,* and *Listrognathus* reach only as far south as the Valley or northern México. On the other hand, *Trachysphyrus* and the *Transfuga* group of *Mesostenus* occur in all three study areas. The *Transfuga* group is mainly Holarctic and Andean, reaching its austral limit in northern Argentina and including only three or four South American species. *Trachysphyrus,* in contrast, has a big Holarctic fauna plus a massive endemic South American radiation of more than 150 species centered in mountainous and/or semiarid to arid parts of the southern half of the continent. Thus the Subandino has 21 *Trachysphyrus,* the Coastal Desert 12, but the Valley only one. Interestingly, the south Texan species, *T. mesorufus,* is a member of the *Planosae* group, the only *Trachysphyrus* stock of South American origin to have invaded Middle and North America. The heterogeneous distributional patterns of Holarctic genera represented in the Valley show that this element has penetrated Middle and South America in different expansions at widely separated times. *Trachysphyrus,* because of its huge endemic South American fauna, probably had reached the southern continent by the middle or late Tertiary (Raven and Axelrod, 1975, p. 422 point out that even by the late Cretaceous the "northern Andes" were "beginning to approach their modern configuration" and thus could have served all through the Tertiary as a suitable habitat for temperate-adapted genera invading from the north.). The *Transfuga* group of *Mesostenus,* mainly Holarctic and in South America practically confined to the Andean region excluding Chile, doubtless moved south with Pleistocene glaciations. Finally, *Gambrus, Trychosis,* and *Listrognathus,* which only reach northern México perhaps were pushed as far as the Valley only by the most recent and severest Wisconsin glaciation.

PHAENOLOGY

Hand collecting and Malaise Trap records of Lower Río Grande Valley mesostenines obtained between June 1973 and March 1977 are summarized in Table 1.

Since hand collecting was possible only between 25 August-9 September, 18 December-25 January, 11–12 March (1–8 April in 1975) and 16 May-10 June, the data furnished in Table 1 show strong bias toward those periods. Fieldwork during February, October, and November, in particular, doubtless would have shown that these months have much larger mesostenine faunas than suggested in the table. Nonetheless, the phaenology emerges as unimodal and invernal with an impressive peak that extends from December to March and includes 390 of the 679 specimens and

TABLE 1. PHAENOLOGY OF VALLEY MESOSTENINES

(Unbracketed numbers indicate net and Malaise Trap totals for each month; numbers in parenthesis the results of the 1976 Malaise survey in Bentsen Park.)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC
1. *G. bituminosus*	—	—	—	—	—	—	—	—	—	—	—	1
2. *G. ultimus*	4	—	—	—	—	—	—	—	—	1(1)	—	1
3. *T. subgracilis*	1	—	—	2(2)	—	—	—	—	—	—	—	—
4. *T. mesorufus*	—	—	—	1	—	—	—	—	—	—	—	—
5. *J. brochum*	1	—	—	—	—	—	—	—	—	—	—	—
6. *J. rubriceps*	—	—	—	1	—	—	—	—	—	—	—	—
7. *L. picta*	24	—	1	1	—	—	—	—	—	—	—	11
8. *C. texensis*	6	—	6	6	1	—	—	—	—	—	—	13
9. *C. compacta*	—	—	1	—	—	—	—	—	—	—	—	—
10. *C. vallis*	—	—	—	—	—	—	—	—	—	—	—	1
11. *C. lamentaria*	—	—	—	—	—	—	—	—	—	—	—	1
12. *M. gracilis*	—	—	4	2(1)	—	—	—	—	—	—	—	—
13. *M. opuntiae*	1	—	—	—	—	—	—	—	—	—	—	—
14. *M. longicaudis*	—	—	5	1	1(1)	—	—	2	3	—	—	—
15. *B. texana*	—	—	—	—	—	—	—	—	—	—	—	1
16. *D. macula*	—	—	2	—	—	1	—	—	13	2	—	3
17. *D. sphenos*	—	—	—	—	1(1)	—	—	—	—	1	2(1)	—

Table 1 (Cont.)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC
18. *D. picta*	—	—	2	—	—	—	—	—	—	—	—	—
19. *D. aspila*	—	—	—	—	—	—	—	—	—	—	—	1
20. *D. pareia*	1	—	—	1(1)	—	—	—	—	—	—	—	—
21. *D. introita*	1	—	14	1	1	—	—	1	4	1	—	4
22. *D. acadia*	—	—	4	—	—	—	—	—	—	—	—	1
23. *L. rufitibialis*	8	—	3	—	1	—	—	—	—	—	—	10
24. *M. agenioides*	2(1)	3(3)	—	2(2)	—	—	—	1(1)	2(2)	—	—	—
25. *M. frontalis*	—	—	—	—	—	—	—	—	1(1)	—	—	—
26. *L. cinctiventris*	2	—	—	1	—	—	—	—	—	—	—	2
27. *L. orbus*	1	—	—	1	—	—	—	—	—	—	—	1
28. *L. leucosoma*	2	—	—	—	—	—	—	—	—	—	—	—
29. *A. pertinax*	12	—	8	5(4)	37(36)	6(2)	2(2)	3(2)	11(5)	30(9)	38(4)	27(1)
30. *P. limitis*	19	—	8	1(1)	2(1)	—	—	—	—	—	—	—
31. *P. stupidus*	—	—	—	—	—	—	—	—	—	—	—	1
32. *P. fulvus*	1	—	2	—	—	—	—	—	—	—	—	2
33. *M. discoidalis*	2	—	2	1	—	—	—	—	1(1)	—	—	3
34. *A. discoidaloides*	47	1(1)	51	8(5)	1(1)	—	5(5)	10(8)	14(11)	19(16)	22(3)	50(2)
Total spp./month	18	2	15	14	9	2	2	5	8	6	4	20
Total specimens/month	135	4	113	41	49	7	7	17	49	55	64	138

30 of the 34 species collected. Only *Trachysphyrus mesorufus* (April), *Joppidium rubriceps* (April), *Diapetimorpha sphenos* (May, October, November), and *Mallochia frontalis* (September) were collected exclusively outside that period. Actually, December and January are the optimum months and yielded 273 specimens and 26 species, of which 23 species became most abundant at that time while three others overlapped into December or January from earlier or later maxima (*Diapetimorpha macula* peaks in September, *D. introita* in March, and *Acerastes pertinax* in May and November). Finally, four species peak in late winter or early spring and/or fall but appear to avoid the early winter (*Cryptanura compacta* in March, *Mesostenus gracilis* in March-May, *M. longicaudis* in March-May and August-September, and *Diapetimorpha picta* in March). Thus there is a large late fall and early winter fauna plus a much smaller exclusively late winter and early spring or spring-fall assemblage, but only minimal activity, and no exclusive species, during the hottest months of June, July, and August. This summer hiatus is demonstrated by the 1976 Malaise survey in Bentsen Park and by exhaustive hand collecting each year in late May and early June and again in the last week of August and the first 9 or 10 days of September. Moisture-loving ichneumonid adults avoid the extreme heat of subtropical summers and attain maximum abundance during the cooler months of the year, when they are less endangered by evaporative water loss and when there are many lepidopterous and coleopterous larvae and pupae to parasitize.

As shown in Table 1, the Bentsen Park Malaise Trap collected a meagre sample of only 12 species and 138 specimens in all of 1976, and one characterized by mid-spring (April-May) and early fall (September-October) peaks of abundance with relatively few specimens captured in December-March and again in June-July. This result derives from the trap's location in cool, humid woods under the deep shade of a large *Pithecellobium*. During winter, woodland mesostenines fly in sunny clearings and at the forest edge but, in warmer parts of the year they increasingly seek the protection of deep shade.

Most Valley ichneumonids fly synchronously in climatically favorable periods. My data do not suggest temporal differentiation of closely related species. This agrees with the general observation that ichneumonids, as parasitoids, mainly avoid competition by rather minute spatial and size differences in host selection. Each species exploits a series of hosts that may be taxonomically diverse but which occurs in a particular micro-habitat and falls within definite size limits.

Reference to the preceding discussions of abundant species, such as *Lanugo picta, Compsocryptus texensis, Acerastes pertinax,* and *Agonocryptus discoidaloides,* shows phaenological variation from year to year as well as from month to month within any given year. Such fluctuations probably result from the variable climate of the Valley (as discussed in the Introduction to this study). Sporadic "killing frosts," which occur about once a decade, devastate some of the Valley's subtropical biota but probably have little effect on ichneumonids. Indeed, mesostenines often become strikingly more abundant in the first warm days after a freeze, suggesting that low temperatures may be necessary to break their diapause. Furthermore, Valley ichneumonids are perfectly adapted to the numerous 4–10 day periods of cloudy, drizzly, cold weather (8–10 degrees C.) triggered in winter by passage of wet cold fronts, since they begin to fly immediately and abundantly within minutes after the sun finally breaks through and temperatures exceed 15 or 16 degrees C. Therefore, it is probably the Valley's unpredictable and often lengthy droughts which exercise the most rigorous density independent control on populations of these hygrophile insects.

Finally, we have some data that permit comparison of Valley mesostenine phaenology with that of other New World subtropical communities.

My three year net and Malaise survey of Mesostenini in the northwest Argentine Subandino (Porter, 1975a) produced 21 species and 38 specimens for January, 14 species and 20 species for February, 8 species and 14 specimens for March, 8 species and 12 specimens for April, no records for May, 2 species and 2 specimens for June, 3 species and 3 specimens for July, 1 species and 1 specimen for August, 7 species and 32 specimens for September, 8 species and 20 specimens for October, 7 species and 9 specimens for November, and 17 species and 32 specimens for December. Subandean mesostenines thus peak in summer (December-February), decrease gradually during autumn (March-April), practically disappear in late fall and winter (May-August), and then build up more or less progressively in spring (September-November). The Subandean summer is warm and most of the year's rain falls between September and April, while the winter months are almost rainless and bring repeated killing frosts. Rainfall and temperature thus regulate the seasonal cycles of both Subandean and south Texan mesostenines but the annual climatic pattern is totally different in each area, producing an invernal peak in the Valley and a vernal maximum in the Subandino.

During 1973, I maintained a Malaise Trap at General Saavedra near Santa Cruz de la Sierra, Bolivia. Saavedra lies at about 18 degrees S. Lat. and less than 400 m. altitude toward the humid extreme of an ecotone between Chaco scrub and the southernmost Amazon Basin rainforest. My trap was in wet forest under deep shade of cecropias, palms, philodendrons and other "tropical" flora. Monthly Malaise records for Saavedra include 6 species and 8 specimens for January, 3 species and 4 specimens for February, 3 species and 3 specimens for March, (April sample lost), 4 species and 8 specimens for May, 8 species and 9 specimens for June, (July sample lost), 19 species and 35 specimens for August, 5 species and 11 specimens for September, 5 species and 6 specimens for October, 9 species and 18 specimens for November, and 2 species and 4 specimens for December. Furthermore, hand collecting at Saavedra in July yielded 41 species and more than 100 specimens of Mesostenini. This fauna consequently peaks during mid-winter and is much scarcer at other times of the year, showing considerable phaenologic resemblance to the Valley fauna. I have no weather data for Saavedra but infer from its flora that the area receives at least 1500 mm. of rain per year. Summer is the warmest and wettest season but all months have significant precipitation and the winter, although relatively dry, is punctuated repeatedly by cold fronts that may bring 5–10 days of persistent drizzle. July and August temperatures range from nightly lows of 10–15 degrees C. to daily highs of around 30 degrees C. but cold fronts may bring minima of 3 degrees C. with mid-day maxima of no more than 12 degrees C. Summer temperatures probably show an average daily range of 25–38 degrees C. The Saavedra climate thus is a little warmer and much wetter than that of the Valley but shows much the same type of variation from month to month and, evidently, has a rather similar effect on the ichneumonids under its control.

HABITAT SELECTION

Of the 34 Valley mesostenine species collected, 21 were taken only in partly to densely shaded woods with considerable undergrowth and particularly in areas covered by *Serjania* vines. Of these, five occurred exclusively in *Salix-Celtis-Fraxinus* gallery woods (*Cryptanura compacta, C. vallis, C. lamentaria, Bicristella texana,* and *Diapetimorpha picta*) while the other 16 generally inhabited not only gallery woods but also the *Celtis lindheimeri-C. pallida* association, *Pithecellobium* thickets, and other comparatively dense types of woods. Perhaps significantly, of the five species limited to gallery woods, all but *Diapetimorpha picta* are tropical forms unrecorded north of the Valley. Some or all of these thus really may prove restricted to the narrow zone of slightly warmer and much more humid micro-climate immediately along the Río Grande.

Semi-open fence rows and woods-edges yielded eight species: *Joppidium brochum, Lanugo picta, Compsocryptus texensis, Diapetimorpha introita, D. acadia, Listrognathus rufitibialis, Pachysomoides fulvus,* and *Agonocryptus discoidaloides.* Only one of these, *J. brochum,* appeared exclusively in this habitat. *A. discoidaloides* also was found abundantly in deep woods while *D. acadia* was collected both in deep woods and open fields. The other five species were shared with open fields only.

Open sunny, weedy, or grassy places provided nine species: *Gambrus bituminosus, Joppidium rubriceps, Lanugo picta, Compsocryptus texensis, Mesostenus longicaudis, Diapetimorpha introita, D. acadia, Listrognathus rufitibialis* and *Pachysomoides fulvus* but only *G. bituminosus, J. rubriceps,* and *M. longicaudis* were taken exclusively from this kind of habitat. It should be noted that the one specimen of *G. bituminosus* occurred in a sandy area near the Río Grande and that *bituminosus* in other parts of its range also seems associated with river banks, lake shores, and sea shores.

With regard to other habitats, *Trachysphyrus mesorufus* was the only mesostenine found in xeric *Celtis pallida-Condalia obovata* scrub and *Mesostenus opuntiae* the single species collected in the even drier *Prosopis-Opuntia* association.

The Valley mesostenine fauna thus includes an exclusively or primarily sylvan component of 21 species plus a smaller series of 12 species that shows a variably marked preference for drier and more open habitats. Logically, the Neotropic element predominates in humid situations while the Sonoran genera are conspicuous in and mostly restricted to woods-edge or field habitats. However, the Neotropic genus *Diapetimorpha* shows differentiation into both habitats, with *D. introita* and *D. acadia* mostly in woods-edges and fields and the other five species confined to woods.

Finally, it should be emphasized that few, if any, Valley mesostenines show definite association with an individual plant species or plant community. Mesostenines generally are so versatile in host selection that each one may occur in almost any physically suitable environment with appropriate vegetation structure, irrespective of the taxonomic composition of the local flora.

DIVERSITY

The first component of diversity is richness or number of taxa inhabiting a particular region. In this study, I have reported 18 genera and 35 species of Mesostenini from the Valley. As already noted, that number agrees rather well with faunas of other arid Middle and South American localities, such as the Peruvian Coastal Desert, with 10 genera and 31 species, or the Argentine Subandino, with 10 genera and 33 species. All these habitats are too xerothermic for optimum mesostenine radiation and contain only a moderate amount of niche space in their simply stratified herbaceous and shrub or herbaceous, shrub, and small tree layers. On the other hand, humid, multilayered subtropical and tropical forests may have seven or eight times the number of mesostenine species present in even nearby deserts. For example, the north Argentine wet forests, Selva Tucumano-Boliviana and Selva Misionera, of which the former in places practically interdigitates with the Subandino, have yielded in 10 years of net and Malaise collecting 40 genera and 237 species of mesostenines. I do not yet have similar data for the northeast Mexican wet forests, which extend along the Sierra Madre Oriental to within 200 km. of the Lower Río Grande Valley, but the fact that five days' hand collecting in a humid ravine at Cola de Caballo near Monterrey (31 May-4 June 1974) produced 12 mesostenine genera (*Glodianus, Lymeon, Rhinium, Toechorychus, Cryptanura, Bicristella, Polycyrtus, Messatoporus, Cestrus, Joppidium, Listrognathus,* and *Baltazaria*) suggests that the difference in mesostenine richness between these localities and south Texas eventually will prove similar to that already documented between the Argentine Subandino and its nearby subtropical forests.

A second component of diversity is the apportionment of individuals among species, often referred to as evenness or equitability. As shown by the following data as to number of specimens collected and percent of total collection, the Valley mesostenine fauna has two extremely common species, six that may be considered moderately scarce, and 26 which are rare to very rare:

1. *A. discoidaloides* — 230, 34.4%
2. *A. pertinax* — 179, 27.7%
3. *L. picta* — 37, 5.5%
4. *P. limitis* — 34, 5.1%
5. *C. texensis* — 32, 4.8%
6. *D. introita* — 27, 4.0%
7. *L. rufitibialis* — 22, 3.3%
8. *D. macula* — 21, 3.1%
9. *M. longicaudis* — 11, 1.6%
10. *M. agenioides* — 10, 1.5%
11. *M. discoidalis* — 9, 1.3%
12. *G. ultimus* — 8, 1.2%
13. *M. gracilis* — 6, 0.9%
14. *D. acadia* — 5, 0.7%
15. *L. cinctiventris* — 5, 0.7%
16. *P. fulvus* — 5, 0.7%
17. *D. sphenos* — 4, 0.6%
18. *L. orbus* — 3, 0.4%
19. *T. subgracilis* — 3, 0.4%
20. *D. pareia* — 2, 0.3%
21. *D. picta* — 2, 0.3%
22. *L. leucosoma* — 2, 0.3%

Each of the 12 mesostenines not listed above was collected only once during my five year survey, so that 35% of this community consists of very rare species.

Partially similar equitability data emerge from my three year study of mesostenines in the northwest Argentine Subandino. Here, 12 of the 33 species collected (36%) were represented by a single specimen each, so that the percent of very rare species in the Subandino and the Valley faunas is almost identical. However, of the other 21 Subandean species, two each accounted for 15% of the total number obtained, 1 for 11%, 1 for 7.1%, 1 for 5.9%, 2 for 4.7% each, 1 for 4.1%, 2 for 2.9% each, 3 for 2.4% each, 5 for 1.8% each, and 2 for 1.2% each. The Subandean fauna thus has greater equitability than the south Texan in that specimens are apportioned more evenly among the commoner species. Here the two most abundant species, *Trachysphyrus doddi* and *Basileucus* sp., together account for 26 specimens each or 30% of all specimens obtained, while the two most common Valley mesostenines make up 62.4% of the total for their region. Moreover, mesostenines in general are much rarer in the Subandino than in the Valley. The entire Subandean sample was only 169 specimens (56 per year), while that from the Valley totalled 679 specimens (135 per year). Thus the Subandean fauna is numerically small and composed entirely of scarce to very rare species while the south Texas fauna is numerically larger and contains several genuinely common mesostenines.

It would be desirable to compare equitability figures for the semiarid Valley and the arid Subandino with data from a comparable long-term survey of mesostenines in some optimum Neotropic wet forest habitat. Although complete information of this type is not yet available, results of my 10 month 1973 Malaise project at General Saavedra, Bolivia may be taken as fairly typical for a humid forest community. At Saavedra, 27 (64%) of the 42 species trapped were represented by one specimen each, so that there are almost twice as many very rare species at Saavedra as in the Subandino or south Texas. Of the additional 15 Saavedra mesostenines, 1 accounted for 10.4% of the total number obtained, 1 for 9.4%, 2 for 7.3% each, 1 for 4.1%, 3 for 3.1% each, and 6 for 2.1% each. This fauna thus shows even more equitability of commoner species than the Subandino. The two most abundant Saavedra mesostenines, *Diapetimorpha* sp. 3 and *Agonocryptus* sp. 1, together account for 10 and 9 specimens respectively, or only 20% of all specimens obtained. On the other hand, 96 specimens were trapped at Saavedra during 10 months and this shows much greater overall abundance than the Subandino records (56 specimens per year by Malaise Traps *and* net), being roughly comparable to my 12 month Bentsen Park Malaise catch of 138 specimens. The Saavedra fauna thus is numerically large but composed entirely of scarce to very rare species.

We can only speculate why evenness shows such marked differences among the three mesostenine communities studied. Saavedra with its many rare species has a benign, thermically and pluvially rather stable climate and the trap employed there was situated in a large patch of undisturbed wet forest, Such environments, where severe physical stress is absent, traditionally are supposed to accommodate large numbers of species in a complex variety of niches determined mainly by selective pressure of interspecific competition. Under these circumstances, reproductive success is less important than niche differentiation for avoidance of competition and many groups are represented by many species, each one of which may be relatively uncommon. Toward the other extreme of the equitability scale, stressed environments have fewer species, some of which are rare since they exist at the limits of their ecological tolerance while others may be disproportionately abundant because some special adaptation allows them to survive the burden of the stress, so that they flourish in a context of minimal competition. On the other hand, drastically stressed habitats, where the main selective pressure is toward mere survival, may have few species, none of which is outstandingly abundant. The arid Subandino, with its relict mesostenine populations surviving in scattered humid refugia, doubtless approximates this last model. Finally, the Lower Río Grande Valley, because of its moderately large fauna including many scarce and two superabundant species, seems consistent with the penultimate case. Here the main natural stress is rather low and very irregularly distributed rainfall but to this are added the potent anthropogenic factors of habitat destruction and pesticide contamination. Very little natural flora remains in the Valley and the existing parks and wildlife refuges are surrounded by heavily sprayed citrus groves, truck farms, and other crop systems. Under these conditions, it is not surprising that a few exceptionally tolerant species, such as *Agonocryptus discoidaloides,* which can thrive in disturbed as well as natural areas, have attained unusually high abundance.

REFERENCES

CAMERON, P.

1886. Biologia centrali-americana Insecta. Hymenoptera. Vol. 1, p. 1–466.

CUSHMAN, R. A.

1930. New species of ichneumon-flies and taxonomic notes. U. S. Natl. Mus. Proc. **76**(25): 1–18.

1931. Notes on ichneumon-flies of the genus *Polycyrtus.* U. S. Natl. Mus. Proc. **78**(14): 1–62.

ODUM, E. P.

1971. Fundamentals of Ecology. Third Edition, p. 1–574. W. B. Saunders.

PORTER, C. C.

1974. A new *Trachysphyrus* of the *Planosae* group from Florida. Florida Entomologist **57**(3): 331–335.

1975a. Relaciones zoogeográficas y origen de la fauna de Ichneumonidae (Hymenoptera) en la provincia biogeográfica del Monte del Noroeste Argentino. Acta Zoologica Lilloana **31**(15): 175–252.

1975b. Mesostenini of the Peruvian Coastal Desert. In press in National Geographic Research Reports for 1975.

RAVEN, P. H. & AXELROD, D. I.

1975. History of the Flora and Fauna of Latin America. American Scientist **63**(4): 420–429.

TOWNES, H. K.

1962. Ichneumon-flies of America north of México: 3. Subfamily Gelinae, Tribe Mesostenini. Bull. U. S. Natl. Mus. **216,** pt. 3, p. 1–602.

1966. A catalogue and reclassification of the Neotropic Ichneumonidae. Mem. Amer. Ent. Inst. **11:** 1–367.

1972. A light-weight Malaise Trap. Entomological News **83**(9): 239–247.

TAXONOMY OF UNITED STATES *LEUCOCHRYSA* (NEUROPTERA: CHRYSOPIDAE)*

BY PHILLIP A. ADAMS
Department of Biological Sciences
California State University
Fullerton, California 92634

This paper is one of a projected series dealing with the taxonomy and identification of United States Chrysopidae. Both of our species of *Leucochrysa* prove to range well into the tropics, where the genus is diverse and abundant.

Bickley and MacLeod 1956 discuss at length the history and possible validity of *Allochrysa.* Banks 1903 separated *Allochrysa* from *Leucochrysa* on the basis of its having a quadrangular rather than a triangular intramedian cell, despite the fact that *L. varia,* the type species of the genus, also has a quadrangular cell. This oversight was rectified by Navás 1917, who correctly synonymized *Allochrysa* with *Leucochrysa,* and erected the genus *Nodita* for the species with a triangular intramedian cell, previously placed in *Leucochrysa* by Banks. Banks followed Navás' usage for tropical species, but inexplicably continued referring all the U. S. species to *Allochrysa.* Bickley and MacLeod took a non-committal stand, justifying retention of *Allochrysa* by suggesting that characters might someday be found which show that these genera are distinct. My examination of many neotropical species has not turned up any such characters. Banks himself referred the Antillean population of *L. insularis* to *Leucochrysa,* and the United States population of the very same species to *Allochrysa.* There appears to be no basis whatever for the continued recognition of *Allochrysa.* It may be superfluous to point out that since *L. insularis* is the type species of both *Protochrysopa* Kolbe 1888 (by monotypy) and *Allochrysa* Banks 1903 (*L. virginica,* by original designation), these genera are synonymous.

In the tropics, the genus *Nodita* merges with *Leucochrysa.* Thus far, the only characters useful for its separation are the venational ones discussed by Banks 1945, which have proved variable and unreliable in many cases, as Banks himself was aware. An example

---

**Manuscript received by the editor June 5, 1977*

is *Leucochrysa risi* Navás, in which many specimens have an intramedian cell resembling that of *Nodita;* this species could be assigned to either genus equally well. The case of *L. negata* is comparable (see below). Species of *Nodita* and *Leucochrysa* from the United States, however, can be separated with fair reliability by the form of the intramedian cell.

Occasional aberrant specimens of other genera with a quadrangular intramedian cell may mistakenly be referred to *Leucochrysa* if other characters are not considered. This is exemplified by *Allochrysa parvula* Banks 1903: 143, the unique type of which is *Chrysopa lineaticornis* Fitch: No data, (Runnymede, Fla., according to description) male, MCZ 11405, *"C. columbiana,* det. E. G. MacLeod" (new synonymy).

The genitalia of both sexes of *Leucochrysa* are fully illustrated here for the first time. In the male, the eighth sternite is more or less distinctly demarked from the ninth; sternites except ninth usually with microtholi. Tignum, gonapsis and gonocristae are absent. The mediuncus (=arcessus) usually bears a small curved median tooth or hook flanked by notches (Fig. 10, 11), no entoprocesses (gonocoxites). In the female, subgenitale small, or entire area posteriorly to seventh sternite broadly sclerotized (*insularis, arizonica, singularis*), ventral pit sometimes far anteriorly (*insularis, arizonica*) or on a separate sclerite (*internata*). Spermatheca pillbox-shaped as in *Chrysopa,* or more frequently elongate and bent (*internata, dolichocera*), spermathecal duct short (*insularis, arizonica*) to extremely elongate (*internata, angrandi*), bursal duct sometimes elaborated (*magnifica*), two bursal glands.

The female genitalia, although tedious to prepare for examination, are surprisingly diverse, offering excellent taxonomic characters. It is imperative that preparations of critical specimens retain the copulatory bursa with its glands, ducts, and connection to the spermatheca intact. Removal of the spermatheca destroys the associated structures, and should be avoided if at all possible.

Leucochrysa colombia Banks
Figures 1–4

Allochrysa colombia Banks 1910: 150. A specimen from "Sta. Margarita, W. Colombia, July, 2700 m" MCZ No. 11999 (not dissected) is designated lectotype. A "cotype" female from Canon del Monte Tolima, Colombia, 1700 m, in the BMNH is designated a paratype. *Leucochrysa colombia,* Banks, 1944: 32.

Leucochrysa claveria Navás 1927. Banks 1944: 135 (synonymy). Although the type could not be located in the Navás collection in 1974, the description is sufficiently complete to indicate Banks' action is probably correct.

Leucochrysa californica Navás 1928: 235, new synonymy. Holotype: "California", Riksmuseum, Stockholm, female. *Allochrysa californica,* Banks 1938: 122. *Allochrysa virginica* (incorrectly), Bickley and MacLeod, 1956: 184.

The identity of *L. californica* has long been a puzzle, as Navás' description does not fit any known species from the United States. The specimen proved to be heavily plastered with moth scales, accounting for his incomplete description of the head markings. The printed label "California" dates from the late nineteenth century (Per Inge Persson, pers. comm.), and perhaps replaced an original handwritten label, now lost, such as "Col" or perhaps even "Cali". As this species is otherwise known only from Colombia, we may presume that the type originated there also.

Description. Head (Fig. 4) pale, labrum, clypeus and frons suffused with wine red; red genal stripe present; on vertex a dark blackish red V-mark bordering the antennal fossae, jointed posteriorly by a pair of slender transverse red marks; membrane of fossae pink or red suffused. Scapes dorsally suffused with blackish red, bearing medial black stripe; pedicel black ringed, short anterior blackish red, flagellar stripe. Pronotum pale yellow green, anterior corners pink suffused, occasionally with two small brown spots. Abdominal tergites 6 and 7 heavily black-marked. In the forewing, the inner gradate series extends far distally, intersecting all but one to three "intermediates" (branches of Rs extending from Rs to pseudomedia, and appearing almost as crossveins). Costal area broad, tallest cell 4.3 times as tall as wide, marginal fork opposite outer psm crossvein, 5 times as long as wide. Dark spot surrounding the outer psm crossvein, and 6 or 7 crossveins near the center of the outer gradate series are dark, narrowly brown bordered. Forewing 23.5 mm long. In female, subgenitale (Fig. 1) narrow, bearing a small pit on the inner anterior surface. Copulatory bursa (Fig. 2) small, bursal duct delicate, moderately long, two bursal gland ducts; spermatheca pillbox-shaped, duct short (Fig. 3).

This species is easily recognized by the inner gradate series extending far basally, broad wings with long costal and marginal cells, and head markings.

Leucochrysa arizonica (Banks)
Figures 5–9, 17–18

Allochrysa arizonica Banks 1906: 98. Holotype: Palmerlee, Ariz., July, male, M.C.Z. No. 11403 (not dissected). Banks 1938: 122; Bickley and MacLeod 1956: 184.

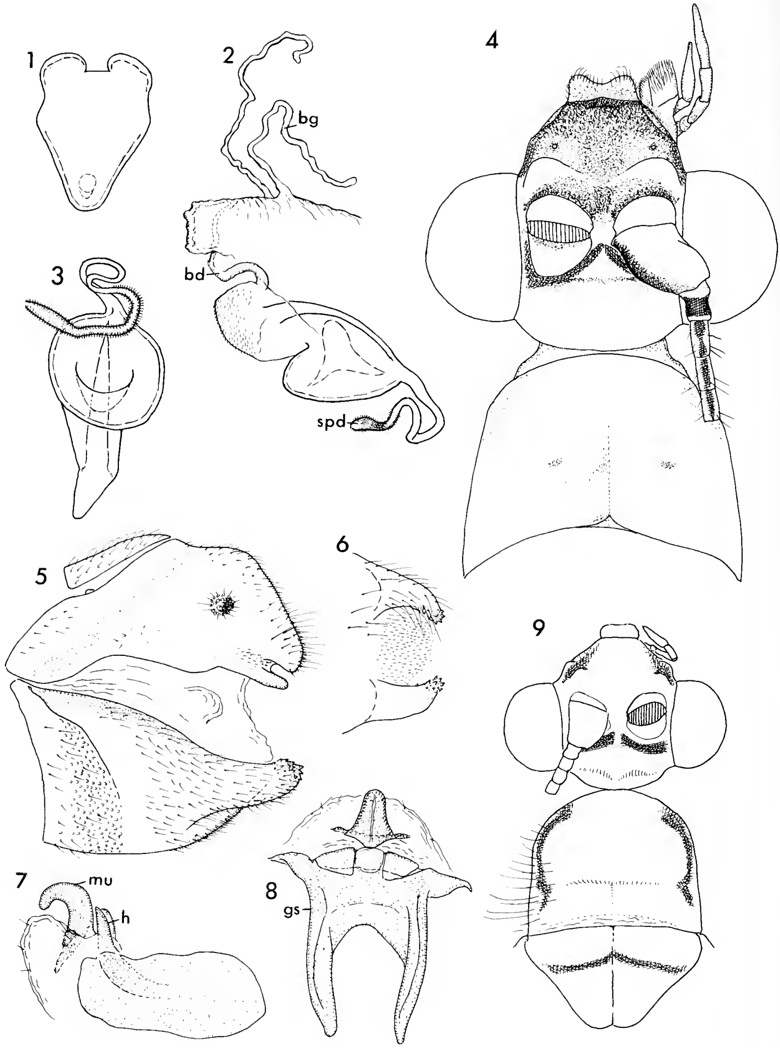
Head, palpi, antennae pale except red marks on gena, vertex, pronotum, mesoprescutum, as in Figure 9. Wings pale, forewing with short red-black marks on middle of several costals, and on anals, pseudocubitals, marginal forks behind pseudocubitus, pseudomedials, basal radials and branches of Rs. First two medial crossveins wholly red, gradates brown. Membrane suffused with brown at basal inner gradate, and at distal pseudomedial crossvein; no brown spot at base of stigma. Height of tallest c-cells 3.0 times width, 19–20 radials, 11–12 inner gradates, series follows psm basad, proximal inner gradate nearly perpendicular to and ending on psm; 10–11 outer gradates, marginal fork nearest last pseudomedial crossvein 5.6 times as long as wide; 10 apparent pseudomedial crossveins, distal crossvein oriented as an extra outer gradate. Hind wing veins pale, dark spot at base of stigma.

Male: sternites 2–8 with microtholi (Fig. 5); sternite 9 bears a pair of denticulate forcipate processes; a field of small microtrichia posteriorly. Ectoprocts notched, ventral lobe hairless; callus cerci black posteriorly. Gonarcus (Fig. 7–8) heavily sclerotized, 3 thin plates form low hood above bluntly hooklike mediuncus; gonosetae sparse, small.

Female: Subgenitale (Fig. 17, 18) as broad as seventh sternite, conspicuously exposed even in dried material, shiny red-brown, laterally bearing downturned angular process; apical pit deep, bordered by two thin nearly vertical ridges. Dorsally to the subgenitale, membrane surrounding oviducal opening and forming floor of copulatory bursa expanded and tanned. Spermatheca pillbox shaped. Copulatory bursa much as in *L. insularis.*

Specimens examined: Arizona: Santa Rita Mts., Madera Can., 12–13–VI–1968, female, Menke and Flint, USNM. Mexico: Michoacán, Jct Hwy 4 and Huetamo Rd., 15 mi. E. Morelia, 8–VII–1947, male, T. H. Hubbell (Univ. of Michigan); Jalisco, Ajijic, 16–18–VII–1966, Flint and Ortiz, 6 specimens (USNM and PAA).

This is a much more robust insect than *L. insularis,* easily recognized by the color markings of the head, and unusual external



Figures 1–4. *L. colombia* (holotype of *L. californica*). Fig. 1, subgenitale, ventral view. Fig. 2, copulatory bursa and spermatheca, left lateral view. Fig. 3, spermatheca, ventral view. Fig. 4, head and pronotum. Figures 5–9, *L. arizonica* (Michoacan, Mexico). Fig. 5, Male abdomen, lateral. Fig. 6, apex of ninth sternite, ventral. Fig. 7, gonarcus and mediuncus, lateral. Fig. 8, same, dorsal. Fig. 9, head and thoracic markings. Abbreviations used in Figs. 1–9: bd — bursal duct, bg — bursal gland, gs — gonarcus, h — hood, mu — mediuncus, spd — spermathecal duct.

genitalia in both sexes. Not previously reported from Mexico, it now appears to be a tropical species, Arizona representing the probable northern range boundary. *L. negata* (Navás) 1913: 316 is very similar, but the gonarcus hood is much more developed, extending almost to cover the mediuncus viewed dorsally; apical process of ninth sternite separated by a distinct v-cleft and with larger teeth, pronotum and head more lightly marked. I suspect that when more material is available, it will prove to be a geographic or developmental variant of *L. arizonica.* This species was described from "Guatemala: Amula, Guerrero, 6000 ft, Aug., H. H. Smith." The only Guerrero listed for Guatemala is at 15°29′N, 88°35′W, at an altitude of less than 2000 ft. It seems probable that *L. negata* is from Guerrero, Mexico, which is much closer to localities for *L. arizonica.*

The holotype of *L. singularis* Navás 1913: 316 was collected simultaneously with that of *L. negata;* both are identical but for the structure of the intramedian cell, the specimen with a quadrangular cell being named *Allochrysa* [now *Leucochrysa*] *negata,* and the other, with a triangular cell, *Leucochrysa* [now *Nodita*] *singularis* (New synonymy; *L. negata* has precedence). Navás' overlooking the identity of these two species, while describing them one after another, seems quite in character.

Leucochrysa insularis (Walker)
Figures 10–16

Chrysopa insularis Walker 1853: 269. Holotype: "Jamaica/*insularis*", male, British Museum (Natural History) (examined). *Protochrysopa insularis* Kolbe 1888: 74.

Chrysopa virginica Fitch 1856: 91. New synonymy. Holotype (not seen, probably lost): Cartersville, Va. Comparison of a male from Virginia with the holotype of *L. insularis* revealed no significant differences. *Nothochrysa virginica,* Banks 1895: 315. *Allochrysa virginica,* Banks 1903: 143, Bickley and MacLeod 1956: 184. *Nothochrysa phantasma* MacGillivray 1894: 170. Six cotypes are present in the MCZ, a male from "West Chop Mass., Aug. 8, 1893, MCZ Type 10479" is designated lectotype. Banks 1895: 315.

Leucochrysa cerverai Navás 1923: 325. New synonymy. Type not found. A long series from the type locality, Santiago de las Vegas, Habana, Cuba, F. Z. Cervera, Navás det., is in the MCZ and there is no doubt as to the identity of this species. The synonymy with *L. insularis* was suggested by Alayo 1968: 57. *Leucochrysa joannisi* Navás 1925: 13, "Santiago de las Vegas, Cuba, July 17, Aug. 20, 1924, F. Cervera". No type specimen designated, and no type found in the Navás collection, 1974. Alayo 1968: 57 (synonymy). There seems to have been no formal description published of this species; it is the color variant of

insularis with brown instead of pale lateral thoracic markings.
Allochrysa virginica ocala Banks 1938: 122. Type: "Lloyd Sink, Jefferson Co., Fla., G. Fairchild coll., Aug. 9, 1935", female, MCZ No. 23184 (examined).

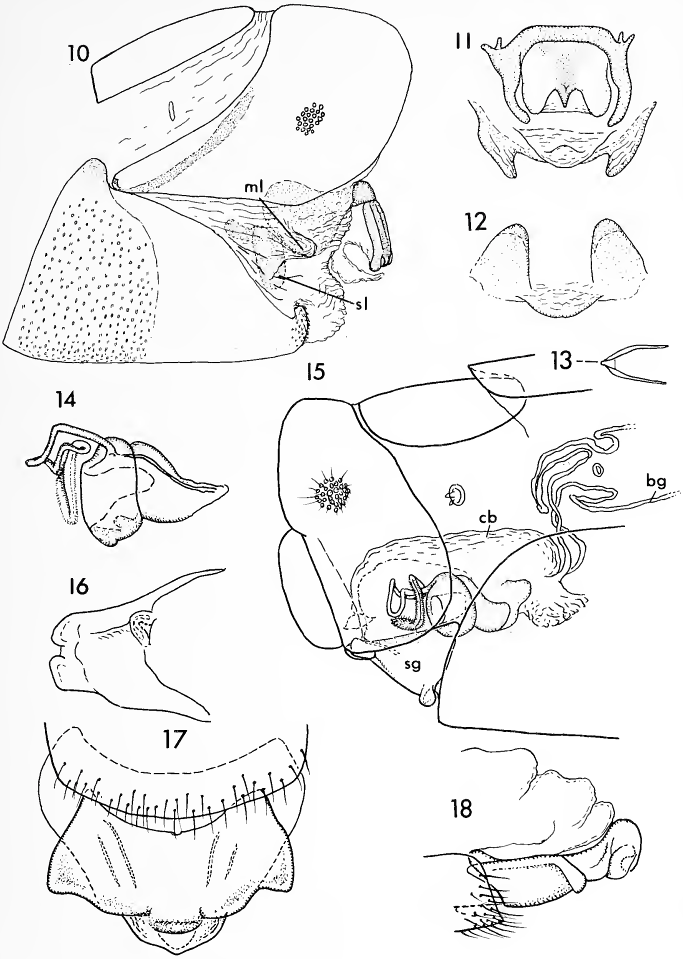
Maculation of this species shows geographic as well as individual variation. Specimens from Florida, Alabama, and the Antilles have a red or brown V mark on vertex bordering antennal fossae and genae are red marked (*L. insularis ocala*). In Georgia and Alabama the V mark, if present, is faint. North of Georgia, the vertex marks are absent and genae are brown marked or pale. The mesonotum bears two brown spots on the prescutal-scutal suture on lightly marked specimens; on heavily marked examples (*"L. joannisi"*) nearly the entire pteronotum is brown or black. The holotype of *L. insularis* has most of the transverse veins in the forewing dark marked. In Florida specimens, the inner gradates are paler, costals pale; dark transverse veins include outer gradates (except apical 3 or 4), ends of proximal r's, 1–3 m, the cubitals, and ends of the anals. The gradates are often bordered by a dark streak. North of Florida, transverse veins are paler.

Male genitalia. Sterna except ninth with microtholi; apex of ninth sternum slightly notched with a small field of lanceolate gonocristae each side (Fig. 10). Mediuncus with median sclerotized band and hook, confluent with semimembranous lateral lobes, gonosaccus without setae (Fig. 11). Laterally to gonarcus a pair of delicate digitiform membranous sacs (Fig. 10), ventrally a pair of lightly sclerotized lobes connected by a membranous flap (shown withdrawn in Fig. 10). A membranous lobe between gonopore and ninth sternite.

Female genitalia. Subgenitale (Fig. 16) broadly sclerotized, expanded anteriorly as pit-bearing lobe adjacent to seventh sternite. Bursal gland ducts very long, unbranched, bursal duct inconspicuous.

The form of the mediuncus is typical for a *Leucochrysa,* but the ventral sclerotized lobes are highly distinctive.

Distribution. Coastal states from Massachusetts to Florida, Puerto Rico, Cuba and Jamaica, also West Virginia, Tennessee (Bickley and MacLeod 1956), Alabama, Mississippi, Arkansas, and Missouri. Range extensions: Ala.: Wilson Dam, F. Q. 9–VIII–1941, J. N. Belkin, LAM. Miss.: Clinton, Hinds Co., 20–V–1960, Bryant Mather, USNM. Ark.: Devil's Den St. Pk., Wash. Co. 12–VI–1966, R. W. Hodges, USNM. Mo.: Columbia, Malaise trap, 7



Figures 10–16. *L. insularis.* Fig. 10, male abdomen, lateral, sclerotized lobes withdrawn. Fig. 11, gonarcus, mediuncus and sclerotized lobes, dorsal view. Fig. 13, hypandrium internum. Fig. 14, spermatheca, dorsolateral. Fig. 15, female abdomen, showing broadly sclerotized subgenitale, and internal structures. Fig. 16, subgenitale, ventral view. Figures 17–18, *L. arizonica.* Fig. 17, apex of seventh sternite and subgenitale, ventral. Fig. 18, same, lateral. Abbreviations used in Figs. 10–16: bc — copulatory bursa, bg — bursal glands, ms — membranous sac, sg — subgenitale, sl — sclerotized lobes.

a.m.-7 p.m., 22–IX–1967, F. D. Parker, USNM; 5 mi. S. Joplin, 25–VI–1968, E. L. Todd, USNM.

Gumilla longicornis (Walker)

Osmylus longicornis Walker 1853: 235. Holotype: "Georgia," "Type, *Osmylus longicornis* Walker, det, D. E. Kimmins", *"Gumilla longicornis* Walk., Long. Navás det." BMNH.

Meleoma longicornis, Hagen 1861: 210.

Leucochrysa longicornis, Banks 1907: 26.

Gumilla ? longicornis, Navás 1912: 189, Krüger 1913: 221.

Allochrysa longicornis, Bickley and MacLeod 1956: 184. Not *A. longicornis* (Gray), Banks 1920: 339, as cited by Bickley and MacLeod 1956: 184.

This insect is not a chrysopid, but an osmylid in which the ocelli are lost, and the antennae are exceedingly elongate. Hagen's referral of *G. longicornis* to the chrysopid genus *Meleoma* seems to have been based solely upon the nature of the antennae. Navás' illustration of the wing characters is reasonably accurate. Additional features are: pronotum articulating above mesothoracic spiracle, claws simple, single aroliar pad, two nygmata between RS-MA and MP in forewing. In hindwing, basal piece of MA ("sinuate crossvein") absent, stem of MP runs close to R; MP2 fused briefly with and appearing to be a continuation of GuA; CuP unbranched, clearly separate from 1A for its entire length. Wing membrane microtrichiated, marginal vein entire except for a few marginal dots near wing apex.

The only other species of this genus, *Gumilla aspersus* Navás 1912: 189, known from a single male specimen from Brazil (Vienna Museum, not seen) is probably the same; Navás' figure of the forewing does not differ in any important respect from that of *G. longicornis.* Two additional specimens from Brazil, Langsdorf, are in the Berlin Museum. There thus seems little question that the type of *G. longicornis* is also from Brazil, not Georgia.

ACKNOWLEDGEMENTS

The following have graciously made material available for study: Peter Barnard — British Museum, Natural History (BMNH), O. S. Flint — U. S. National Museum (USNM), K. K. Günther — Museum für Naturkunde, Berlin, Charles Hogue — Los Angeles County

Museum of Natural History (LAM), T. H. Hubbell — Univ. of Michigan, John Lawrence — Museum of Comparative Zoology, Harvard (MCZ), Per Inge Persson — Riksmuseum, Stockholm.

LITERATURE CITED

ALAYO, P.

1968. Los Neurópteros de Cuba. Poeyana Ser. B(**2**): 1–127.

BANKS, N.

1895. New neuropteroid insects. Trans. Amer. Entom. Soc. **22:** 313–316.

1903. A revision of the nearctic Chrysopidae. Trans. Amer. Entom. Soc. **29:** 137–162, pl. II.

1906. Three new species of Neuroptera. Psyche **13:** 98–100.

1907. Catalogue of the neuropteroid insects (except Odonata) of the United States. Amer. Entom. Soc., Philadelphia, 53 pp.

1910. New South American neuropteroid insects. Proc. Entom. Soc. Washington **12:** 146–160.

1920. New neuropteroid insects. Bull. Mus. Comp. Zool. Harvard **64:** 299–362, pl. 1–7.

1938. New Chrysopidae and species new to the United States. Canad. Entom. **70:** 118–122.

1944. Neuroptera of Northern South America. Part 3. Chrysopidae. Boletín de Entomología Venezolana **3:** 1–34.

1945. A review of the Chrysopidae (Nothochrysidae) of Central America. Psyche **52:** 139–174.

BICKLEY, W. AND E. MACLEOD.

1956. A synopsis of the nearctic Chrysopidae, with a key to the genera (Neuroptera). Proc. Entom. Soc. Washington **58:** 177–202.

FITCH, A.

1856. First and second reports on the noxious, beneficial, and other insects of the State of New York. Albany, 336 pp.

GRAY, G.

1824–1833. *In* Griffith: Animal kingdom **15:** 331, pl. 72, Fig. 3 (not seen).

HAGEN, H.

1861. Synopsis of the Neuroptera of North America. Smithsonian Misc. Coll. 347 pp.

KOLBE, H.

1888. Die geographische Verbreitung der Neuroptera und Pseudoneuroptera der Antillen. Arch. f. Naturgesch. 54 Bd. I, Hft. **2:** 153–178, pl. 13.

KRÜGER, L.

1913. Osmylidae. IIIa. Nachtrag zur Literatur und Katalog. Stettiner entomologische Zeitung **74:** 218–224.

NAVAS, L.

1912. Insectos neurópteros nuevos ó poco conocidos. Memorias de la Real Academia de Ciencias y Artes de Barcelona Ser. III, **10:** 135–202.

1913. Les chrysopides (Ins. Névr.) du Musée de Londres. Annales de la Société scientifique de Bruxelles **37:** 292–330.

1925. Crisópidos (Ins. Neur.) neotrópicos. Revista Chilena de Historia Natural **29:** 8–13.
1927. Insecta nova, series XII. Mem. Pontif. Accad. Nuovi Lincei Ser. II, **10:** 1–10.
1928. Insectos del museo de Estocolmo. Revista de la Real Academia de Ciencias de Madrid **24:** 28–39.

MACGILLIVRAY, A. D.
1894. New species of *Nothochrysa.* Canad. Entom. **26:** 169–171.

WALKER, F.
1853. Catalogue of the specimens of neuropterous insects in the collection of the British Museum. Part III: 193–476.

EGG GUARDING BY MALE ASSASSIN BUGS OF THE GENUS *ZELUS* (HEMIPTERA: REDUVIIDAE)

By J. Scott Ralston*
Western Carolina University
Cullowhee, North Carolina 28723

Introduction

Sporadic accounts of parental care of offspring in the Hemiptera-Heteroptera have appeared in the literature and are summarized by Hussey (1934) and Odhiambo (1959). In all but one or two of these cases only the female guards the brood; the only well documented exception is the reduviid *Rhinocaris albopilosus* in which only males guard the broods (Odhiambo, 1959).

The present paper is a summary of observations on the form and function of brood guarding behavior of a reduviid species (*Zelus* sp.) in which males guard the brood. My observations were made during January and February 1975, in the vicinity of Cali, Colombia in a dry tropical forest zone (Espinal and Montenegro, 1962). There the bugs are common in the outer branches of *Pithecelobium dulce* (Leguminosae), a tree locally known as the "chiminango." During the course of this study I observed approximately 60 different males with broods.

Egg Structure and Placement

The cylindrical, dark brown eggs occur in tight masses, with about 5 to 15 eggs in each mass. The eggs are about 0.3 mm in diameter, about 1.2 mm long and are attached to a branch or leaf by one end. Each egg projects from the substrate at a right angle and is in direct contact with other eggs in the mass. Freshly laid eggs are brown with fine, cream-colored seals at their exposed ends. Older unhatched eggs have darker seals and are partly covered with a slimy substance. Hatched eggs lack the seal, which is broken as the nymph leaves the egg.

---

*Present address: Department of Biochemistry, N.C. State University, Raleigh, N.C.

Manuscript received by the editor August 8, 1977.

Brood Guarding Behavior

Generally the female deposits more than one egg mass in a small area and this appears to be the number of egg masses a male will guard. I observed individual males guarding as few as one to as many as seven egg masses. The male (body length 9–10 mm) usually assumes a guarding position directly over the egg masses or will stand not more than 3–4 cm from the nearest egg mass.

Two simple tests were conducted to compare the behavior of guarding and non-guarding (not positioned near any egg mass) males. In the first test, which may have simulated the approach of a large predator, I passed my hand within about 10 cm of each male. Thirteen guarding males were tested; one took flight and the others simply dodged to one side to avoid my hand. With repeated passes of my hand no escape behavior other than dodging was triggered. Seventeen non-guarding males were similarly tested: nine flew away; another five dodged to avoid my hand at first but with one or two repeated passes they too flew away; the remaining three only dodged to avoid my hand. In the process of grasping 44 guarding males for marking or removal during another part of this study, I found that none took flight; the only reaction was to dodge my hand. Application of the chi-square test to these data shows that guarding males are significantly ($p < 0.01$) less likely to flee from a potential predator than are non-guarding males.

The second test involved a model parasite made of a bit of black tape attached to the end of stiff nylon line on the end of a long hollow glass tube. I carefully presented the model parasite so that the male would only perceive the model. Of the ten guarding males tested, one avoided the model completely, one exhibited no reaction, and seven others readily attacked the model by grasping it with the forelegs. The attacks appeared especially aggressive when the model came close to the egg masses. The tenth male, which was about 7 cm from his egg masses, avoided the model when it was brought near him. However, when the model approached the egg masses the male was guarding, he rapidly moved to attack it.

The non-guarding males were less ready to attack the model wasp. Of eight non-guarding males tested, only one readily attacked the model. Four males avoided the model parasite but when touched by it they did attack. The other three non-guarding males avoided the model completely. The chi-square test results show that there was a significant ($p < 0.01$) difference between the guarding and non-guarding males in readiness to attack the model parasite.

After hatching, the nymphs appeared to stay very close to the eggs and guardian male for several days (a maximum of seven days in one case). In one instance in the field I watched a male capture a small insect about 15–30 cm from the egg masses where the nymphs were gathered. He promptly returned to the nymphs with the insect and the nymphs fed on it. I attempted unsuccessfully to repeat this observation in the lab with a few males, several nymphs, and tiny insects. Dr. William Eberhard (personal communication) reports seeing recently (February 1977) a guarding male holding a prey with a cluster of nymphs gathered around apparently sucking the prey.

Rates of Parasitism

On January 28, I finished marking 22 males guarding egg masses (control group) as well as the sites of the egg masses. The males were marked with white airplane dope on the anterior dorsal surface of the thorax. This did not appear to interfere with their normal functioning. I also removed 22 males from the masses they were guarding and marked the sites of the egg masses (experimental group). Each tree in which I made the study contained both control and experimental groups distributed roughly at random. However, if different groups of egg masses were very close together, I labeled them all control or all experimental so that the presence of a nearby male would not affect parasitism of unguarded eggs. The purpose of this experiment was to see if the presence of the guarding male affected the rate of parasitism of the eggs.

On February 20, I collected 57 egg masses from the marked sites with guarding males and 63 egg masses which had been left unguarded. Of the 57 guarded egg masses, 12 (21%) had been parasitized (distinguished by eggs with unbroken seals and tiny exit holes near their attached ends); whereas 35 (55%) of the 63 unguarded egg masses had been parasitized. A chi-square test shows that the difference between the rate of parasitism of unguarded and guarded egg masses is statistically significant ($p < 0.01$). Five tiny wasp parasites of the genus *Telenomus* (Scelionidae) hatched from one egg mass in the experimental group soon after it was collected.

Discussion

Odhiambo (1959) points out that broodguarding Hemiptera exhibit a strong tendency to remain with egg masses when they are disturbed in ways that in other situations would cause them to take flight. I found this to be true for *Zelus* males.

A few direct observations and some circumstantial evidence indicate that broodguarding in Hemiptera helps to protect eggs from egg parasites (Odhiambo, 1959). I have tested this hypothesis for *Zelus* in two ways and the results of both tests strongly support the hypothesis. There is no evidence, such as that found by Eberhard (1975) in his study of egg guarding by pentatomid bugs, that the guarding male makes the eggs more vulnerable to certain parasites.

My observation and an observation by Eberhard show that *Zelus* parental care continues during early nymphal life in the form of feeding and perhaps protection.

Further study of *Zelus* broodguarding should be directed towards answering questions such as the following: What is the genetic relationship between the males and the eggs which they guard? I would predict that the guarding male is the genetic father of at least some of the eggs he guards; otherwise there would be little or no selective advantage in the guarding behavior. How common is the parental feeding which was observed? Exactly how do the males react to real parasites and predators? How does the number and distribution of egg masses affect egg rearing efficiency?

ACKNOWLEDGMENTS

The author wishes to extend his thanks to the following: Dr. William Eberhard, University del Valle, Cali, Colombia, for his guidance and suggestions during the course of this study; Dr. Frederick Coyle, Western Carolina University, for helping to arrange this study and for his interest and help in writing this paper; J. L. Herring, U. S. Department of Agriculture, Beltsville, Maryland, U.S.A., for identifying *Zelus;* and P. M. Marsh, U. S. Department of Agriculture, Beltsville, Maryland, U.S.A. for identifying *Telenomus.*

REFERENCES

EBERHARD, W. G.
1975. The ecology and behavior of a subsocial pentatomid bug and two scelionid wasps: strategy and counter-strategy in a host and its parasites. Smithsonian Contrib. Zool. **205:** 1–39.

Espinal, L. S. and E. Montenegro.
1962. Formaciones Vegetales de Colombia. Instituto Augustin Codazzi, Bogota.
Hussey, R. F.
1934. Observations on *Pachycoris torridus* (Scop.), with remarks on parental care in other Hemiptera. Bull. Brooklyn Ent. Soc. **29:** 133–45.
Odhiambo, T. R.
1959. An account of parental care in *Rhinocoris albopilosus* Signoret (Hemiptera-Heteroptera: Reduviidae), with notes on its life history. Proc. Royal Ent. Soc., London. (a) **34:** 175–185.

REPRINTS OF ARTICLES BY W. M. WHEELER. — The Cambridge Entomological Club has available for distribution numerous reprints of articles by Professor W. M. Wheeler. These were stored in Professor Wheeler's office at Harvard University at the time of his death in 1937 and they have recently been turned over to the Cambridge Entomological Club by Dr. Ralph Wheeler and Miss Adeline Wheeler. Included are about 12,700 individual copies of 250 publications by Dr. Wheeler.

In accordance with a vote of the society in April of this year, a committee has been appointed to administer the distribution of the reprints. The price of the reprints has been set at the rate of 5¢ a page (including postage); for orders under $5 there will be in addition a 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 Ave., Cambridge, Mass. 02138. Checks should be made payable to the Cambridge Entomological Club. — F. M. Carpenter, editor.

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 B-455, Biological Laboratories, Divinity Ave., 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.

ISSN 0033-2615

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 84 June, 1977 No. 2

CONTENTS

CAMBRIDGE ENTOMOLOGICAL CLUB

Officers for 1977–1978

President	Gary D. Alpert
Vice-President	John A. Shetterly
Secretary	Robert Robbins
Treasurer	Frank M. Carpenter
Executive Committee	Martha Fisher Katherine Horton

EDITORIAL BOARD OF PSYCHE

PSYCHE is published quaterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: $8.00 for United States and Canada, $9.50 for other countries. Single copies, $2.50.

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 $23.50 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, 1977, Psyche (Vol. 84, No. 1) was mailed November 30, 1977

The Lexington Press, Inc., Lexington, Massachusetts

PSYCHE

Vol. 84 June, 1977 No. 2

PAIRING BEHAVIOR IN *HODOTERMES MOSSAMBICUS* (ISOPTERA)[1]

BY R. H. LEUTHOLD[2] AND O. BRUINSMA

Division of Animal Physiology, Zoological Institute,
University of Bern, Engehaldenstr. 6, CH-3012 Bern, Switzerland;
and The International Center of Insect Physiology and Ecology,
P.O. Box 30772, Nairobi, Kenya

INTRODUCTION

The dispersal flight of termites, especially of those species living in savannah areas with alternating dry and wet seasons, is generally related to the beginning of a rainy period. The precise time of flight may be controlled by exogenous or endogenous factors and varies from species to species. Most species fly at dawn or dusk or at night whereas the few daylight-fliers usually swarm only under humid atmospheric conditions. After individual landing the alates of both sexes will meet in pairs. A typical "calling" posture of the female was observed in many species and was interpreted by several authors as chemical attraction. However, no precise evidence for this interpretation was given from field observations and no data about the spatial range of attraction were specified. After meeting, the sexes of many species proceed in "tandem", a typical formation, in which the male usually follows the female closely on the search for a suitable nesting site. The termite considered herein, *Hodotermes mossambicus,* is a dry grass harvesting species, exceptionally adapted to survive under extreme climatic conditions of semi-arid grasslands. The species differs in several aspects from other termites: the workers forage in relatively loose formation above ground often in sunshine and are able to use individual op-

---

[1] Research supported by the Swiss National Foundation, grant no. 3.2810.74.

[2] A short summary of this subject is part of a communication presented in Proc. VIII Congr. IUSSI 1977, Wageningen.

Manuscript received by the editor November 28, 1977.

tical orientation in contrast to the usual feature of foraging columns confined under galleries or in narrow pheromone trails (Leuthold *et al.,* 1976). In contrast to other termites, they have functional compound eyes and darkly pigmented body surface. Alate imagines and workers carry their own water supply in specialized water sacs, according to Watson *et al.* (1971). We had the opportunity to observe carefully the pairing behavior of *H. mossambicus* on a single swarming day (9.4.1976) in Olorgesailie, Kenya. This study revealed an unusual modification also in the pattern of pairing behavior. The reproductive dispersal flight occurs during the hot period in the afternoon, often during full sunshine on the day after a rainfall. The roles of male and female were found reversed relative to the behavior observed in other termites. A mechanism of pheromonal sex attraction was clearly concluded from the behavior. Unfortunately, another flight during which we expected to carry out planned experimental analysis did not occur during our available observation time.

OBSERVATIONS

The climate of Olorgesailie, the area of observation in the great Rift Valley near Nairobi, is characterized by extensive dry periods and sporadic rainfall of 300–400 mm per year, concentrated in the months of February to May and to a lesser extent from October to November. Swarming of *H. mossambicus* in this area takes place after substantial rainfall following the main dry season (recorded data of rainfall that released flight: 1.3 mm, 35 mm and 21.2 mm). In this area the swarming often extends over several rains if the showers are only weak and sporadic. Swarming was recorded on (23.12.1971), 8.1.1973, 25.2.1973, (20.2.1974), 9.4.1976 and 3.4.1977.[3] The time of swarming recorded was always in the afternoon under sunny conditions on the day following rainfall. One expected flight did not occur with overcast sky and slight drizzle.[4]

---

[3] Partly recorded by Mr. Kannugi, warden at the prehistoric site in Olorgesailie. The figures in parentheses are not well documented.

[4] Hewitt and Nel (1969) reported flight after a latency time of 4 to 6 days after the first substantial summer rains, in the Orange Free State in South Africa. They did not mention the meteorological conditions before and during flight. It seems worthwhile to collect more data in both areas to decide whether the populations in the two zones of very different latitude (1.6°S and 29°S) behave differently in this respect.

The swarming referred to in this paper occurred on 9.4.1976 around 16.30 h (sunshine). After a short dispersal flight of less than 100 m the alates landed individually on the ground, shed their wings and started running about. [Behavioral details of this sequence have been described by Hewitt and Nel, 1969.] The MALES rambled with their abdomens raised in "calling" position and their huge sternal glands exposed (Fig. 1) in search of a digging ground. If they found a suitable place, they started excavating a hole by flicking dust particles out with their legs and often carrying out soil bits with their mandibles. They held their abdomens permanently in "calling" posture as long as they were unpaired. The unpaired FEMALES, on the other hand, repeatedly climbed on elevated structures, such as grass stems, apparently for "sniffing" for the male's scent. They clearly perceived the presence of a male from a distance of at least 2.5 m up-wind. They obviously became excited and ran slightly zig-zag towards the calling male, without ever failing to reach the goal (Fig. 2). The joining of a female with a digging male was analyzed from two film sequences: the female touched the male's abdomen with her antennae. On this stimulus the male turned around through 180° and palpated the female's abdomen intensively. With that stimulus, apparently, the male terminated calling behavior by lowering the abdomen and retracting the sternal gland. Henceforth, no other female was attracted, not even from as close as a few cm. The pair met either during the male's exploratory run or on the male's digging site. In the latter case the female participated in excavating behavior. In the first case she followed him in loose formation on the search for digging terrain. However, no rigid pattern such as that referred to as "tandem run" was ever observed. In suitable ground the digging pair disappeared from the surface within minutes. If the substrate was too hard or if the pair was attacked by ants, the male went on in search of another place, followed by the female. In the postflight behavior the male was always the attracting and leading partner and the female actively hunted for him. If the female was experimentally removed from the pair, the male resumed calling behavior. However, reproductives collected in petridishes did not resume sex attraction behavior when separated and tested the day after flight in the laboratory nor did a crushed male sternal gland under those conditions attract any female.

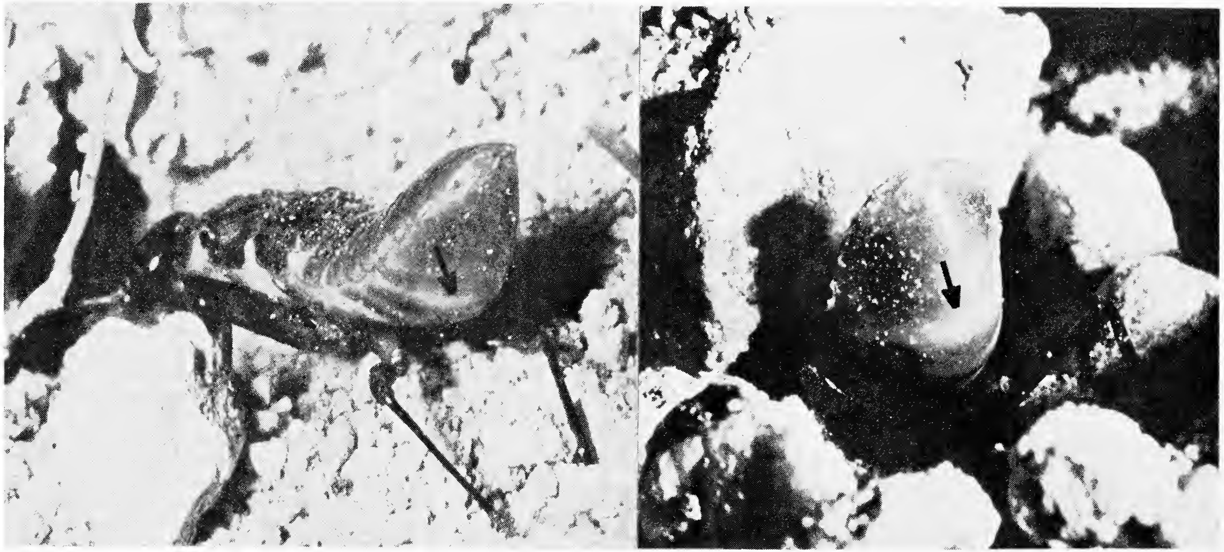


Figure 1. *Hodotermes mossambicus:* dealate male in "calling" posture and at the same time excavating a hole. The zone of the sternal gland is widely protruded (light area marked with arrow).

AIRBORNE PHEROMONAL ATTRACTION

A female motivated for pairing is clearly attracted from a distance apparently by a volatile chemical stimulus from the male. When the female crossed a zone 250 cm or less down-wind from the male, an immediate reaction of intensified excitement and orientation towards the male was always observed. [Eleven observations on the natural ground were recorded in which some females were used for a second run after experimental displacement. Reactions over distances up to 3 m or even more seemed to be possible but have not been systematically recorded. The wind was a light breeze, windspeed in one case determined roughly 1.5 m/sec.] The possibility that visual cues from the male could be responsible for the accurate female orientation was clearly disproved, since the same pattern of orientation was observed when the male was not visible to the female. Another argument for pheromone mediated orientation is the strong correlation of sex attraction response with the exposure of the male sternal gland. When this was retracted (after a female had joined the male) another searching female was no longer attracted, even if the male was visible. Females within the active space of attractive pheromone approached the goal in a fast agitated run (5 to 10 cm/sec) performing a characteristic orienting pattern (Fig. 2). The female's body-axis altered its direction in short irregular turns, performing an irregular broken zig-zag line. In superimposed movement the insect walked a greater waveline or zig-zag along the main axis leading to the source. A female in up-wind position relative to the male oriented positively only at distances closer than 6 to 10 cm. This was observed under natural conditions and after experimental displacements of the female. The observed overall pattern of orientation (Fig. 2) is principally compatible with the theoretical model of airborne chemical orientation as reviewed and discussed by Farkas and Shorey (1974). This postulates, first, motivation of the insect by the chemical stimulus to anemotactic orientation, i.e. steering in general up-wind direction. Secondly, the course is finely adjusted by a mechanism of orientation (e.g. osmoklinotaxis, osmotropotaxis or a combination) that involves correction of the lateral deviation from the central axis of the aerial trail and enables the insect to remain within the odor plume. At close range, where the gradient of concentration

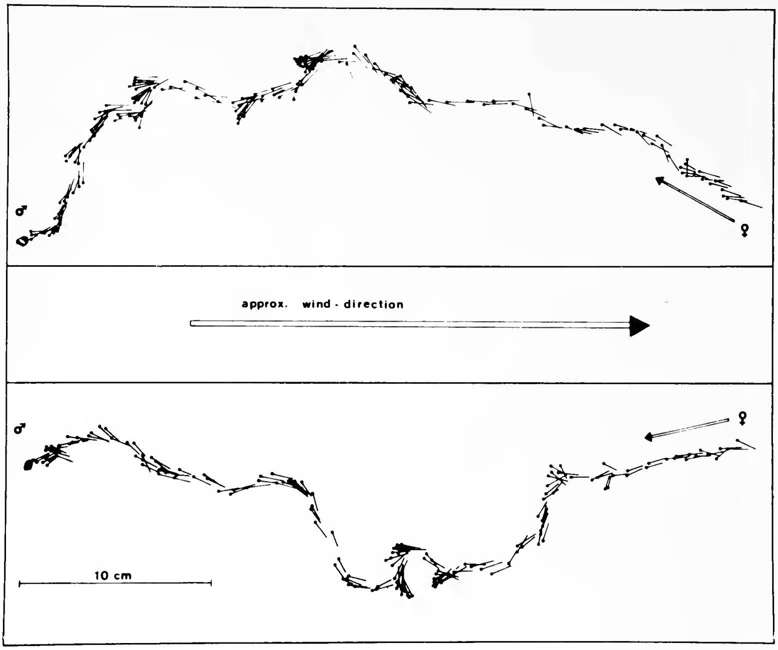


Figure 2. Two walking patterns of females orienting up-wind towards the "calling" male, redrawn in sequence of 1/18 sec from ciné film. The small dots represent the position of the female's head, the tails indicate the body axes. The wind was a light breeze of unknown speed, the direction was approximately determined with cigarette smoke.

is assumed to be steep, direct osmochemotactic orientation is postulated without the need of air movement. An experimentally proved analysis of the postulated mechanisms has not been firmly worked out so far, and neither can the answer be given for the case of *Hodotermes* sex attraction. This species, however, appears to be an ideal subject for experimental analysis because of the insistent motivational impetus in the performance of postflight behavior except for the difficulty in catching the swarming time.

The Sternal Gland

The sternal gland in termites is known as the source of the trail pheromone (Stuart, 1969 and 1976; Bruinsma *et al.,* in prep.). The involvement of the gland in sexual attraction during the imagines'

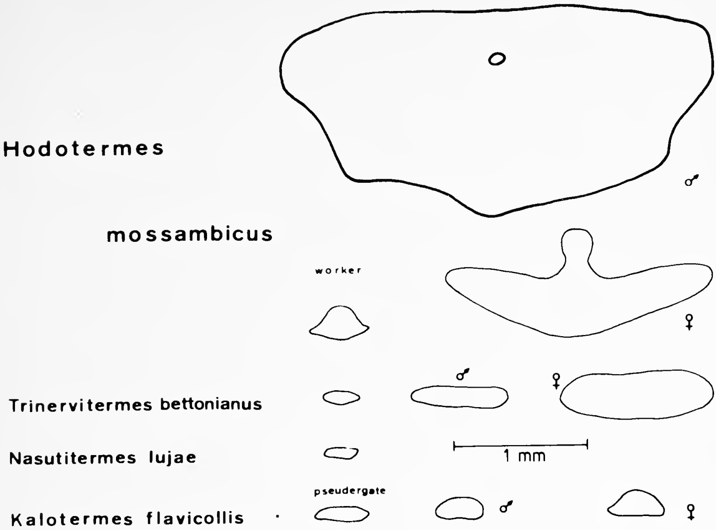


Figure 3. Comparative sizes of termite sternal glands: the contours of the glands in top view of *H. mossambicus*, reproductive male and female (after flight) and major worker; those of *T. bettonianus*, characterized by Leuthold and Lüscher (1974) as unusually hypertrophic in the reproductive caste; those of other species [*N. lujae* after Pasteels (1965), *K. flavicollis* from own drawings]. The glands were drawn from fresh whole-mount preparations in Ringer solution.

postflight behavior had been assumed from calling behavior by several authors (reviewed by Stuart, 1969). A few species have been more closely analyzed: In *Kalotermes flavicollis* (Kalotermitidae) calling females have been only occasionally observed with exposed sternal glands (Wall, 1969). A more intensive relationship of the sexes was found in the tandem behavior in which either the male or the female could be leader. Both sternal and tergal glands were experimentally verified as sources of sex attraction from laboratory bioassays. The sternal gland of the female was exclusively male attractive. The male tergal gland was dominantly attractive to females and to a lesser extent to males, and the female tergal gland was slightly active towards both sexes (Wall, 1971). Pasteels (1972) reported calling courtship but no distinct tandem pattern in *Zootermopsis nevadensis* (Hodotermitidae). In most cases the female was the calling partner but apparently for the first time also a male was seen calling. Extracts of sternal glands released reciprocal attraction between the sexes. The glandular secretions of imagines were found to be sex specific and different from the trail pheromone of the nymphs. *Reticulitermes flavipes* (Rhinotermitidae) performs distinct female calling courtship and tandem behavior with the female leading (Buchli, 1960). Reciprocal attraction of extracted sternal glands was found between males and females (Stuart, 1975). In *Trinervitermes bettonianus* (Termitidae) the attracting and leading partner is always the female, as it usually is for the family. The calling female exposes both tergal and sternal glands (Leuthold, 1975). The former attracts on longer range distances, up to 12 cm; the latter on short distances, up to 1.5 cm in the laboratory. Both glands are involved in holding the tandem connection, but the sternal gland is more important in this function (Leuthold, to be published). Furthermore a powerful trail is deposited during tandem run. The imaginal sternal gland pheromone may not be different from the worker trail pheromone (Quennedey and Leuthold, 1977). The relative volume of the female gland, however, is unusual and reaches 7 times that of the male and 65 times that of the worker gland (Fig. 3), and trail activity was found to be 1200 times as high as that of a worker gland (Leuthold and Lüscher, 1974).

The sternal gland of *Hodotermes* (Hodotermitidae) is the largest termite sternal gland ever reported (comparative sizes in contours of various species are represented in Fig. 3). The morphology of the gland in *Hodotermes* is complex and it seems that different glandular structures are differently developed in the various castes [A study of morphology is in preparation by Quennedey and Leuthold]. Trail activity of the sternal gland of *Hodotermes* male was lower than that of the worker gland and not different from the control (male sternal plates without the gland). The extracts were tested in the bioassay described by Leuthold *et al.* (1976). The apparent function of the male gland is airborne female attraction. The pheromone produced is definitely different from the trail pheromone of the workers. [Unfortunately no attractant test in the field with isolated or extracted glands could be carried out during the single swarming event available.] As mentioned above, the attracting and leading partner in courtship was always the male as far as we have observed. However, Hewitt and Nel (1969) apparently have seen both sexes calling in the same species in the Orange Free State in South Africa. This would bring light to the question of the unknown function of the female sternal gland, which is obviously different in shape from that of workers and reproductive males (Fig. 3) and yields the same trail-activity as a worker gland when extracted and tested in the standard trail-bioassay.

DISCUSSION

Dispersal flight in *Hodotermes mossambicus* was observed during full afternoon sunshine on open land. This is a rather exceptional behavior in termites (Nutting, 1969) and comprises considerable hazards of desiccation and predation. How do the alates prevent desiccation? According to Watson *et al.* (1971) the imagines have specialized water sacs (salivary reservoirs) which they fill after flight by active water uptake (in the laboratory). The authors did not say whether or not water is carried along during the flight. This would seem useful, in our opinion, to compensate for water loss during flight and post-flight behavior and for the initial development of the colony in case no other rain falls after swarming. As mentioned above, a low rainfall of only 1.3 mm may trigger flight for the following day. This may occasionally be the only rain for a longer period of time. On the day of flight the soil surface is still slightly humid but probably not sufficiently so for the insects to imbibe free water. Therefore, it would be interesting to investigate the question of water storage in the hot semi-arid zones of Kenya. The hazard of predation on open land on sunny afternoons is considerable. Birds are extremely active and are efficient predators during the time of swarming. We have furthermore observed significant predation by lizards, ants, and salticid spiders. However, a good percentage of all the swarmed imagines escapes predation thanks to the very efficient system of pairing. *Hodotermes mossambicus* together with two other hodotermitid species (*Anacanthotermes* sp: Clément, 1956) are, to my knowledge, the only observed species where the attracting partner is already digging while still single. *Hodotermes mossambicus* represents the only documented case in termites of airborne chemical sex attraction on long distance. In most observed cases pairing took place efficiently within seconds or a few minutes from alighting. If pairing was not successful by the time the male's excavation had reached the depth to enable him to disappear underground, he stopped digging or started another hole. However, we did not observe such a case except when the approaching females were experimentally removed. The question arises: why does *Hodotermes* fly during the time of highest predation and desiccation and not, like many other species, under damp and rather dark conditions during or soon after rain? Some aspects of adaptation to the extreme habitat are considered: in the arid areas the dry soil is often dusty and does not absorb the water rapidly. The rains often are short, heavy thunderstorms. After a first rainshower the soil is generally flooded or muddy and swarming during or shortly after the rain would be fatal. Waiting for a repeated rainfall, when the soil is wet enough to absorb, as do certain other termites (e.g. *Trinervitermes bettonianus*), could possibly mean waiting forever, since rainshowers may be very sporadic. The day after rain the soil is still humid, and if the sky is clear in the afternoon there is little risk for another flood immediately after the flight. Such a situation may be interpreted as a suitable flying condition from this point of view. It is worth mentioning that the species generally is obviously challenged to sunlight, as revealed also in the workers' pigmentation, their developed compound eyes and sunlight orientation.

SUMMARY

Swarming in *Hodotermes mossambicus* was always observed at the beginning of a rainy period in afternoons during sunshine, the day after a first rain.

The dealate male exposes his sternal gland for airborne female attraction ("calling") (Fig. 1). The male sternal gland is the largest ever found in termites (Fig. 3). The male begins with excavating into the soil while calling. The female (running about) is stimulated by the male pheromone from 250 cm up-wind and orients in a winding zig-zag run towards the calling male (Fig. 2). After they join, the male stops "calling" and the female takes part in digging. The behavior of "tandem run" was not observed. The pair disappears within minutes from the surface.

REFERENCES

BRUINSMA, O., M. KAIB, R. H. LEUTHOLD AND G. D. PRESTWICH.
Trail Pheromones in Termites, Evidence for a Multicomponent System.
BUCHLI, H.(in preparation)
1960. Les Tropismes lors de la Pariade des Imagos de *Reticulitermes lucifugus,* Vie Milieu **11:** 308–315.

Clement, G.
1956. Observations sur l'Essaimage d'Anacanthotermes ochraceus Burm., Bull. Soc. entomol. France, **61:** 98–103.

Farkas, S. R. and H. H. Shorey
1974. Orientation to a Distant Pheromone Source, in: Birch, Pheromones, North-Holland Publ. Comp. Amsterdam-London, 81–95.

Hewitt, P. H. and J. J. Nelel
1969. The Influence of Group Size on the Sarcosomal Activity and the Behaviour of *Hodotermes mossambicus* Alate Termites, J. Insect Physiol. **15:** 2169–2177.

Leuthold, R. H.
1975. Orientation Mediated by Pheromones in Social Insects, in: Pheromones and Defensive Secretions in Social Insects, Proc. Symp. Int. IUSSI, Dijon, 197–211.

Leuthold, R. H. and M. Luscher
1974. An Unusual Caste Polymorphism of the Sternal Gland and its Trail Pheromone Production in the Termite *Trinervitermes bettonianus,* Insectes Soc. **21:** 336–341.

Leuthold, R. H., O. Bruinsma and A. van Huis
1976. Optical and Pheromonal Orientation and Memory for Homing Distance in the Harvester Termite *Hodotermes mossambicus* (Hagen), Behav. Ecol. Sociobiol. **1:** 127–139.

Nutting, W. L.
1969. Flight and Colony Foundation, in: Krishna and Weesner, Biology of Termites, Academic Press, **1:** 233–282.

Pasteels. J. M.
1965. Polyethisme chez les Ouvriers de *Nasutitermes lujae,* Biol. Gabonica **1:** 191–205.
1972. Sex-Specific Pheromones in a Termite, Experientia **28:** 105–106.

Quennedey, A. and R. H. Leuthold
1977. Fine Structure and Pheromonal Properties of the Polymorphic Sternal Gland in *Trinervitermes bettonianus* (Isoptera, Termitidae). (accepted in Insectes Soc.)

Stuart, A. M.
1969. Social Behaviour and Communication, in: Krishna and Weesner, Biology of Termites, Academic Press, **1:** 193–232.
1975. Some Aspects of Pheromone Involvement in the Post Flight Behaviour of the Termites *Zootermopsis angusticollis* and *Reticulitermes flavipes,* in: Pheromones and Defensive Secretions in Social Insects, Proc. Symp. Int. IUSSI, Dijon, 219–223.
1976. Some Aspects of Communication in Termites, Proc. XV Int. Congr. Entomol. Washington, 400–405.

Wall, M.
1971. Zur Geschlechtsbiologie der Termite *Kalotermes flavicollis* (Fabr.) (Isoptera), Acta Tropica **28:** 17–60.

THE ORIENTATION OF MIGRANT AND NON-MIGRANT MONARCH BUTTERFLIES, *DANAUS PLEXIPPUS* (L.)

By James E. Kanz*
Department of Biology
Tufts University
Medford, Massachusetts 02155

Introduction

Many species of butterflies migrate (Nielsen and Nielsen, 1952; Tilden, 1962; Williams, 1951, 1958). The fall southward migration of the North American Monarch butterfly, *Danaus plexippus* L., is a classic example of long-distance insect migration (Urquhart, 1960, 1976; Walker, 1914; Williams, Cockbill, Gibbs, and Downes, 1942). Evidence from tagging studies indicates that the same butterflies traveling south in the fall return northward the following spring (Urquhart, personal communication). It is unlikely, however, that fall migrants from the northern latitudes (48° N) return as far north in the spring.

Johnson (1969), Urquhart (1960), Williams et al. (1942), and Williams (1958) have provided descriptive information on several aspects of *D. plexippus* migration. However, little experimental work exists on the isolation of environmental orientation cues and their role in the seasonal movements of the Monarch. Baker (1968a) hypothesized an evolutionary scheme for the development of sun-orientation in a butterfly's search for new habitats. Using field data on general flight directions of migrating European butterflies, Baker (1968a,b) determined that sun orientation was apparently used by *Pieris rapae, P. brassicae, P. napi, Maniola jurtina, Aglis urticae,* and *Inachis io* during their migrations. This paper reports which environmental orientation cues are used by caged migrant and non-migrant Monarchs, and suggests how such cues are used.

---

*Present address: Marine Biomedical Institute, University of Texas Medical Branch, 200 University Boulevard, Galveston, Texas 77550.

Manuscript received by the editor August 20, 1977.

MATERIALS AND METHODS

Experiments used laboratory-reared and "wild-caught" Monarch butterflies (*D. plexippus* L.) of both sexes. The laboratory colony was reared from the egg under mid-summer conditions: 24°C under a 15:9 hour light/dark schedule (Kanz, 1973; Urquhart and Stegner, 1966). Some laboratory-reared Monarchs were reared under a photoperiod advanced 6 hours. Predominantly laboratory-reared animals were used for summer experiments. Wild-caught migrants were used in fall tests. Fall migrants were maintained in the field in frame cages (3 × 3 × 2½ m) covered with nylon netting and placed over patches of golden rod and asters.

Summer experiments with non-migrants were conducted in an open field in Lexington, Massachusetts. Studies with fall migrants were conducted at the Eastern Point Audubon Sanctuary in Gloucester, Massachusetts. Eastern Standard Time (EST) was used for summer and fall experiments.

Experimental orientation cages were circular (80 cm diameter) and mounted on a rotatable base. The floor of the cages was marked off into 45° sectors. The periphery (20 cm height) and top were wire screening. Entrance was through a door in the top. Two types of orientation cages were used: (1) transparent-periphery cages with both terrestrial and celestrial cues visible and (2) opaque-periphery cages with a beige strip of no-glare cloth around the periphery so only celestial cues were visible.

Experiments were conducted under sky conditions ranging from clear to overcast. Orientation cages were placed in the center of a field so that terrestrial cues were symmetrical about the cages. Terrestrial cues were distant enough so as not to be visible to animals in opaque-periphery cages. Cages were oriented to true north and the cages could be rotated to any desired azimuth.

Male or female Monarch butterflies (N = 10–20) were released into an orientation cage, and data collection started 15 min later. Cage positions of the Monarchs were monitored at intervals ranging from 1 to 15 min and positions were scored on circular data sheets divided into 45° sectors. Each animal's position in relation to true north could be designated within ± 5°. With few exceptions, the cage position recorded for each animal was a resting position (i.e., the butterfly was not in flight). Following each reading, the cage was usually rotated. The side of the cage from which the observations were made was randomized, but always excluded those sides directly toward and away from the sun. The presence of the experimenter during a reading (an elapsed time of 10–30 sec) did not appear to affect the butterflies' positions. Unless otherwise noted, animals were used for only one experiment and then released with vanishing azimuths recorded; males or females were used in a particular experiment.

The butterflies' orientation cage positions were converted to azimuths with a protractor. These orientation azimuths were then treated as a circular distribution and the following parameters obtained for each observation time (Batschelet, 1965; Greenwood and Durand, 1955): (1) mean orientation direction (θ); (2) a grouping factor (r) indicating the extent to which the butterfly azimuths for an observation were concentrated about the θ for that observation; (3) an angular deviation (AD) for θ; and (4) the probability (P) of r occurring by chance. Computer plots were made for θ and the sun azimuth values as a function of time of day. The orientation response of the Monarchs was considered significant when the P for a distribution of animals (in the orientation cages or vanishing azimuths) was $\leqslant 0.05$.

Other data recorded at each reading included: (1) time of day; (2) temperature; (3) humidity; (4) surface wind velocity (with a Taylor 3105 anemometer) and direction; (5) sun azimuth and altitude computed from a Nautical Almanac and Tables of Computed Altitude and Azimuth for the appropriate latitude. Ambient temperature for the fall tests (10°–18° C) was lower than for summer (18°–32° C) experiments. When ambient temperatures fell below 16° C, the butterflies displayed sunning behavior: turning away from the sun and spreading the wings in order to increase surface area exposed to sun and thus body temperature (Kanz, 1973; Urquhart, 1960). Sunning is often accompanied by shivering (Kammer, 1968, 1970; Urquhart, 1960), and was only seen in fall migrants. Sunning Monarchs were indicated on the data sheets and in subsequent analyses, computation of θ, AD, r and P with and without sunning Monarchs were made.

RESULTS

Field Behavior of Migrant and Non-Migrant Monarch Butterflies

Non-migrant summer Monarchs left their overnight roosting trees as soon as ambient temperatures permitted flight (approximately 13° C) and engaged in feeding and mating throughout the day until sunset.

Fall migrating Monarchs passing through Gloucester, Massachusetts, frequently remained in the area for several days, depending upon weather conditions. Fall migrants left overnight roosting trees to feed (except when it rained) when ambient temperatures exceeded 10°–12° C (Kanz, 1973); mating occurred infrequently. At approximately 1600 hrs (EST) the butterflies returned to their roosting trees. This cycle was repeated each day until migration resumed. Fall migratory flights occurred between 1000 and 1400 hrs, EST (Brower, personal communication; Urquhart, personal comminication). Fall migratory flight occurred with north, northeast, or northwest winds.

Butterfly Orientation in Opaque Periphery Cages

Laboratory-reared, non-migrants oriented toward the sun's azimuth throughout the day when the sun was the only environmental cue available (Fig. 1). To examine the possibility that this orientation was actually a shade-seeking response (i.e., orienting to the shaded area of the cage and thus the side toward the sun) a sunshade was positioned so that a shadow was cast over the half of the orientation cage facing the sun. If butterflies were seeking shade, their cage positions should fall within the shaded area of the cage. If Monarchs were sun-orienting, the butterflies would move toward the sun's azimuth, stopping as they entered the shaded portion of the cage and their cage positions would fall along the shade line cast by the sun-shade. For such an experiment, 59% of the butterflies' cage positions were within ± 5 cm of the shade line; and 72% of the cage positions were on the lid. Therefore, sunward orientation of caged, summer, non-migrants seemed to be an orientation to the sun and not an attempt to seek shade.

Without celestial or terrestrial cues (overcast day), laboratory-reared, summer, non-migrants displayed a random orientation pattern (Fig. 2). With the sun visible, the mean absolute difference between a given θ and the sun's azimuth for that θ (i.e., $\overline{|\theta\text{–sun azimuth}|}$) was 23° for opaque periphery cage, laboratory-reared, non-migrants, and 99° without the sun visible (Table I). Seventy-three percent of the sun-visible readings, versus 2% of the no-sun readings, showed significantly different Monarch cage distributions

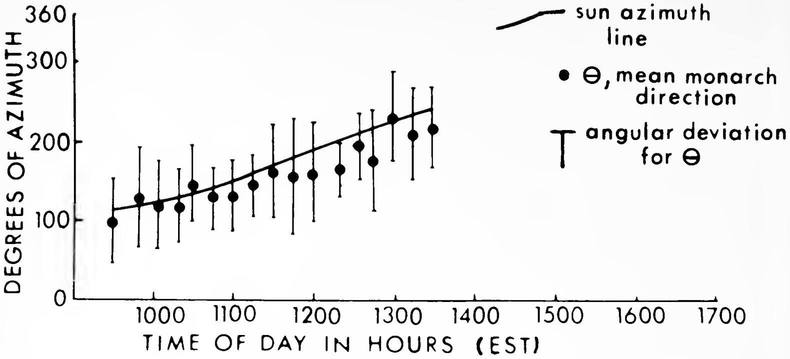


Fig. 1. Orientation of laboratory-reared, summer, non-migrants in an opaque periphery cage on a clear day. θ's lie close to the sun azimuth line throughout the course of the test.

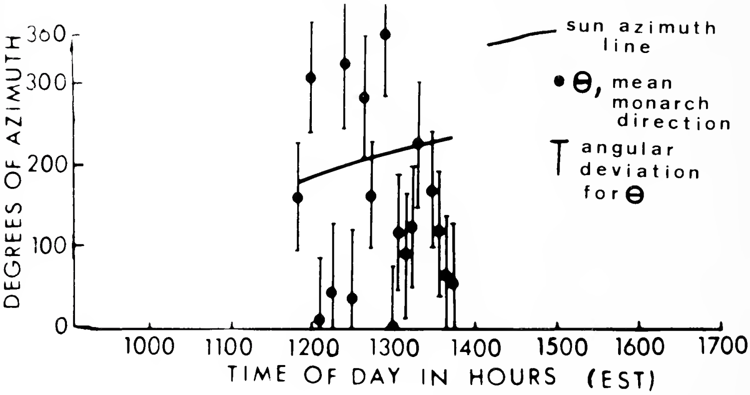


Fig. 2. Random mean orientation of summer, laboratory-reared monarchs in opaque periphery cages on an overcast day.

(Raleigh Test, $P \leqslant .05$). Thus, caged non-migrant Monarchs responded to the sun as an orientation cue. Two tests under sun-visible and no-sun-visible conditions using wild-caught summer, non-migrants, paralleled the results with laboratory-reared animals: wild-caught non-migrants, sun-oriented on clear days but oriented randomly on overcast days. However, if summer Monarch followed the azimuth of the sun, their daily movement would be to the south. Such a movement is inconsistent with the random wandering observed for summer non-migrants (Urquhart, 1960). Therefore, the sun orientation of summer non-migrant Monarchs in opaque cages with the sun visible may have been an escape reaction (see Discussion).

Fall migrants in opaque periphery cages also displayed a sun orientation when the sun was visible (Fig. 3): mean$|\theta$–sun azimuth$|$ = 39°, 31% of the readings showing significant Monarch concentrations about the mean orientation direction (Table I). Low ambient temperatures during fall tests (10°–18°C) compared to summer tests (18°–32°C) might be one reason for the difference in sun-orienting response between the two populations. However, the data suggest that caged fall migrants sun-orient when the sun is their sole orientation cue. Sun orientation would result in fall migrants moving south, the direction Monarch butterflies take during their fall migration. A distinction can be seen between the sun orientation of fall migrants and summer non-migrants in opaque periphery cages: the mean$|\theta$–sun azimuth$|$ value for fall migrants was not as consistent throughout the day as it was for non-migrants. Caged fall migrants showed a mean orientation direction closer to the sun's azimuth (mean$|\theta$–sun azimuth$|$ = 31°) from 1000 to 1400 hrs (EST) than before or after this time period (mean$|\theta$–sun azimuth$|$ = 44° and 52°, respectively). The 1000–1400 hrs time period corresponds to the migratory period of fall migrants (Brower, personal communication; Kanz, 1973; Urquhart, personal communication; Kanz, 1973; Urquhart, personal communication). The sun-orienting response of non-migrants on the other hand, was consistent, or even improved, throughout the course of the day (30°, 27°, and 12°, respectively for prior to 1000 hrs, 1000–1400 hrs and after 1400 hrs). This suggests that there is more to the sun orientation of fall migrants than a sun-orienting escape response.

The wider divergence of θ's from the sun's azimuth in the fall tests cannot wholly be ascribed to cooler autumn temperatures in the morning and late afternoon hours. Two fall experiments, including that illustrated in Fig. 3, were conducted when ambient temperatures ranged from 13° to 16°C. This temperature range was less than or equal to that recorded for the time period 1000–1400 hrs for all but two of the remaining fifteen tests of this series (i.e., fall migrants in opaque periphery cages with the sun visible). Caged migrants from these two tests still showed a mean orientation closer to that of the sun's azimuth during the observed 1000–1400 hr migratory period. The orientation of caged fall migrants was random on overcast days (Table I).

Table I. Orientation Statistics from Opaque Periphery Cage Experiments

Experimental Conditions	N^{Φ}	AD*	Mean $\lvert\theta$-sun azimuth$\rvert$¶		P^{Ψ}
Summer non-migrants:§					
clear day	72	51°	23°		73%
overcast day	33	70°	99°		2%
Summer non-migrants,§ overcast day, photoperiod advanced six hours:	14	72°	real sun azim. 98°	shifted sun azim. 72°	0%
Summer non-migrants,§ clear day sun-shade blocking sun for 1/2 of test:					
shade present	84	72°	92°		18%
shade absent	84	51°	17°		79%
Fall migrants:					
clear day	248	64°	39°		31%
overcast day	24	66°	86°		16%
Fall migrants, clear day, sun-shade blocking sun:	15	73°	118°		5%

Φ number of butterflies

* mean absolute difference between each θ's of each test series

¶ mean absolute difference between each θ and sun azimuth

Ψ percentage of observations in which Monarch cage distribution was significantly different from uniform (at the 5% confidence level)

§ laboratory reared under summer conditions

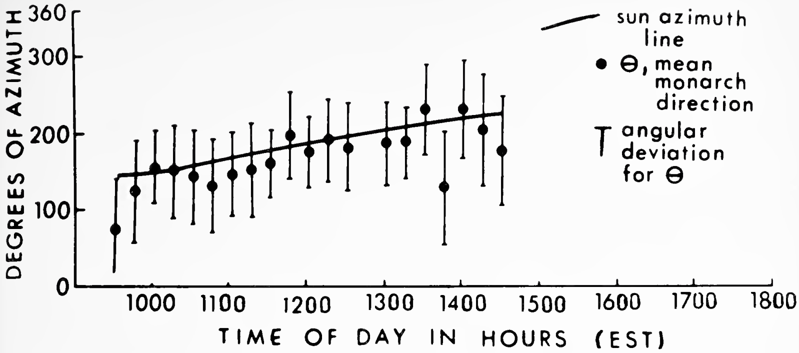


Fig. 3. Orientation of fall migrants captured in the field and tested in opaque periphery orientation cages on a clear day. The orientation displayed by these migrants was a sun orientation.

The consistently random orientation of all Monarchs in no-sun tests, and the random orientation of summer non-migrants reared under a photoperiod advanced 6 hours and tested on no-sun days (Table I), argue against a time-compensating, sun-compass orientation in experiments with opaque periphery cages. von Frisch (1967) showed that a patch of blue sky subtending an angle of only 10° to 15° was not only sufficient for the honeybee to localize the sun's position, but also that the honeybee was capable of a sun-compass orientation using polarized light. The sun's position can be uniquely described for most times of the day by the pattern of polarized light (Stockhammer, 1959; von Frisch, 1967). Experiments with summer laboratory-reared non-migrants and fall Monarchs suggested that the sun orientation of these animals was dependent on the sun being directly visible. On partly cloudy days, opaque periphery cage non-migrants and fall migrants oriented randomly when the sun was obscured by clouds but sun-oriented when the sun was not obscured by clouds. Summer non-migrants (laboratory-reared) and fall migrants, in opaque cages with a sun-shade blocking the sun but the remainder of the sky visible, showed a random orientation with the shade in place and a sun orientation when it was removed (Table I).

Orientation in Transparent Periphery Cages

Tests performed with transparent periphery orientation cages exposed Monarchs to terrestrial as well as celestial orientation cues.

Table II. Orientation Statistics from Transparent Periphery Cage Experiments

Experimental Conditions	N[Φ]	AD	Mean |θ-sun azimuth|[¶]	P[Ψ]
Summer non-migrants:[§]				
clear day	51	69°	73°	13%
overcast day	25	68°	90°	14%
Fall migrants:				
clear day	100	56°	40°	54%
overcast day	31	67°	102°	33%

Φ number of butterflies
* mean angular deviation for the θ's of each test series
¶ mean absolute difference between each θ and sun azimuth
Ψ percentage of observations in which Monarch cage distribution was significantly different from uniform (at the 5% confidence level)
§ laboratory reared under summer conditions

The orientation of summer laboratory-reared, non-migrant Monarchs in transparent periphery cages was random with or without the sun visible (Table II), and was comparable to the random orientation shown by opaque periphery cage non-migrants and migrants in the absence of sun cues. Therefore, the presence of terrestrial cues over-rides the sun-orienting escape response of non-migrant Monarchs. It is possible that using terrestrial instead of sun cues each non-migrant butterfly persisted in its orientation cue for escape. These experiments demonstrate that the majority of non-migrant Monarchs chose terrestrial rather than sun cues for orientation when both were available.

Fall migrants, exposed to both terrestrial and sun cues, continued to orient to the sun's azimuth (Fig. 4, Table II) with an orientation closer to the sun's azimuth from 1000–1400 hrs, EST, than either before or after this period ($|\theta$–sun azimuth$|$ value being 35°, 52° and 77°, respectively). An exception was seen in one sun-visible test, in which θ's from most significantly grouped animals maintained an approximately 240° heading (southwest). However, this occurred only once and one cannot determine whether terrestrial or celestial cues were used. Random orientation resulted with terrestrial cues present but sun clues absent (Table II). The persistent sun orientation of fall migrants, when the sun and terrestrial cues were visible, is additional support for the hypothesis that the sun orientation of fall migrants is a migratory response and not merely an escape response.

Flight Directions Following Release

Monarchs were released after each experiment and an azimuth reading taken on the vanishing direction of each butterfly using a Silva compass compensated for declination angle. Only those butterflies that flew to the horizon were used in the analysis of Monarch vanishing directions. All Monarchs exhibited speed flight (Urquhart, 1960) immediately upon release. Occasionally Monarchs showed a feeding flight pattern with short randomly directional flights between flowers. When feeding flight took a butterfly to the horizon of the test field within 2 minutes, its azimuth at the periphery was included in the analysis; if feeding flight persisted, the vanishing azimuths of such animals were excluded from computations. Flight altitudes of released Monarchs were evenly divided between those above and below approximately 8 meters.

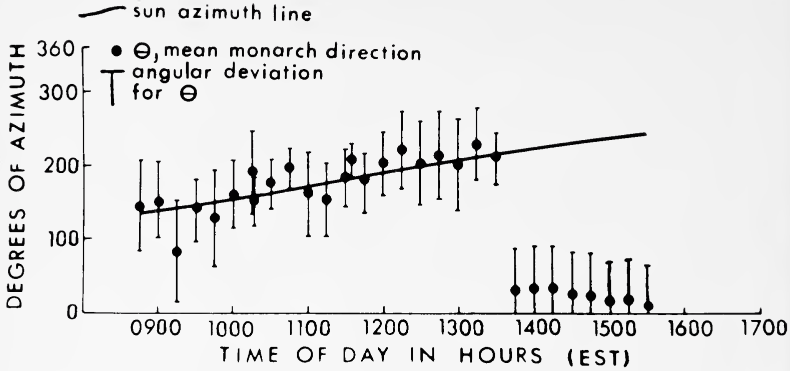


Fig. 4. Orientation displayed by fall migrants in a transparent periphery cage on a clear day. In contrast to summer non-migrants, fall migrants continue to sun-orient in the presence of both sun and terrestrial cues. Readings beginning at 1345 hrs (EST) were an artifact of a sudden ambient temperature drop.

The results of summer Monarch releases with the sun visible showed that most vanishing azimuths appeared to be down-wind rather than toward the sun (Fig. 5). Only the releases of (c), (f) and (h) were significantly grouped about their respective mean orientation direction. Vanishing azimuths for summer non-migrants on overcast days were down-wind (Fig. 6). The distribution of releases in all but (c) were significant about their respective θ's. The releases of (f), with only a light surface wind, appear to be in the direction of the sun's azimuth even though the sun's position was obscured by clouds. However, most of these butterflies flew at an altitude $\geqslant 20$ m and, therefore, likely encountered stronger winds. The vanishing directions of summer Monarchs, therefore, appeared more influenced by wind than by sun. Vanishing azimuths were more scattered with light winds ($\leqslant 5$ mph or 8 km/hr). Low flight enabled Monarchs to fly against head winds that exceeded 10 mph (16 km/hr). Thus, Monarch flight direction was greatly influenced by the wind but was not competely determined by wind direction.

Figure 7 shows the patterns of vanishing azimuths for fall migrants when the sun was visible. All 20 distributions were significant about their respective θ's. The vanishing azimuths generally corresponded to the direction in which the wind was blowing with the exception of (a), (m) and (t). The releases of (a) occurred from a site that was surrounded by water except to the west; Urquhart

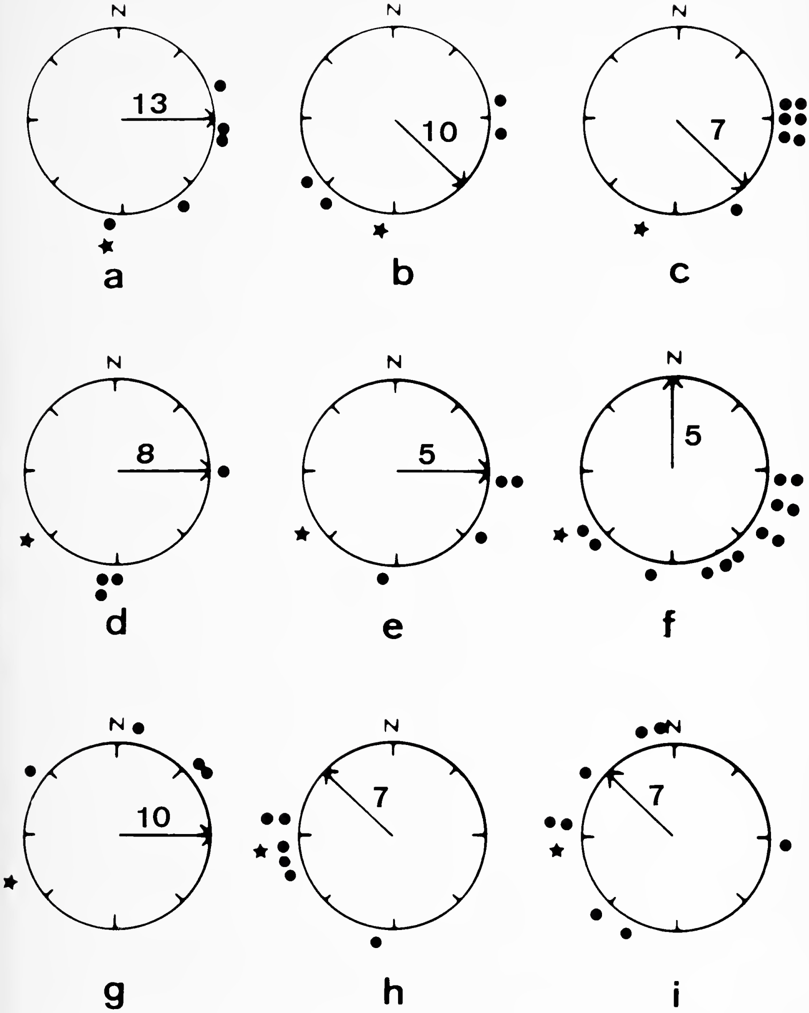


Fig. 5. Release orientation for summer monarchs on clear days. For each circle: Dot indicates the vanishing direction of a butterfly; star indicates sun position at the time of release; radial arrow indicates direction in which wind was blowing and its velocity in miles per hour; N indicates true north. Most vanishing azimuths are seen to be down-wind.

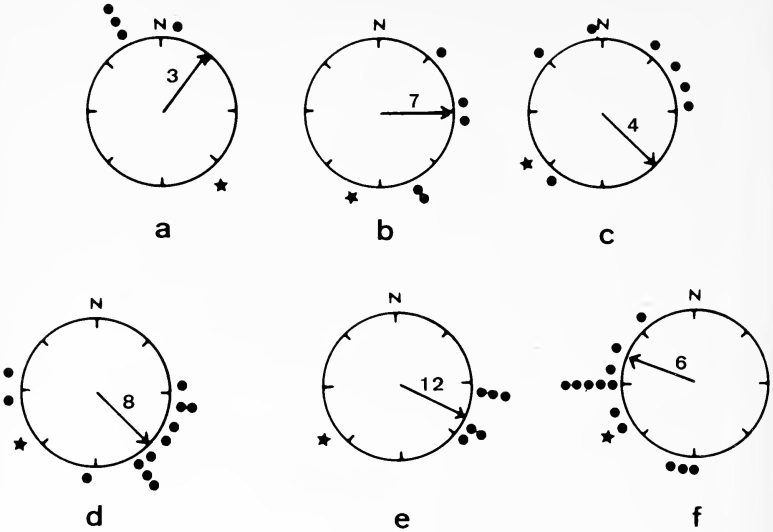


Fig. 6. Release orientation for summer monarchs on overcast days. Symbols are as in Fig. 5. Most vanishing directions were down-wind.

(1960) has observed that Monarchs tend to avoid flying over water when possible. Most flights in (m) were low to the ground, as was true for the majority of flights showing vanishing azimuth into the wind. The releases of (t) occurred at 1600 hrs (EST) when migrants return to roosting trees for the night. The roosting trees for migrants at Gloucester were west and northwest of the release and feeding sites. Thus, the migrants of (t) were possibly returning to their roosting trees; however, it is unclear why the butterflies in (c) chose a similar direction at 1300 hrs (EST) with the same wind velocity as in (t).

Vanishing directions appeared to be down-wind, particularly when winds exceeded 10 mph (16 km/hr) unless the butterfly flew low to the ground. Two-way analysis of variance between the mean angular deviation of 22° for (h), (i), (k), (l), (n) and (o) and the mean angular deviation of 42° for the remaining fourteen release distributions indicate significant differences (F = 9.5, df = 16, $P <$ .01). In the former case, the wind was blowing in the same direction (southwest) as the sun's azimuth. In the latter case, the wind and sun azimuth directions did not coincide. Analysis of variance of

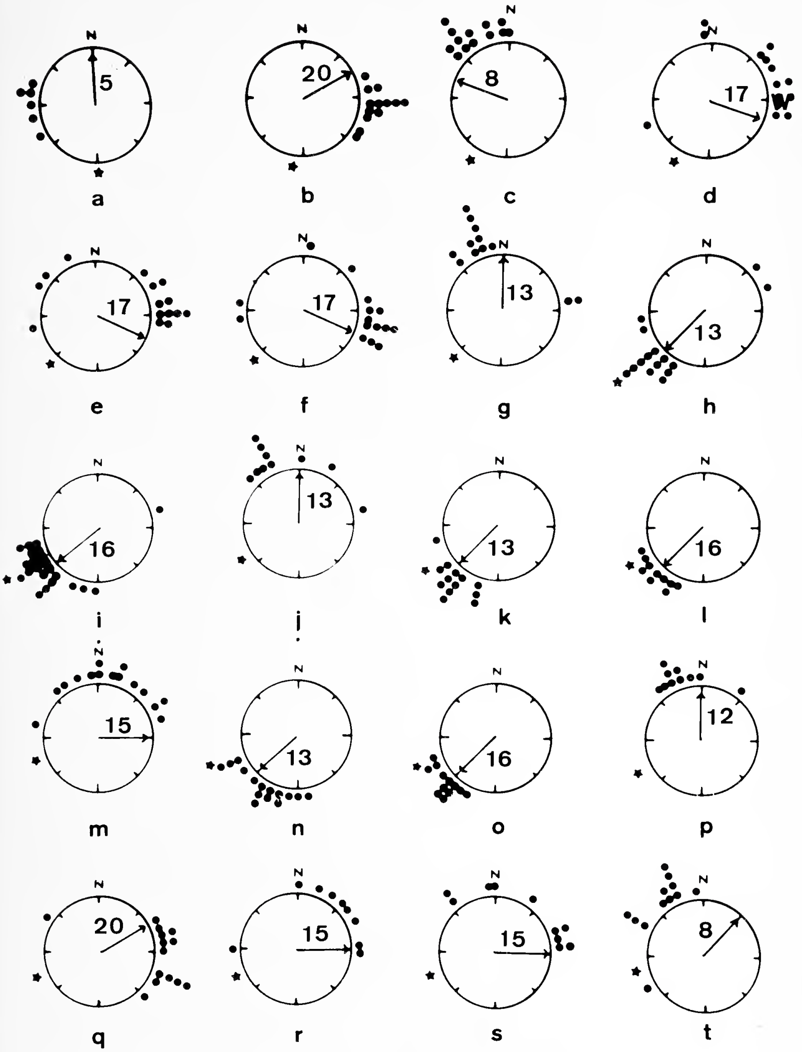


Fig. 7. Vanishing directions of fall migrants on clear days. Symbols are as in Fig. 5. Most releases flew down-wind but distributions for north and northeast winds are tighter than those for southerly winds. See text for discussion.

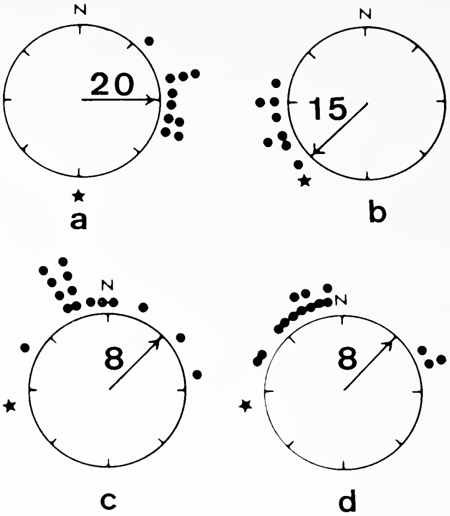


Fig. 8. Vanishing directions for fall migrants released on overcast days. Symbols are the same as in Fig. 5. Monarchs flew generally down-wind.

angular deviations for winds of 13 mph (21 km/hr) shows that the mean AD of 17° for distributions (h), (k) and (n) with the sun and wind in the same direction was significantly smaller than the mean AD of 28° for distributions (g), (j) and (p) with sun and wind directions dissimilar ($F = 4.9$, $df = 5$, $P < .1$). The same was true for winds of 16 mph (26 km/hr) where the mean AD (18°) for (i), (l) and (o) with sun and wind to the southwest was significantly smaller than the mean AD (46°) for (d), (e), (f), (m), (r) and (s) with the sun and wind directions dissimilar ($F = 30.8$, $df = 8$, $P < 0.005$). Therefore, these data suggest that fall migrants were not just flying with prevailing winds but were also orienting toward the sun.

The vanishing azimuths for fall migrants released on overcast days were predominantly down-wind and each distribution was significant about its θ (Fig. 8). Releases (c) and (d) occurred at 1630 hrs and 1700 hrs (EST), respectively, and could be examples of the roosting orientation described for Fig. 7 (t).

Thus, although the sun is an important cue in oriented flight, fall migrants utilize favorable winds to facilitate migration, but display oriented flight without the aid of the wind.

DISCUSSION

The experiments reported here were designed to delineate the role of the sun in Monarch orientation. The sun was selected as the most probable cue in the orientation of Monarch butterflies for several reasons: (1) the Monarch is a diurnal animal and the sun is a prominent cue in its environment; (2) a positive phototaxis has been reported in a number of Lepidoptera (Brandt, 1934; Collins, 1935; Dolley, 1916; Jander, 1963; and Kelsheimer, 1935); (3) the sun has been shown to be important in the orientation of a number of animals (Hasler, 1967; Schmidt-Koenig, 1961; Taylor and Ferguson, 1969; and von Frisch, 1967), including migrating European butterflies (Baker, 1968a,b).

Non-migrant Monarchs (laboratory-reared) demonstrated a sun orientation when tested in an opaque periphery orientation cage with the sun visible. This response was termed an escape response. A sun-orienting escape response for Monarch butterflies is appropriate for three reasons. First, the most prominent orientation cue available to Monarchs in opaque periphery cages on a clear day is the sun. Second, when fast escape flight is warranted, Monarch escape would be linear and, therefore, fastest when the animals use a constant cue, such as the sun, for orientation. Third, when followed by a predator, a sunward escape response would put the sun in the predator's line of sight thus making it more difficult for the Monarch to be detected.

The orientation of summer non-migrants was random with both terrestrial and celestial cues present. If Monarchs were attempting to escape, the sun did not appear to be their orientation cue. This random orientation was believed to be indicative of the orientation of uncaged, non-migrant, Monarchs during the summer, since summer animals are known to wander randomly (Urquhart, 1960). Verheijen (1958) has criticized phototaxis experiments on the basis that the test situations eliminated scattered and reflected light, therefore making the illumination of the animal's environment unnatural. Illumination conditions (as well as conditions in general) during Monarch testing in transparent periphery cages, more closely approximated a natural field situation for Monarchs than the conditions encountered with opaque periphery cages. Thus the responses of transparent periphery cage butterflies might be expected to more accurately represent Monarch orientation.

It has been assumed that Lepidoptera displaying positive phototaxis (Johnson, 1969) were flying directly toward a light source. Hsiao (1973), however, has found that the corn earworm moth, *Heliothis zea,* flies toward a dark band surrounding the light source. Hsiao suggested that this Mach band explanation (Graham, 1966) could explain the attraction of night-flying moths to ultraviolet light sources: moths seek darkness characteristic of their diurnal behavior, although they appear attracted to ultraviolet light. Hsiao's results raise the possibility that sun orientation of Monarch butterflies is an orientation to either (1) a Mach band surrounding the sun, or (2) a Mach band perceived between the sun and the darker horizon. However, the Monarch is a diurnal butterfly, not a nocturnal moth, and butterflies generally seek sun-light areas instead of shaded areas (Klots, 1961).

Data from experiments with caged butterflies might represent landing orientation. However, when observations were made (at times ranging from 1–15 min after cage rotation), few, if any, Monarchs were in flight or landing. In general, the butterflies were either stationary or walking.

The location and shape of the horizon in opaque vs transparent periphery cages could also have affected Monarch orientation. Orientation to mountain tops by many Coccinellidae (Hagen, 1962), and to tree tops by the Scolytid beetle, *Conophthorus coniperda* (Henson, 1966), is presumably based on horizon-orientation. Nevertheless, sun orientation by fall migrant Monarchs persisted in spite of horizon differences between opaque and transparent periphery orientation cages. It seems unlikely, therefore, that the cage orientation of these insects was significantly affected by horizon differences. The orientation displayed by summer non-migrants was different in the two types of cages. This difference might reflect an horizon influence, but other factors, such as the presence or absence of terrestrial cues, are equally likely.

When the sun was visible, fall migrant Monarchs oriented to the sun's azimuth regardless of the type of orientation cage. In contrast, non-migrant orientation was sunward only in opaque periphery cages. One explanation for this difference in orientation response could be that a sun-orienting escape response is stronger in fall migrants than in summer non-migrants. Tables I and II show that the sun orientation of fall migrants (opaque or transparent periphery cages) was not as conclusive, statistically, as the sun orientation of summer non-migrants in opaque periphery cages. Furthermore, a stronger escape response could be expected to be positively correlated with a greater overall level of activity within a cage. It was found, however, that cage activity during fall tests was less than cage activity during summer tests.

The tendency of fall migrants to orient more closely to the sun's azimuth during the observed fall migratory period (1000–1400 hrs, EST) was another feature distinguishing fall migrant sun orientation from escape response sun orientation. A sun orientation restricted to the period 1000–1400 hrs would offer several advantages to Monarchs migrating south: (1) A restricted sun orientation encompasses an arc of 60° to 70° compared with an arc of 160° to 180° resulting from all-day sun orientation and the 60°–70° arc rarely deviates from the desired south to southwest migratory direction. (2) Consequently, the distance traveled, and time and energy expended, would be less. Tunmore (1960) has suggested a similar scheme for bird navigation. (3) A restricted sun orientation also obviates the necessity of sun-compass orientation to explain the precision of the Monarch's long-distance fall migration. The data suggest that the restricted sun orientation was independent of temperature (for ambient temperatures greater than 13° C). (4) Since the highest autumn temperatures generally occur between 1000 hrs and 1400 hrs (EST), fall migrants would be migrating during the warmest part of the day.

If fall migrants use sun orientation, then spring migrants returning north might use a negative sun orientation. Reversed orientation by insects between leaving and returning to a site is well known (Geir, 1960; Johnson, 1969; Kennedy and Booth, 1963; Pickens, 1934; and Shephard, 1966).

Monarch migrations are undoubtedly affected by winds. However, while Monarch migrations appear to be aided by prevailing winds, they are not as dependent on them as locusts (Waloff, 1946, 1958) and aphids (Johnson, 1954, 1969). Figure 7 showed that the distributions of release azimuths were tighter when migratory and down-wind directions coincided than when the two directions differed. Furthermore, several instances were recorded (Kanz, 1973) where fall and spring migrants were engaged in directed migratory flights with little or no wind. The prevailing surface wind patterns for up to 500 m altitude (Prevailing Direction, Mean Speed and

Fastest Mile of Wind, U.S. Weather Bureau) for September and October would facilitate a southwestward movement of Atlantic Coast migrants in the fall, and for March and April would facilitate a north and northeastward movement of migrants passing north through Mexico and Texas. Prevailing wind patterns for March and April suggest a possible explanation for why the population of Monarch butterflies in the United States (excluding the West Coast population) is proportionally greater east than west of the Mississippi River (Urquhart, personal communication). Strong March and April winds from the north, west, and northwest in northern Texas and Nebraska, could force spring Monarchs, orienting by a negative sun-orientation, to the east and northeast. Therefore, even a broad northerly orientation for spring migrants might still result in biasing the summer population toward the eastern half of the United States. Thus, it might not be necessary for Monarchs to possess a restricted negative sun orientation in order to assure a northeasterly movement in the spring.

SUMMARY

Non-migrant and fall migrant male and female Monarch butterflies, *Danaus plexippus* L., orient toward the azimuth of the sun when confined in circular orientation cages with only celestial cues present. When both terrestrial and celestial cues are present, non-migrants exhibit random directionality similar to the flight of free-flying summer non-migrants while fall migrants orient to the sun's azimuth. Both fall migrants and non-migrants exhibit a random cage distribution under overcast sky with or without terrestrial cues. The sun orientation of fall migrants is believed to be a migratory response resulting in a southward movement. Such orientation differed from the sun orientation of non-migrants which appears to be an escape response. Upon release, migrants and non-migrants tend to fly with the wind. No conclusive indication of sun-compass or polarized light orientation in migrants or non-migrants was evident. No sex differences in orientational responses were observed.

ACKNOWLEDGMENTS

I wish to thank Dr. E. S. Hodgson for his advice and support during this study. In addition, I am indebted to Dr. F. A. Urquhart of the University of Toronto and Dr. L. P. Brower of Amherst

College for their help in establishing a laboratory colony of Monarch butterflies. I would also like to thank Ms. Mary Kanz for her assistance throughout the field studies. This research was supported, in part, by funds derived from an NIH Career Development Award to Dr. K. D. Roeder, Tufts University.

REFERENCES

BAKER, R. R. (1968a). A possible method of evolution of the migratory habit in butterflies. *Phil. Trans. R. Soc.* (B), 253, 309–341.

BAKER, R. R. (1968b). Sun orientation during migration in some British butterflies. *Proc. R. ent. Soc.* (A), 43, 89–95.

BATSCHELET, E. (1965). Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. AIBS Monograph, Washington, D.C.

BRANDT, H. (1934). Die Lichtorientierung der Mehlmottle *Ephestia Kuehniella Zeller. Z. vergl. Physiol.*, 20, 646–673.

COLLINS, D. L. (1935). Comments upon phototropism in the codling moth with reference to the physiology of the compound eyes. *J. econ. Ent.*, 28, 103–106.

DOLLEY, W. L. (1916). Reactions to light in *Vanessa antiopa*, special reference to circus movements. *J. exp. Zool.*, 20, 357–420.

GEIR, P. W. (1960). Physiological age of codling moth females (*Cydia pomonella* (L)) caught in bait and light traps. *Nature, Lond.*, 185, 709.

GRAHAM, C. H. (1966). *Vision and Visual Perception.* New York: John Wiley and Sons.

GREENWOOD, J. & DURAND, D. (1955). The distribution of length and components of the sum of n random unit vectors. *Ann. math. Statist.*, 26, 233–246.

HAGEN, K. S. (1962). Biology and ecology of predaceous Coccinellidae. *A. Rev. Ent.*, 7, 289–326.

HASLER, A. (1967). Underwater guideposts for migrating fishes. In: *Animal Orientation and Navigation*, pp. 1–20. Corvallis, Oregon: Oregon State University Press.

HENSON, W. R. (1966). The analysis of dispersal mechanisms in *Conophthorus coniperda Sz.* Biometeorology 2. *Proc.* III *Int. Congr. Biomet.* (Pau, 1963), pp. 541–549.

HSIAO, H. S. (1973). Flight paths of night-flying moths to light. *J. Insect. Physiol.*, 19, 1971–1976.

JANDER, R. (1963). Insect Orientation. *A. Rev. Ent.*, 8, 95–114.

JOHNSON, C. G. (1954). Aphid migration in relation to weather. *Biol. Rev.*, 29, 87–118.

JOHNSON, C. G. (1969). *Migration and Dispersal of Insects by Flight.* London: Methenun and Co., Ltd.

KAMMER, A. E. (1968). Motor patterns during flight and warm-up in Lepidoptera. *J. exp. Biol.*, 48, 89–109.

KAMMER, A. E. (1970). Thoracic temperature, shivering, and flight in the monarch butterfly *Danaus plexippus* (L). *Z. vergl. Physiol.*, 68, 334–344.

Kanz, J. E. (1973). The orientation of non-migrant and migrant monarch butterflies (*Danaus plexippus*). Ph.D. Dissertation. Medford, Massachusetts: Tufts University.

Kelsheimer, E. G. (1935). Response of European corn borer moths to colored lights. *Ohio J. Sci.*, 35, 17–28.

Kennedy, J. S. & Booth, C. O. (1963). Free flight of aphids in the laboratory. *J. exp. Biol.*, 40, 67–85.

Klots, A. B. (1951). *A Field Guide to the Butterflies.* Boston: Houghton Mifflin Co. (The Riverside Press).

Nielsen, A. & Nielsen, E. T. (1952). Migration of the pieride butterfly *Ascia monuste* L. in Florida. *Ent. Meddr.*, 26, 386–391.

Pickens, A. L. (1934). *Termites and Termite Control* (Ed. by C. A. Kofoid). Los Angeles: University of California Press.

Prevailing Direction, Mean Speed, and Fastest Mile of Wind; from *National Atlas of the United States.* U.S. Weather Bureau, U.S. Department of Commerce, Washington, D.C.

Schmidt-Koenig, K. (1961). Sun navigation in birds? *Nature, Lond.*, 190, 1025–1026.

Shephard, R. F. (1966). Factors influencing the orientation and rates of acitivity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Can. Ent.*, 98, 507–518.

Stockhammer, K. (1959). Die Orientierung nach der Schwingungsrichtunglinear polarisierten Lichtes und ihre sinnesphysiologischen Grundlagen. *Ergebn. Biol.*, 21, 23–56. Summarized in: *The Dance Language and Orientation of Bees* by Karl von Frisch (1967). Cambridge, Mass.: Harvard University Press.

Tables of Computed Altitude and Azimuth, Latitudes 40°–49° N. Inclusive (1962). U.S. Navy Hydrographic Office, Publication No. 214, Volume V. Washington, D.C.: U.S. Government Printing Office.

Taylor, D. H. & Ferguson, D. E. (1969). Solar cues and shoreline learning in the Southern Cricket Frog, *Acris gryllus*. *Herpetologica*, 25, 147–149.

The National Almanac, for Years 1970–1973. Issued by the U.S. Naval Observatory. Washington, D.C.: U.S. Government Printing Office.

Tilden, J. W. (1962). General characteristics of the movement of *Vanessa cardui* (L). *J. Res. Lepidop.*, 1, 43–49.

Tunmore, B. G. (1960). A contribution to the theory of bird navigation. *Proc. XII Int. Ornith. Cong., Helsinki*, pp. 718–723.

Urquhart, F. A. (1960). *The Monarch Butterfly.* Toronto, Canada: University of Toronto Press.

Urquhart, F. A. (1976). Found at last: The Monarch's winter home. National Geographic, *150* (12): 161–173.

Urquhart, F. A. & Stegner, R. W. (1966). Laboratory techniques for maintaining cultures of the monarch butterfly. *J Res. Lepidop.*, 5, 129–136.

Verheijen, F. J. (1958). The mechanisms of the trapping effect of artificial light sources upon animals. *Archs. neerl. Zool.*, 13, 1–107.

von Frisch, K. (1967). *The Dance Language and Orientation of Bees.* Cambridge, Mass.: Harvard University Press.

WALKER, J. J. (1914). The geographical distribution of *Danaida plexippus* L. (*Danais archippus* F.) with especial reference to its recent migration. *Entomologist's mon. Mag.*, 50, 181–193, 224–237.

WALOFF, Z. (1946). A long-range migration of the Desert Locust from Southern Morocco to Portugal, with an analysis of concurrent weather conditions. *Proc. R. ent. Soc.* (A), 21, 81–84.

WALOFF, Z. (1958). The behaviour of locusts in migrating swarms. *Proc. X Int. Congr. Ent., Montreal,* 2, 567–570.

WILLIAMS, C. B. (1951). Seasonal changes in flight direction of migrant butterflies in the British Isles. *J. Anim. Ecol.,* 20, 180–190.

WILLIAMS, C. B. (1958). *Insect Migration.* London: Collins Press.

WILLIAMS, C. B., G. F. COCKBILL, M. E. GIBBS, J. A. DOWNES (1942). Studies in the migrations of Lepidoptera. *Trans. R. ent. Soc., Lond.,* 92, 101–283.

REDESCRIPTION OF *XENICOPODA* MOORE AND LEGNER (COLEOPTERA: STAPHYLINIDAE, OMALIINAE), WITH SUPPLEMENTARY NOTES*

By Margaret K. Thayer

Museum of Comparative Zoology, Harvard University,
Cambridge, Mass. 02138

Introduction

Moore and Legner (1971) described a new genus and species of Omaliinae, *Xenicopoda helenae,* on the basis of a unique specimen of undetermined sex collected on Mt. Wilson, California. The major distinguishing character they noted for this genus (op. cit. and Moore and Legner, 1974) was the bizarrely modified protarsi, quite unlike any previously described in the Omaliinae.

Since then I discovered a series of six *X. helenae* in the H. C. Fall Collection at the Museum of Comparative Zoology. Examination of these specimens showed that the unusual front tarsi found on the type are present only in males. Females have normal female omaliine protarsi, slender and with equal tarsal claws. This distinct difference between the sexes and the availability of additional specimens of *Xenicopoda* made it seem worthwhile to publish an amplified description of the genus. Detailed study of the type and the six other specimens also led to the discovery of a number of discrepancies between the specimens and the original description. The proportions as given in the description and as shown in the original habitus drawing are rather distorted, owing partly, perhaps, to the fact that the type is somewhat curled up. Proportions based on careful measurements of the seven available specimens will be mentioned below. The head shape in the original drawing is rather distorted as well, and a new figure is given.

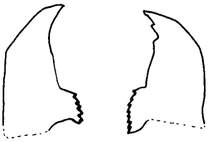
**Manuscript received by the editor November 3, 1977*

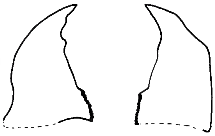
REDESCRIPTION

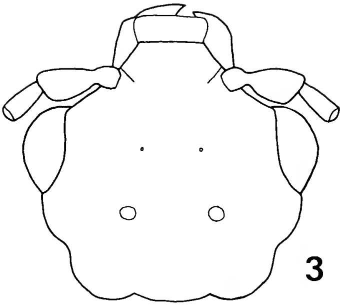
Length: mean 2.5 mm (2.0–2.7 mm), measured as is (slightly curled); estimated actual length 3.0 mm (2.5–3.6 mm).

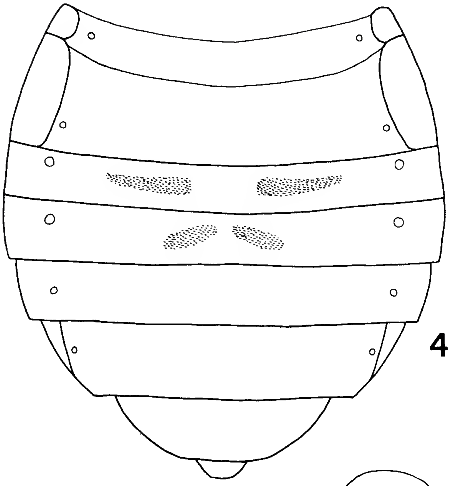
Head about seven-tenths as long as wide (from clypeal apex to nuchal constriction), epistomal sulcus absent (fig. 3). Vertex with well-impressed dorsal tentorial pits and small, rather obscure pale ocelli. (The dorsal tentorial pits are presumably what Moore and Legner (1971) meant by anterior tentorial pits. The latter are actually very slight depressions antero-medial to the antennal insertions, indicated by short lines there in figure 3.) Weak nuchal constriction across dorsal surface just behind ocelli. Faint microsculpture on dorsal and ventral surfaces of head. Labrum nearly rectangular with rounded anterior corners, about 2.2 times as wide as long; margins entire. Mandibles as illustrated (figs. 1, 2) with well-developed molar areas composed of many small, sharp, buccally directed teeth. Maxillary palp four-segmented, more or less filiform, with first segment small; second and third segments larger, subequal to each other, more or less obconical; fourth segment at least twice as long as wide (2.1–3.3x, mean 2.5x), tapering toward apex, the whole segment twice as long as the third, but narrower than its apex. Labial palp three-segmented, each segment slightly longer and narrower than the preceding; third segment two to three times as long as wide. Gular sutures distinctly separate, closest at a level just before the hind margins of the eyes and diverging anterior and posterior to this. Antenna filiform, basal segments distinctly longer than wide, more distal ones becoming successively shorter and broader up to tenth segment, which is very slightly wider than long. First five or six antennal segments glabrous except for sparsely scattered long setae; segments six or seven to eleven with shorter setae in addition. The shorter setae become progressively denser on the more distal segments, while the longer setae diminish in number and become increasingly restricted to the apical area of each segment.

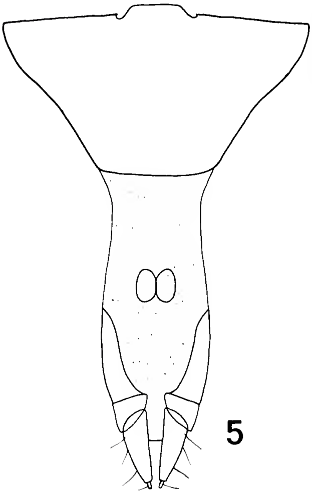
Pronotum about seven-tenths as long as wide, about half as long as elytra; fairly evenly convex except for a small median basal depression; lateral margins evenly arcuate, slightly explanate in basal half; reticulate microsculpture on dorsal surface. In ventral view, postcoxal process of pronotum extends about halfway from lateral

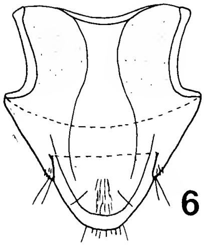

1

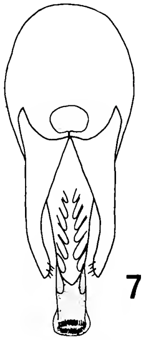

2

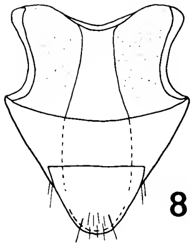

3


4


5


6


7


8

pronotal margin to midline of prothorax. Procoxa and protrochantin very strongly and sharply carinate externally. Prosternum with short acute process barely extending between procoxae externally. Mesosternum not longitudinally carinate, having a fairly even surface with no distinct depressions fitting against procoxae; with a short rounded process between mesocoxae. Mesocoxae slightly separated, but meso- and metasternum not touching externally. Metasternum without external process between mesocoxae, with a short pair of processes between metacoxae. Metacoxa triangular in ventral view, with posterior surface slightly excavate. Apex of coxa slightly explanate laterally, overlapping part of the trochanterofemoral joint when the leg is in a retracted position. All tibiae with vague row of spines along part or all of outer face. Tibiae and tarsi slender except male prolegs as described below. Metatarsus about three-fourths as long as metatibia, first four segments subequal in length, fifth about twice as long as each of first four. Pair of empodial setae between claws on all tarsi, generally about half as long as claws.

Elytra together about 1.1 times as long as wide; without microsculpture between punctures; probably extending to about the apex of tergite 4 in life. Elytral epipleuron delimited by a distinct lateral keel. Wings fully developed, with a typical omaliine folding pattern (my unpublished data).

Abdomen with fine reticulate microsculpture on dorsal and ventral surfaces; intersegmental membranes with brick-wall pattern (with occasional irregularities) typical of Omaliinae (see Hammond, 1971); sternites of segments 2 and 3 apparently without a keel between metacoxae; tergites 2 and 3 somewhat sclerotized, 4 and following more so; tergites 4 and 5 each with a pair of small patches of medially-directed microtrichia ("pruinose" or "tomentose" spots of authors; see fig. 4); only segments 3 and 7 bearing paratergites ("margined segments"), segment 2 with sternites extending onto dorsal surface, other segments with narrow membranous joint di-

---

Figs. 1–8. *Xenicopoda helenae* Moore and Legner. 1–2. Mandibles; 1., ventral; 2., dorsal view. 3. Head, dorsal view (large circles = ocelli, small circles = dorsal tentorial pits). 4. Abdomen, segments 2–8 and (male) genital segment, dorsal view. 5. Eighth abdominal sternite and external female genitalia, ventral view. 6–8. Male genitalia; 6., Genital segment, ventral view; 7., Aedeagus (as positioned within abdomen), dorsal view; 8., Genital segment, dorsal view. Membranous areas of genitalia stippled. Scale line = 0.5 mm.

rectly between tergite and sternite; sternite 8 with median basal process as illustrated in figure 5.

Male: Protibia abruptly broadened just beyond base, its maximum width about twice that of a mesotibia; apical half of outer face with an irregular row of spines intermixed with a few setae; rounded notch at apex on outside of tibia. Protarsus with first four tarsomeres expanded: the first a pedunculate triangle, next three roughly triangular with their anterior apical corners successively more prolonged; ventral surfaces of first four segments with large strap-like setae (except medially); fifth tarsomere distinctly curved ventrally, apex twice as wide as base. Anterior protarsal claw much longer and thicker than all other tarsal claws, about four-fifths as long as protarsus. Posterior protarsal claw normal. Empodial setae on protarsus shorter than usual, about one-fourth as long as posterior claw. Peg setae (see Hammond, 1972) appear to be absent from legs. Genital segment and aedeagus as in figures 6–8. Aedeagus with parameres dorsal within abdomen, internal sac with dense armature.

Female: Protibia slender, similar to meso- and metatibia, spinose along entire outer face. Protarsus narrow (as meso- and metatarsus), fifth tarsomere only slightly wider at apex than at base; normal slender setae on ventral surface of tarsomeres 1–4. All tarsal claws similar in size and shape. Genitalia as in figure 5, sclerotized spermatheca apparently absent.

Material examined: CALIFORNIA: Los Angeles Co.: Mt. Wilson, 6–III–46, G. P. Mackenzie (Holotype, male) [California Academy of Sciences]; Pasadena, Echo Mt., 18–III–16, 3500 ft., (1 male, 1 female) [Museum of Comparative Zoology]; (Los Angeles Co.?) Pomona Mts., II–22 (2 males, 1 female) [MCZ]. Santa Barbara Co.: Santa Barbara, 8–II–91 (1 male) [MCZ].

DISCUSSION

The distinctive protarsi of *Xenicopoda* males may be modified to facilitate grasping females during copulation. There seem to be no corresponding special structures in females, but both the pronotum and the elytra have fairly sharp lateral margins. Assuming that a male mounts a female dorsally (I have collected *Eusphalerum* mating this way), he might use his protarsi to grasp her pronotum or elytra in either of two ways: 1) with his tarsi dorsal and tarsal claws ventral to the lateral edge of the body; 2) with the anterior side of the tarsus (including anterior protarsal claws) dorsal and posterior side ventral to the lateral edge of the body. The bifurcate nature of the second to fourth protarsal segments of the male and the lack of setae along the midline of the tarsus lend some credence to the latter hypothesis, but of course only direct observation of mating can confirm or deny any of this speculation. Why only one genus, out of all known Omaliinae, has these tarsi remains a mystery. The large strap-like setae on male *Xenicopoda* protarsi also may be an aid to grasping females in copulation. The presence of modified protarsal setae in at least the males is characteristic of nearly all omaliine genera I have seen (approximately 40, of which at most 5 lack these setae entirely). The form of the modified setae varies: some, like those of *Xenicopoda,* are strap-like, while others are spatulate, more or less like those of *Xanthonomus* Bernhauer, as illustrated by Steel (1955). Those of other genera form a continuum between these two types. Rarely, females also have modified setae on the protarsi, and in *Eusphalerum, Amphichroum,* and *Pelecomalium,* modified setae are found on all tarsi of both sexes, although in all these cases the setae of the males seem to be broader than those of the females. Males of several genera have modified setae on their mesotarsi as well as on their protarsi.

Most Omaliinae have a pair of paratergites on the second through seventh abdominal segments. In their description of *Xenicopoda,* Moore and Legner (1971) stated that paratergites are present on the fourth and fifth "visible abdominal segments" (=sixth and seventh segments), although their figure seems to show paratergites on the seventh and eighth segments. Examination of a cleared *Xenicopoda* specimen reveals that only the third and seventh segments bear paratergites. The second segment appears at first to have paratergites, but closer examination reveals that the sternite extends continuously onto the dorsal surface, whereas there is a membranous articulation between paratergites 3 and 7 and their respective sternites. *Xanthonomus* appears to have a similar abdomen, but has paratergites present only on the seventh segment (Steel, 1955, description and figs. 1–2; also I have examined specimens of an apparently undescribed *Xanthonomus* sp. in the Bernhauer Collection). I do not intend to imply, however, that these two genera are related because of their similarity in abdominal structure.

To include females of *Xenicopoda* in Moore and Legner's (1974) key to North American omaliine genera, couplet 29 should be replaced by the following:

29(28) Abdomen lacking paratergites except on segments 3 and 7; male with large unequal protarsal claws, anterior one much longer and thicker than posterior, sometimes nearly as long as tarsus .... *Xenicopoda* Moore & Legner

—Abdomen with paratergites on segments 3 through 7; protarsal claws equal in both sexes, same size as those on meso- and metatarsi 30

There are no ecological data on any of the specimens seen. Examination of one cleared specimen, however, revealed the gut to be packed with pollen grains, as in *Eusphalerum* spp., *Amphichroum* spp., *Pelecomalium* spp., and some *Elonium* spp. which are found on flowers. The presence of a mandibular mola composed of small sharp teeth is fairly restricted within the Omaliinae, but all of the above-named genera except *Elonium* share this character with *Xenicopoda.* (*Brathinus* spp. and *Olophrum* spp., which are not floricolous, also have molar surfaces composed of separate teeth, but the teeth differ in size, shape, and orientation from those of *Amphichroum, Eusphalerum, Pelecomalium,* and *Xenicopoda.*) Pollen-feeding in *Elonium* may well be a secondary development, as most species of this genus seem not to be found on flowers; this possibility makes the lack of a toothed mola in the flower-dwelling *Elonium* species less surprising. The other genera mentioned are apparently entirely floricolous as adults. This evidence and the collection dates on the seven known specimens of *Xenicopoda* suggest that an intensive search in February and March on flowers in the fairly restricted area where the genus has been collected might turn up additional specimens of this interesting beetle.

The genus *Xenicopoda* was placed in the tribe Anthophagini by its authors. For the time being it may remain there, pending badly-needed further study of the higher classification of the Omaliinae.

ACKNOWLEDGEMENTS

I would like to thank D. H. Kavanaugh, California Academy of Sciences, for the prompt loan of the type of *Xenicopoda helenae;* H. S. Dybas and E. H. Smith, Field Museum of Natural History, for the opportunity to study the type of *Xanthonomus toxopeanus*

(Bernhauer) and to borrow specimens of *Xanthonomus* sp.; Nancy Hinnebusch for typing the manuscript; and especially my husband, A. F. Newton, Jr., for continual encouragement and advice in the preparation of this paper.

REFERENCES CITED

HAMMOND, P. M.

1971. The systematic postition of *Brathinus* LeConte and *Camioleum* Lewis (Coleoptera:Staphylinidae). J. Ent. (B) **40**(1): 63–70.

1972. The micro-structure, distribution and possible function of peg-like setae in male Coleoptera. Ent. Scand. **3:** 40–54.

MOORE, I. AND E. F. LEGNER.

1971. A new genus and species of rove beetle from California (Coleoptera: Staphylinidae). Coleopt. Bull. **25:** 51–53.

1974. Bibliography (1758 to 1972) to the Staphylinidae of America north of Mexico (Coleoptera). *and* Keys to the genera of the Staphylinidae of America north of Mexico exclusive of the Aleocharinae (Coleoptera: Staphylinidae). Hilgardia **42**(16): 511–563.

STEEL, W. O.

1955. Notes on the Omaliinae (Col., Staphylinidae) (7) The genus *Xanthonomus* Bernhauer. Entomol. Mon. Mag. **91:** 275–278.

ASSOCIATIONS BETWEEN FLIES AND SPIDERS: BIBIOCOMMENSALISM AND DIPSOPARASITISM?*

By
Michael H. Robinson and Barbara Robinson

Smithsonian Tropical Research Institute
P.O. Box 2072, Balboa, Canal Zone, Panama

There are numerous records in the arachnological and entomological literature of relationships between spiders and flies other than the simple case of predator and prey. Bristowe (1941:362–370) reviewed a number of cases of parasitism and commensalism. Flies of the superfamily Drosophiloidea are involved in a number of more or less complex relationships with spiders. Chloropids parasitize spiders' egg cocoons and may actually perch on adult spiders (Bristowe, 1941:367) while milichiids share food with spiders (Richards, 1953). McMillan (1975) has recorded an association between milichiid flies of the genus *Desmometopa* and two species of large Australian orb-weaving spiders. The flies moved about the host web and fed on prey items as they were being consumed by the spiders. In addition, the milichiid moved onto the host and apparently cleaned the mouthparts and anal region of the spider. McMillan does not state whether the flies remained on the spiders when they were not actively cleaning them nor does he state how many flies were present on the spider at any one time. We here report on several different associations between flies and spiders, all of which are commensal (in the broadest sense). We found milichiids associated with the golden-web spider *Nephila clavipes,* unidentified flies were found as commensals of *Argiope savignyi,* and chloropid flies were found in a similar relationship with *Argiope argentata.* All these relationships were discovered in Panama. We describe a case of milichiid commensalism with a predatory hemipteran and suggest that the complex relationship between *Nephila* and the milichiids may have evolved from such a relatively simple stage. We think that the term commensalism is not sufficiently specific to describe some of the relationships reviewed here and suggest two possible additions to the terminology of symbioses.

**Manuscript received by the editor October 31, 1977.*

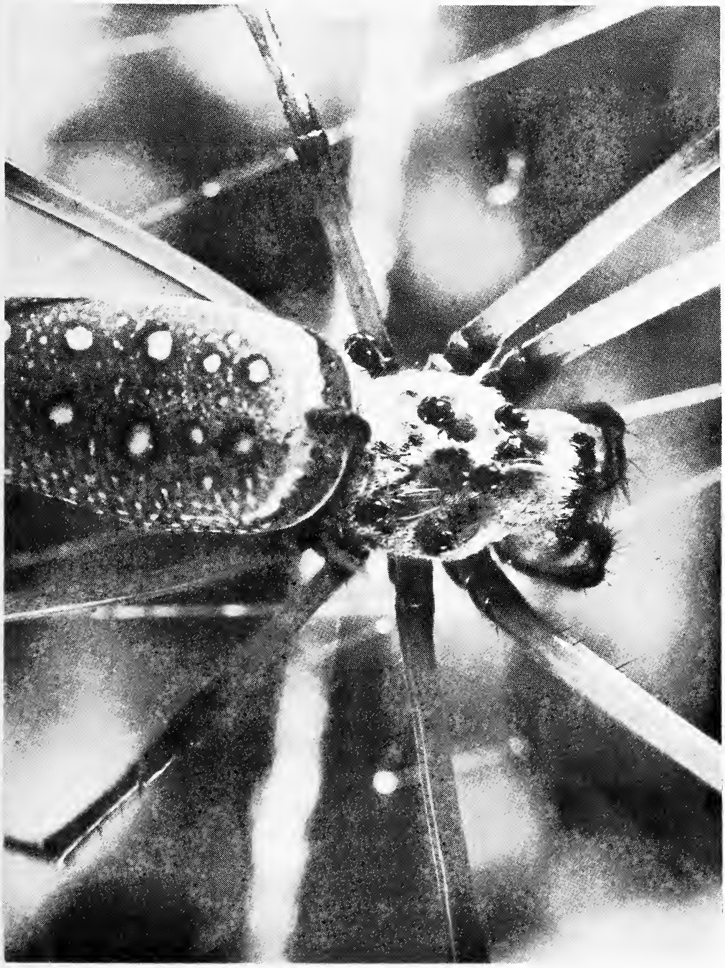


Figure 1. Dorsal surface of cephalothorax and part of abdomen of adult female *Nephila clavipes.* Eight milichiid flies can be counted on the spider.

Nephila clavipes and flies of the genus *Phyllomyza*

We first found flies associated with *Nephila clavipes* in January 1976, on Barro Colorado Island, Canal Zone, Panama. We subsequently found similar flies associated with this spider at a number of localities in the Canal Zone and elsewhere in Panama. Flies from four adult female *N. clavipes* at four different sites were collected. They were identified (see acknowledgments) as belonging to the genus *Phyllomyza* and all belonging to the same (undetermined) species. All eleven insects were females. The flies rest on the dorsal surface of the spider and usually aggregate on the cephalothorax. Figure 1 shows eight flies resting on this area. The flies remain on the spider for long periods of time and are virtually inactive. When we set out to determine what the flies were doing sitting on the body of the spider we ran into a major practical problem. The *Drosophila*-sized flies were really too small to observe with the unaided eye. This problem was solved by adapting a stereo-binocular microscope for horizontal use, mounted on a camera tripod (Robinson & Smythe, 1976). With this device, under field conditions we could watch the insects under 10× or 20× magnification. It became apparent that on the cephalothorax of the spider the flies were not doing anything other than grooming themselves, sporadically shifting position and occasionally defecating. The bodies looked entirely normal and there was no evidence of oviposition or of penetrative feeding on the spider itself. (The mouthparts of milichiids could clearly not be used for piercing the spider's cuticle and sucking its internal fluids, but at this stage we did not know what the flies were.) Eventually we decided to feed the spider. This went through all phases of its predatory behavior without disturbance to the flies. Prey capture involved rushing out to attack the prey, biting it, wrapping it in silk, removing it from the web, transporting it back to the hub and there wrapping it once again before hanging it and feeding (details in Robinson & Robinson, 1973, for *Nephila maculata* apply broadly to *N. clavipes*). This predatory sequence involves a great deal of violent movement, in space and of the spider's legs, throughout which the flies simply sat tight.

At the hub the spider passed secretions into the prey and after about eight minutes the whole surface of the insect was covered in a film of liquid. At this stage the flies left the body of the spider and clustered on the surface of its prey. There they could be seen dabbing at the liquid with their extended mouthparts. They quickly became swollen with food and their abdomens in particular were distended and almost spherical. The intersegmental membranes became very clearly visible and extended. After feeding the flies returned to the spider's cephalothorax. This timing of movement onto the prey item to coincide with its liquifaction seems to be fairly precise. It occurred in five out of five instances in which we provided the spider with prey and watched the whole process from its inception. The spider on which we made these observations disappeared after four days and we replaced it (on the still-intact web) with an adult female *Argiope argentata.* Two flies settled on this spider and fed once on her prey before disappearing. (It is noteworthy that the *Argiope* was able to locate and successfully attack prey on the structurally very different *Nephila* web. This has provided us with a useful tool for further studies of araneid predatory behavior.)

We saw very few cases where the spider reacted to the presence of the flies. Araneids seem to make very few responses to the activities of their larger kleptoparasitic associates, the theridiids of the genus *Argyroides* (see Robinson & Olazarri, 1971:34–5; Robinson & Robinson, 1973:32).

Argiope savignyi and unidentified flies

While carrying out observations on *Argiope savignyi* in an insectary at Curundu, Canal Zone, Panama, the prey of two separate adult female spiders was visited by flies that did not alight on the spider at any stage. The flies "appeared from nowhere" and fed on liquifying prey items from which the spider was simultaneously feeding. On one occasion the spider's prey was a pentatomid and the entire insectary in which we were working was flooded with the penetrating odor of the hemipteran's defensive secretion. In the second case (Figure 2), the prey was a moth. In both instances the flies alighted on the spider's prey and never moved onto the spider at any stage. After feeding they simply flew off. We were unable to catch the three flies involved.

Argiope argentata and *Conioscinella* sp.

While censusing *Argiope argentata* along the Old Gamboa Road, Summit, Canal Zone, we found an adult female of this species consuming a half-digested acridiid. On this prey were two small flies

Figure 2. *Argiope savignyi* feeding on a moth, two flies (marked) are visible on the prey.

that we succeeded in collecting. They were identified as chloropids of the genus *Conioscinella.* Several species of chloropids are known to parasitize the egg cocoons of spiders (see, for instance, Bristowe, 1941:366–7).

Milichiids and a reduviid

At the La Fortuna dam site, Chiriqui, Panama, one of us (MHR) observed a reduviid *Zelus trimaculatus* Distant, feeding on a sting-less bee (*Trigona cupira* Sm.) which was impaled on the bug's proboscis. Around the prey item was a large number of small flies all apparently feeding. Eight of these flies were captured, many escaped. The flies were identified as *Neophyllomyza* sp.

Discussion

The relationship between *Phyllomyza* sp. and its host *Nephila clavipes* is one that involves prolonged contact between the two species. We suspect that the same flies may remain on the spider for days at a time, leaving only to make very short feeding forays. Our attempts to paint-mark the tiny flies failed utterly so we cannot be certain on this point. In any case, the association seems to us to be distinctly more specialized than that described by McMillan (1975) for *Desmometopa* sp. Of course, this is a matter of interpretation. However, it is possible to suggest an evolutionary pathway from commensalism without contact (the reduviid and *Argiope savignyi* associates) through commensalism plus feeding excursions onto the host, to commensalism with sustained non-trophic contact. If the flies were cued into food sources by olfactory stimuli, as seems possible, then the pathway would involve a reduction of the detection distance. The strategy of waiting on the host must involve some interesting mechanism that allows the fly to "evaluate" the odds on food being available within its own feeding timescale. At some stage the fly may be faced with "deciding" whether to remain with a spider on the off-chance that it will catch food or using its remaining food reserves to fly off in search of another (more successful?) host. In this respect, the fly may be at an advantage over the kleptoparasitic theridiid spiders that also associate with *N. clavipes.* It can probably range over greater distances, more quickly, in search of a new host than can the spiders. At least three species of theridiids associate with the golden-web spider; at least one of these regularly shares the host's meal, at the hub of the web (Vollrath, in press). Such kleptoparasitic spiders are small, but differ from the milichiids in having mouthparts capable of penetrating insect cuticle.

Spiders of the genus *Nephila* may be particularly suitable as hosts for this kind of associate, They are large, build very efficient webs that are operated 24 hours per day, and show a considerable degree of web-site tenacity. The other large, diurnal, orb-web spiders in Panama build much more ephemeral webs that are more susceptible to damage (they are nothing like as strong). They probably spend much less time on their webs at any one site, a situation which may be less favorable to the development of a protracted association. The fact that the only time we have seen milichiids resting on an *Argiope* was when this spider had been placed on a *Nephila* web could indicate that the flies respond to some characteristic of the web in finding their hosts. On a recent trip to Papua New Guinea (May 1977), one of us (MHR) looked at over 500 adult *Nephila maculata,* hoping to find flies resting on the spider. None were found. Bristowe (1941:369) reports that R. N. Champion Jones saw a small fly crawl over the palps of *Nephila maculata* in India. Conceivably this is a case where a less sustained association has evolved.

As far as the milichiids are concerned it is at least possible that their relationship with *Nephila* may be more than a trophic one. The fact that all the *Phyllomyza* sp. that we collected were females is disturbing. The fact that we found *Conioscinella* feeding on the prey of *Argiope argentata* makes it possible that the egg parasites of araneids could also be commensals. The reverse could be true.

There is some problem about finding terms that accurately describe the relationship of the milichiids to their host(s). They are clearly commensals (in the broad sense) since they "share a table" with their hosts. However, they rely on the host liquifying the prey, they *drink* alongside the host and could perhaps be called *bibiocommensals.* The presence of fairly large numbers of flies feeding on a prey item *could* reduce the amount of food available to the host in a significant way, in which case the term parasite would be justifiable. A drinking parasite would be a *dipsoparasite* and this term is (to us) more euphonious than bibiocommensal.

ACKNOWLEDGMENTS

We thank the Insect Identification and Beneficial Insect Introduction Institute, USDA, Beltsville, Maryland (Chairman, Dr. L. Knutson), for identifying all the insects involved in this study. The experts involved were: C. W. Sabrosky, J. L. Herring, and S. W. Batra. Dr. Sabrosky drew our attention to a number of published works on the relationship between milichiids and spiders; this additional help is greatly appreciated.

REFERENCES

BRISTOWE, W. S.: The comity of spiders. Volume 2. Ray Society, London 1941

MCMILLAN, R. P.: Observations on flies of the family Milichiidae cleaning *Araneus* and *Nephila* spiders. West Australian Naturalist, **13:** 96 (1965)

RICHARDS, O. W.: On commensalism of *Desmometopa* with predacious insects and spiders. Proc. roy. ent. Soc. (Lond.) Ser. C. **18:** 55–56 (1953)

ROBINSON, M. H. AND OLAZARRI, J.: Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius): (Araneae: Araneidae). Smith. Contr. Zool. **65:** 1–36 (1971)

ROBINSON, M. H. AND ROBINSON, B.: The ecology and behavior of the giant wood spider *Nephila marculata* (Fabricius) in New Guinea. Smith. Contr. Zool. **149:** 1–76 (1973)

ROBINSON, M. H. AND SMYTHE, N.: A technique for observing the behavior of small animals under field conditions. Psyche **83:** 210–212 (1976)

THE LARVA OF *PLATYSTETHUS SPICULUS* ERICHSON (COLEOPTERA : STAPHYLINIDAE) AND ITS OCCURRENCE IN BOVINE FECES IN IRRIGATED PASTURES*

By E. F. Legner and Ian Moore

Department of Entomology, University of California,
Riverside, California 92521

Platystethus is a relatively small genus (35 described species) with only two species being known to be indigenous to the United States. The Nearctic species were reviewed by Moore and Legner (1971). The larva of one of these, *P. americanus* Erichson, was described and illustrated by Paulian (1941). The larvae of the other species, *P. spiculus* Erichson, is described here. It goes to *Platystethus* in Paulian's (1941) key to the genera of the larvae of the Staphylinoidea. Several larvae were taken by Berlese extraction as previously described (Legner et al., 1975) in company with many adults of *P. spiculus* in bovine manure that, at the time, contained no other staphylinids. Ten to 25 1 L samples were taken at random from bovine feces deposited in green and dry irrigated pastures at 3 sites near Calexico, California between 9 AM and 11 AM over several sample dates from October 22, 1974 to April 22, 1975. Two age groups of manure were distinguished: 12 hr and 24–48 hr old.

KEY TO THE LARVAE OF THE SPECIES OF *PLATYSTETHUS* INDIGENOUS TO THE UNITED STATES

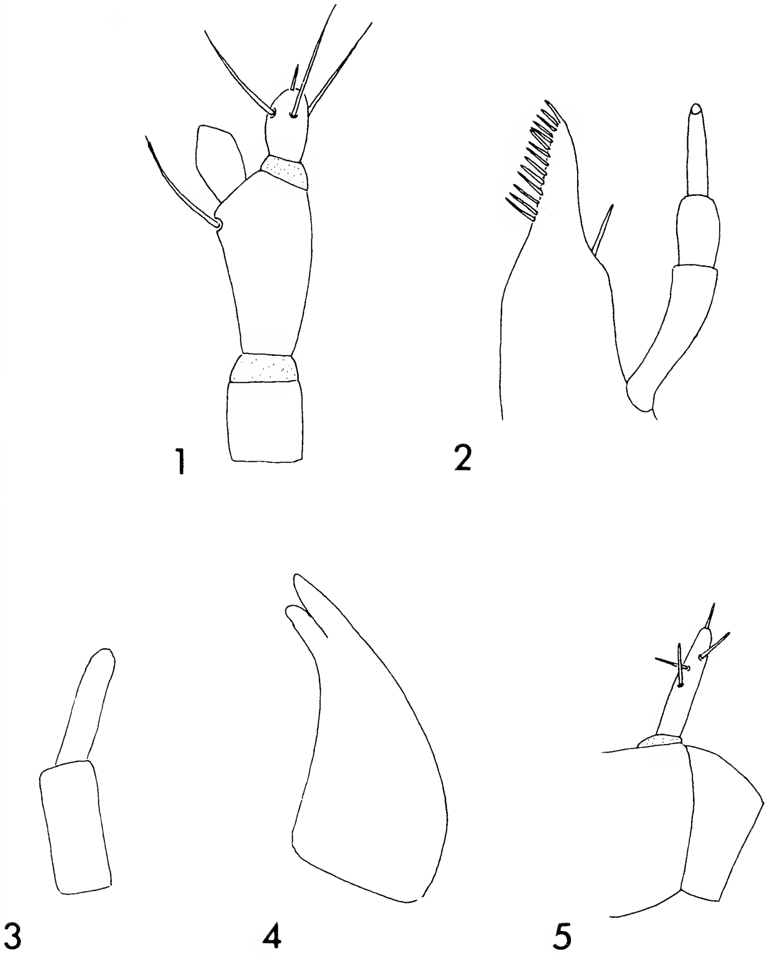
1. Acorn-like seta at apex of second antennal segment equal in size to third antennal segment .... *spiculus* Erichson
   Acorn-like seta at apex of second antennal segment only half as long as third antennal segment .... *americanus* Erichson

Larva of *Platystethus spiculus* Erichson

Length 3.8 mm. Body elongate, pale, integuments mostly transparent with the head and mouthparts tinged with brown, the man-

---

**Manuscript received by the editor June 10, 1977.*



Figures 1–5. Larva of *Platystethus spiculus*. Fig. 1, antenna; Fig. 2, maxilla; Fig. 3, labial palpus; Fig. 4, right mandible, dorsal view; Fig. 5, pseudopod and urogomphus.

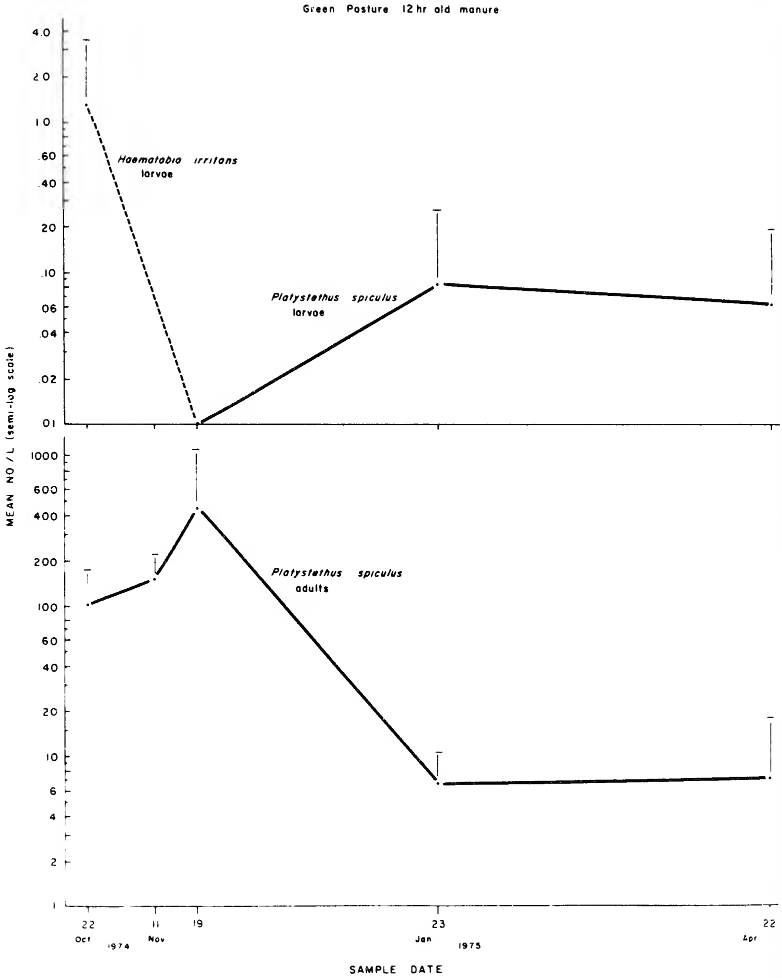


Figure 6. Average density of *Platystethus spiculus* and *Haematobia irritans* larva, in 12-hr-old bovine feces from green, irrigated pastures; Calexico, California, 1975 (+ 05 Conf. limit shown above each mean).

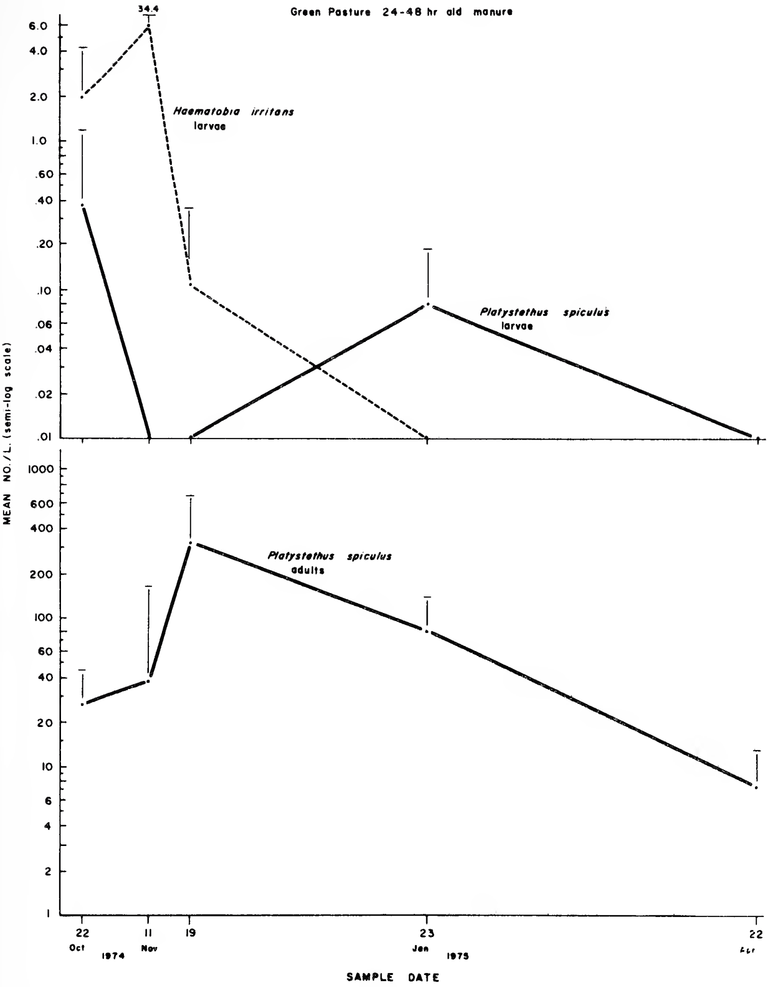


Figure 7. Average density of *Platystethus spiculus* and *Haematobia irritans* larvae, in 24-48-hr-old bovine feces from green, irrigated pastures; Calexico, California, 1975 ($+^{t}$ 05 Conf. limit shown above each mean).

dibles darkest. Head oval, about one-fourth wider than long, with a single ocellus very near outer apical angle of the head at the base of mandible. Labrum simple, a little wider than long. Antennal fossa located near the outer, apical angle of the head at the base of the mandible. Antenna three-segmented; first segment about as wide as long; second segment about one-fourth wider than first and twice as long, widest near apical fourth, with a large acorn-like seta at obliquely truncate component of apex, about as long as third segment; third segment less than one-third as long as second segment and a little more than one-third as wide. Mandibles stout at base, arcuate, with two teeth at apex in dorsal view. Maxillary palpus three-segmented; first segment longest, about three times as long as wide; second segment about as wide as first and almost half as long; third segment a little longer than second but only about half as wide, apex pointed. Lacinia gradually, irregularly narrowed to apex, with a series of stout setae internally in apical half and a single large seta in the middle on the outer edge. Labial palpus two-segmented, segments of about equal length, first segment wider than second. Pronotum about as wide as head but a little shorter, with two setae at anterior margin and two in each lateral series. Mesonotum and metanotum each about as wide as pronotum but a little shorter, each with four transversely arranged discal setae and with one large seta and two small setae in the lateral series. Abdomen with nine segments, first segment about as wide as metanotum but not quite as long, segments progressively slightly increasing in width and length through eighth which is slightly wider and about as long as metanotum; each with four setae along the posterior margin and three in the lateral series. Pseudopod short and stout. Urogomphus one-segmented, cylindrical, about four times as long as wide, tapered to apex.

Five specimens taken from field-manure in company with adults at Calexico, Imperial county, California, 21 October 1974, E. F. Legner collector.

This species is similar to Paulian's (1941) description and illustration of *P. americanus,* except that the acorn-like seta at the apex of the second antennal segment is as large as the third antennal segment whereas in *P. americanus* it is only half as long.

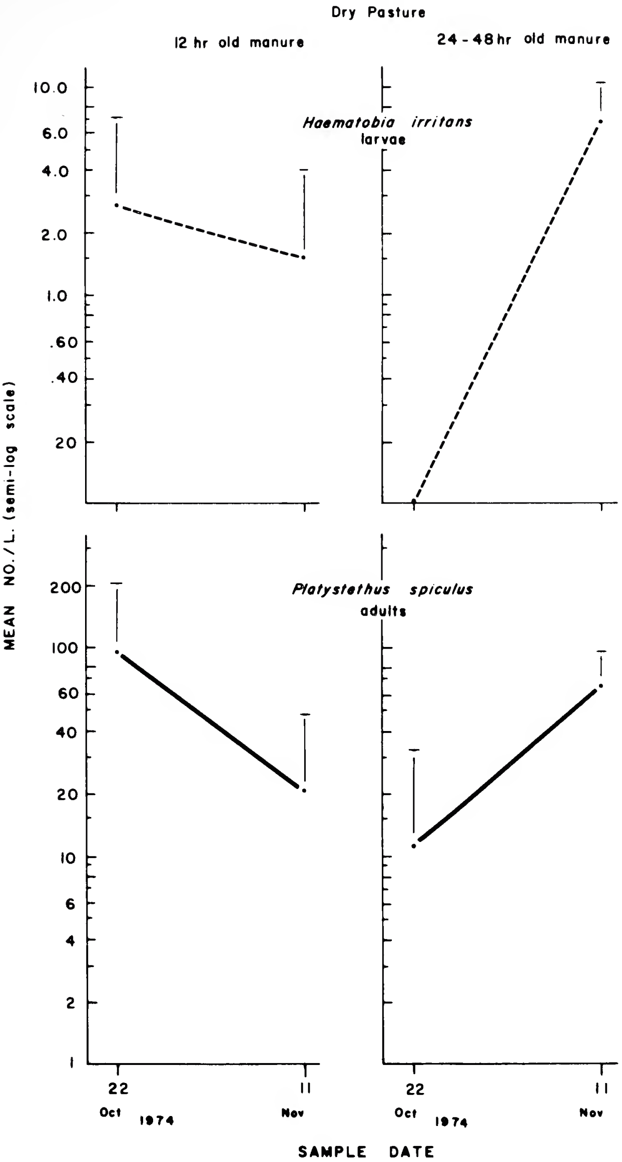


Figure 8. Average density of *Platystethus spiculus* and *Haematobia irritans* larvae, in 12- and 24-48-hr-old bovine feces from dry pastures; Calexico, California (+' 05 Conf. limit shown above each mean).

FIELD OCCURRENCE

Larvae of the horn fly, *Haematobia irritans* Linnaeus, occurred in bovine feces in pastures in association with adults and larvae of *Platystethus spiculus*.

There was no continuous coincidence of *P. spiculus* larvae and adults with *H. irritans* larvae (Figs. 6–8). Therefore, alternative food would have been necessary to sustain *P. spiculus* during period of *H. irritans* scarcity or absence.

The occurrence of *P. spiculus* larvae was exceptionally low in the manure habitat, certainly not sufficiently dense to account for the comparative high adult abundance (Figs. 6 & 7), and no larvae were detected in dry pastures (Fig. 8).

It appears that *P. spiculus* adults are initially attracted to fresh bovine feces in green pastures where some eggs are laid (Fig. 6). Attraction to dry pastures is not as great, and apparently no eggs are laid judging from the absence of larvae (Fig. 8). The adult density is maintained for at least 24 hrs (Fig. 7). The majority of the larvae of this species may occur subterraneously below and surrounding the bovine fecal droppings.

Hinton (1944) has shown that in the European *P. arenarius* (Fourcroy) larvae and adults feed on manure and are facultative feeders on carrion; that eggs are laid in a brood chamber in or partly beneath manure and protected by the female until hatched. Whether similar sub-social behavior exists with the American species has not been determined.

LITERATURE CITED

HINTON, H. E.
1944. Some remarks on sub-social beetles, with notes on the Biology of the staphylinid, *Platystethus arenarius* (Fourcroy). Proc. Royal Ent. Soc. London, (A): **19:** 115–118, 15 Figs.

LEGNER, E. F., G. S. OLTON, R. E. EASTWOOD AND E. J. DIETRICK.
1975. Seasonal density, distribution and interactions of predatory and scavenger arthropods in accumulating poultry wastes in coastal and interior southern California. Entomophaga. **20** (3): 269–283.

MOORE, I. AND E. F. LEGNER
1971. A review of the Nearctic species of *Platystethus* (Coleoptera:Staphylinidae). Pan-Pac. Entomol. **47:** 260–264. 1 Fig.

PAULIAN, R.
1941. Les premier états des Staphylinoidea. Étude de Morphologie Comperee. Mém. Mus. Nat. Paris, n. ser., **15:** 1–361; 1365 Fig., 3 L.

DRAGLINE-FOLLOWING BY MALE LYCOSID SPIDERS[1]

By William J. Tietjen

Department of Zoology, Ohio University, Athens, Ohio 45701

Wolf spiders stalk or ambush their prey rather than build prey-capture webs. Production of silk by lycosids is important during aerial dispersal via ballooning (Richter, 1970b) and, in some, during post-immobilization wrapping of prey (Rovner and Knost, 1974), and construction of egg sacs or sperm webs (Richter, 1970a). During locomotion both sexes lay down silk draglines that are generally assumed to have a stabilizing or security function (Richter and Van der Krann, 1970). In addition, female draglines induce courtship behavior in male conspecifics and, in some species, males are reported to have followed a female trail, but no systematic analyses of the dragline-following behavior have been attempted (Bristowe and Locket, 1926; Engelhardt, 1964; Kaston, 1936).

The present study is concerned with the trail-following behavior of male *Lycosa rabida* and *L. punctulata.* Specific areas of investigation include determination of the use of various appendages during following, analysis of cues involved in initiating and maintaining trail-following, and an interspecific comparison of trail-following behavior.

Methods

Penultimate and young adult instars of *L. rabida* and *L. punctulata* were collected near Amesville, Athens County, Ohio, USA, during 1974 and 1976. *L. rabida* were collected late June through July while *L. punctulata* were collected mid- to late September.

Animals were housed separately in 13 × 7 × 6.5 cm plastic cages painted on two sides to afford visual isolation between animals in adjacent cages. A paper substratum in each cage collected silk used in some experiments and facilitated periodic cleaning of the cages. Water was provided ad libitum via a cotton-stoppered vial, and two *Tenebrio* sp. larvae were provided per week as food. Cages

---

[1] This study was supported by National Science Foundation Grant BNS 76-15009 to J. S. Rovner.

Manuscript received by the editor September 9, 1977.

containing males were located on shelves along one wall of the laboratory that received indirect sunlight. Laboratory humidity was not controlled (range 36–56% RH) and temperature ranged from 23–28° C. Cages containing females were placed in a controlled environmental chamber (Frease model 818) at 15° C night and 20° C day and 53–56% RH, with a photoperiod approximating natural conditions. The lower temperatures were necessary to retard female development and to delay onset of eggsac production, which even occurs eventually in unmated females, making them useless for further experimentation. Females were removed from the environmental chamber and allowed sufficient time to warm to room temperature before experimental use.

In order to lay draglines along predetermined trails spiders were anesthetized with CO_2. A thread leash, secured to a hemostat, was tied around the cephalothorax of each spider between the second and third pairs of legs. Upon recovery, the spider was led along a path such that the dragline was laid either directly on the substratum to form "ground lines" or suspended above the substratum by being laid across horizontally placed glass rods to form "aerial lines" (Fig. 1). Lines connecting parts of an artificial plant made of wood dowels were also called "aerial lines." Male draglines or imitation draglines (nylon thread or human hair) were laid in either a continuous or discontinuous manner with the female trail during some experiments.

The test trail was then surrounded by glass walls to provide an arena (54 × 64 cm), the position of which was rotated in a random manner between experimental runs. The position, length, and direction of the dragline, including attachment disks (produced by the spider to fix the dragline to a substratum) were recorded on a diagram of the completed path.

Test males were of two physiological conditions: (1) unprimed males, which had not encountered female silk for the previous 72 hr and (2) primed males, which were induced to court in response to substratum silk from a female cage, and then tested 1 hr later for dragline-following behavior. Experimental trials began when a male released into the arena contacted and explored a female line with his palps. Trials lasted for 5 min, during which time data were recorded in shorthand notation from a distance of 0.5–1.0 m from the experimental males. To test the response of males to various types of silk, males were released into cages containing either lepi-

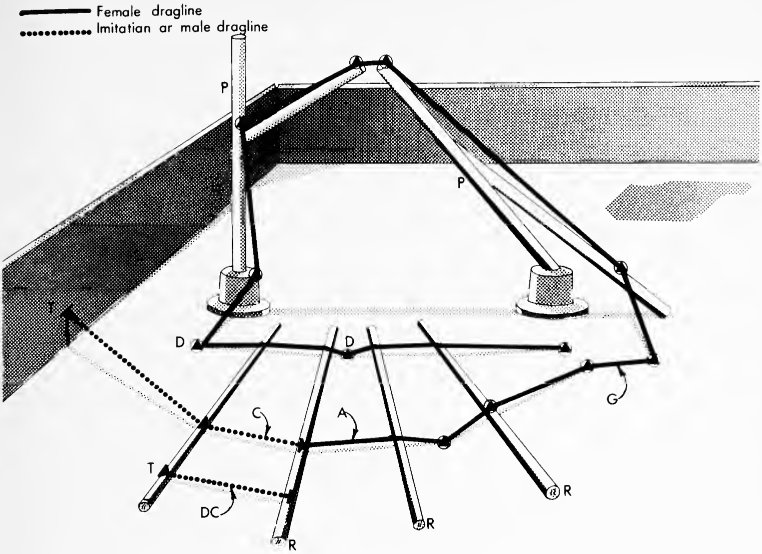


Figure 1. Diagrammatic summary of a typical trail including attachment disks (D) and female *aerial* lines (A). Female *ground* lines (G) and imitation draglines are laid contiguously (C) and discontiguously (DC) with the female dragline. Small strips of masking tape (T) attach imitation dragline to the wall of the arena and to 5-mm diameter glass rods (R). Glass rods were usually parallel and 9–11 cm apart. When artificial "plants" (P) were incorporated into the experiment, female trails up to 236 cm in length were constructed.

dopteran silk or conspecific male or female silk. Male *L. punctulata* were also exposed to female *L. rabida* silk. Clean cage cards were used as controls. A positive response by males to the silk consisted of exploring the silk and initiating courtship behavior within 5 min.

Statistical analyses of data were performed according to the methods of Conover (1971) and Sokal and Rohlf (1969). All means are accompanied by their standard errors.

RESULTS

COMPARISONS OF YEARLY SAMPLES

No difference was found in trail-following behavior between 1974 and 1976. Unprimed male *L. rabida* showed no difference in frequency of following-behavior ($\chi^2 = 0.0$, $df = 1$, $P > .50$) and in total distance followed during the 5-min test period (Mann-Whitney test, $T = 173, P > .80$). Primed male *L. rabida* showed no difference in frequency of following ($\chi^2 = .504$, $df = 1$, $P > .70$) or in total distance followed (Mann-Whitney test, $T = 229.5$, $P > .56$). Male *L. punctulata* showed no difference in the frequency of following ($\chi^2 = 2.5$, $df = 1$, $P > .90$) or in total distance followed (Mann-Whitney test, $T = 235.5$, $P > .84$). Therefore, data for the two years were pooled for analysis.

DESCRIPTION OF DRAGLINE-FOLLOWING

Males of both species followed conspecific female lines. Although high speed (36–180 fps) cinematographic analysis indicates that there are slight differences in the use of appendages during dragline-following (Tietjen, unpublished data), the two species exhibit many similarities. Upon contacting the silk line for the first time, males tend to examine it with alternating movements of the palps such that the dorsal surface of the palp contacts the line and moves anteriorly along it. Such behavior is soon terminated if the line is a male's or is an imitation. Dragline-following results if the line is that of a female conspecific. Males usually wander to the edge of the arena and walk around the periphery if chemo- and mechano-exploratory behavior is terminated.

In both species, dragline-following is characterized by the male straddling the silk so that it passes medially beneath him. Although the first pair of legs may occasionally pluck at the line, the palps are the most important appendages used. The palps are alternately moved forward and back, making contact with the silk on their medial surface rather than on the dorsal surface, which is used during the initial contact with the line. Experiments conducted under red light (Kodak safelight Filter No. 1) and with blinded animals indicated that vision is not necessary for dragline-following. Males may accompany their dragline-following behavior with elements of courtship or, more typically, interrupt dragline-following with separate bouts of courtship behavior.

DRAGLINE-FOLLOWING BY *LYCOSA RABIDA*

Both primed and unprimed male *L. rabida* followed female *aerial* draglines. Unprimed males exhibited a lower incidence of dragline-following, with 84.6% of primed and 65.2% of unprimed following ($\chi^2 = 5.83$, $df = 1, P < .025$). Comparing only those males that

Table I: Performance of Male *Lycosa rabida* and Male *L. punctulata* During Dragline-Following of Conspecific Male, Female, and Imitation Silk.

	L. rabida		*L. punctulata*
	Primed	*Unprimed*	*Pooled*
Number of males tested	52	69	57
number following	44	45	40
number not following	8	24	17
Distance (cm)			
$\bar{Y}$ total distance	23.1 ± 2.3	26.7 ± .2	56.9 ± 8.7
$\bar{Y}$ polarity	+ 7.9 ± 3.3	− 6.5 ± 4.2	+ 5.3 ± 2.4
Courtship			
Frequency	27.2%	26.6%	12.5%
$\bar{Y}$ latency (min)	1.4 ± .4	1.1 ± .3	1.4 ± .8
Imitation and male draglines			
number followed	7	4	0
number not followed	6	12	16
Ground lines			
number followed	0	0	13
number not followed	18	9	4

followed draglines, no significant difference was found in the total distance followed between primed and unprimed animals (Mann-Whitney test, $T = 1069.5$, $P > .72$). No males of either group followed *ground* lines, although they would usually examine such lines with their palps (Table I).

None of the male *L. rabida* followed isolated imitation draglines; and chemoexploratory behavior to such lines was exhibited only five times. Males in the process of following a female line would occasionally follow imitation and male draglines laid contiguously with the female trail (Table I). Once, a male following a female line continued on and followed the entire length of a human hair that constituted an 8.5 cm interruption in the female trail, losing no momentum in his following behavior. Male draglines were followed four times, human hairs were followed six times and nylon thread was followed once.

The polarity of each male's trail was calculated as the difference between total distance traveled in the same direction as the female trail was laid and total distance traveled in the opposite direction. Primed males exhibited a positive polarity by following the correct direction more often than the incorrect direction ($\chi^2 = 7.36$, $df = 1$, $P < .01$), and by traveling further in the correct direction along the female trail (Wilcoxon test, $T = 252.5$, $P < .01$). Unprimed males did not show a directional preference ($\chi^2 = 0.0$, $df = 1$, $P > .50$; Wilcoxon test, $T = 525$, $P > .64$; Table I).

Primed and unprimed male *L. rabida* showed no difference in the frequency of courtship during dragline-following ($\chi^2 = .613$, $df = 1$, $P > .50$) or in the elapsed time during a test before courtship was observed (= courtship latency) (Mann-Whitney test, $T = 70.0$, $P > .54$; Table I). Primed males that courted showed no correlation between total distance of dragline followed and courtship latency (Spearman's rho, $\rho = + .026$, $P > .53$). Unprimed males courting early in the test showed decreased total dragline-following (Spearman's rho, $\rho = + .692$, $P < .01$). Comparing primed and unprimed males that both courted and followed draglines, no difference was found in the total amount of dragline-following (Mann-Whitney test, $T = 747.0$, $P > .65$).

DRAGLINE-FOLLOWING IN *LYCOSA PUNCTULATA*

L. punctulata was a more difficult species to study experimentally than *L. rabida.* Females often would not lay the required lines and both sexes tended to break the lines by catching a claw on them, and the males by running through the lines.

In 1974, 9 of 10 males in each group exhibited dragline-following. The total distance followed for primed ($\bar{Y} = 63.1 \pm 20.7$ cm) and unprimed ($\bar{Y} = 63.1 \pm 17.5$ cm) males did not differ significantly between the two groups (Mann-Whitney test, $T = 47.5$, $P > .57$). Incidence of courtship did not differ between the two groups with primed males courting during one and unprimed males courting during three of the trials ($\chi^2 = 1.25$, $df = 1$, $P > .70$). Data for the two groups were pooled for further analysis.

In 1976 only unprimed males were used. During 34 trials 23 males followed a mean total distance of 52.4 ± 11.3 cm. No differences were found between pooled 1974 data and the 1976 (all unprimed) data for incidence of following ($\chi^2 = 3.41$, $df = 1$, $P > .05$), or for distance followed (Mann-Whitney test. $T = 235.5$, $P > .77$). Unprimed males in 1976 exhibited courtship three times during dragline-following; no difference in courtship frequency was found between the pooled 1974 data and those for 1976 males ($\chi^2 = 0.34$, $df = 1$, $P > .70$). In order to have a larger data base the data were pooled for both years.

Unlike male *L. rabida,* male *L. punctulata* initiated dragline-following at ground lines and appeared to use their palps in a manner similar to chemoexploratory behavior. Male *L. punctulata* rarely examined isolated male lines or imitation lines; of 16 that did palpate these lines, none followed them (Table I). Males exhibited a positive polarity ($\chi^2 = 4.33$, $df = 1$, $P < .05$), and traveled a greater distance in the correct direction along the female trail (Wilcoxon test, $T = 255.5$, $P < .03$).

Males that courted during dragline-following showed no correlation between courtship latency and distance followed (Pearson's *r*, $r = + .700$, $P > .90$). No difference in distance followed was found between males that courted during dragline-following and those that did not (Mann-Whitney test, $T = 93.0$, $P > .58$). Courtship latency of males placed on a female substratum was affected after dragline-following; those which had recently followed a dragline exhibited a mean courtship latency of 0.66 ± .29 min ($N = 23$) compared with 2.30 ± 0.25 min ($N = 20$) for those which had not (Mann-Whitney test, $T = 52.0$, $P < .0001$).

COURTSHIP RESPONSES TO VARIOUS TYPES OF SILK

Male *L. rabida* courted in response to silk in a female cage in 50% of the trials. Courtship latency in response to female silk was 2.30 ± .25 min. The incidence of courtship in response to female silk differed from the courtship frequency in response to a clean cage, lepidopteran silk and male *L. rabida* silk ($\chi^2 = 33.99$, $df = 3$, $P < .001$). The incidence of courtship did not differ among the latter three conditions ($\chi^2 = 2.05$, $df = 2$, $P > .70$). (Table II).

Male *L. punctulata* courted in response to female conspecific silk in 61.1% of the trials and exhibited a mean courtship latency of 2.55 min ± .44 min. The incidence of courtship in response to female conspecific silk, female *L. rabida* silk, lepidopteran silk, a clean cage and male *L. punctulata* silk differed significantly ($\chi^2 = 35.93$, $df = 4$, $P < .001$), while courtship frequency did not differ among the latter four test conditions ($\chi^2 = 2.10$, $df = 3$, $P > .50$).

To simulate the effects of dew under natural conditions, silk trails of females of both species were sprayed with a fine mist of distilled water and were air dried (= washed lines). Draglines so

Table II. Courtship Responses to Various Types of Silk by Male *Lycosa rabida* and Male *L. punctulata*.

	Experimental Silks				
	Clean cage	*Female conspecific*	*Male conspecific*	*Female heterospecific*	*lepidopteran*
L. rabida					
number tested	20	40	20	0	20
number courting	1	20	0	—	0
number not courting	19	20	20	—	20
$\bar{Y}$ courtship latency (min)	1.27	2.30 ± .2	—	—	—
L. punctulata					
number tested	20	18	20	20	20
number courting	2	11	1	0	1
number not courting	18	7	19	20	19
$\bar{Y}$ courtship latency (min)	4.06 ± .7	2.55 ± .7	4.93	—	4.57

treated lost elasticity and drooped between the supporting glass rods. Both unprimed male *L. rabida* ($N = 10$) and unprimed male *L. punctulata* ($N = 10$) exhibited short bouts of chemoexploratory behavior at washed lines, but neither species exhibited courtship or trail-following behavior during the 5-min trials.

DISCUSSION

Trail-following has been observed in a variety of arthropods. Terrestrial chemical trails are often employed by eusocial insects, but such trails are detected by the receiver as a rapidly decaying vapor cloud above the substratum and provide no directional information (Wilson, 1971). Lepidopteran larvae (*Malacosoma, Hyponomeuta* and *Thaumetopoea*) have been observed to follow silk trails from their nest to a food source; but tactile information provided by the silk is unimportant, and the pheromone decays within a few minutes (Fitzgerald, 1976; Wigglesworth, 1966). Wolf spider trails differ from the above examples in function (mating vs. food), in the use of a contact rather than an olfactory pheromone, and in the presence of an inherent polarity. Silk lines in the laboratory up to 4 days old will elicit following-behavior in male *L. rabida* and male *L. punctulata;* and a cage substratum with female silk elicits courtship behavior for over a month (Tietjen, unpub. data), indicating that the spider pheromone does not decay over a relatively long period of time.

Female lycosid spiders exhibit low motility during the breeding season and adopt a "sit and wait" reproductive strategy; the highly active males seek out the females (Hallander, 1967a, 1967b; Hollander, 1972; Muma, 1973; Richter, et al., 1971). Mathematical modeling of females laying no silk trails and silk trails of various lengths indicates that the presence of silk effectively increases the size of the female target as perceived by the searching male (Tietjen, unpub. data). Thus, the ability of male *L. rabida* and *L. punctulata* to follow conspecific female draglines to the source increases the reproductive success of these males over spiders that depend on chance encounters in a heterogeneous environment. Female silk also alerts the male to the presence of a female conspecific and, as shown in *L. punctulata,* decreases the courtship latency. The latter two functions effectively reduce the likelihood of intraspecific cannibalism (Platnick, 1971).

Contact sex pheromones associated with the female dragline are known to induce courtship in conspecific male spiders (Dijkstra, 1970; Dondale and Hegdekar, 1973; Hegdekar and Dondale, 1969). Results from the present study support the hypothesis that a pheromone associated with the female dragline elicits courtship in receptive males, i.e., these behaviors are not dependent exclusively upon tactile information provided by the silk. Both *L. rabida* and *L. punctulata* are found with a variety of other spider species. Dependence on a pheromone to elicit sexual behavior in males would reduce the chances of males following draglines of other species and thereby adversely affecting the time budget allocated for reproductive purposes.

The propensity of male *L. rabida* not to follow ground lines which cannot be plucked by the palps (thereby providing little tactile input) and their occasional following of imitation draglines, which provide no chemical cues, indicate that the pheromone is responsible only for initiating the following behavior in males. Once a male is following a dragline, tactile cues appear to be adequate. Males are expected, however, to occasionally sample the trail for female pheromone, as only 38% of male and imitation dragline contacts during female dragline-following resulted in following by males, and most imitation draglines were not followed the entire length.

Male *L. punctulata* followed ground lines, but did not follow male and imitation draglines. This species appears to depend upon the female pheromone for initiating and for maintaining dragline-following. Apparently, male *L. punctulata* are either more sensitive to tactile input provided by ground lines, or more sensitive to pheromonal cues than male *L. rabida,* or both.

The differential sensitivity to tactile and chemical cues exhibited by the two species may be related to microhabitat preferences. *L. punctulata* is found in the lower levels of the herbaceous stratum (Eason and Whitcomb, 1965) in which one expects a greater diversity and density of spiders (Whitcomb, Exline and Hite, 1963) and consequently more draglines. Many lycosids of similar or larger size are found within this microhabitat of which male *L. punctulata* could be potential prey, including *L. helluo* and *L. carolinensis.* Continuous sampling for female pheromone during dragline following reduces the likelihood that males will follow another species' trail in a high silk density microhabitat. In addition, due to the greater foliage density at this level, many draglines could be expected to be laid directly on a substratum. A greater sensitivity to tactile and/or chemical cues could allow male *L. punctulata* to follow such ground lines.

L. rabida, on the other hand, is found high in the herbaceous stratum (Eason and Whitcomb, 1965; Kuenzler, 1958) and is associated with lower interspecific silk densities derived mainly from smaller species such as salticids and oxyopids. Foliage density is less, and a greater volume of open space is found at this level. Fewer female silk trails would be expected to be found directly on this substratum. Under these conditions the sensitivity to tactile and/or chemical cues exhibited by *L. punctulata* would not be required for efficient dragline-following by male *L. rabida.*

Silk lines are destroyed mechanically in the field by wind and the activities of animals. Moisture resulting from rain and early morning dew inactivates the female pheromone found on unbroken lines (Dondale and Hegdeker, 1973; Hegdeker and Dondale, 1969). All of these effects reduce the likelihood that males will follow draglines laid the previous day.

Male *L. punctulata* and primed male *L. rabida* may be able to extract directional information from the female dragline, though it is unlikely that a pheromone concentration gradient could provide the directional information since the pheromone remains active over long periods of time. Examination of female *L. rabida* silk under a light microscope (450×) as well as scanning electron microscope inspection of female *L. punctulata* silk (1000×) indicate no evidence of structural features on the dragline which could provide directional information to males.

Spiders are able to detect slight changes in web tension through vibration receptors during prey capture, web building, and courtship (Robinson, 1969; Walcott, 1969; Witt, 1975). Such variations in tension, related to the direction in which the dragline was laid, could provide directional information to dragline-following males. If present, the tension differential may be related to the structure of the attachment disk by which the silk is fixed to a substratum. As the dragline enters the attachment disk it is tightly wound, whereas the silk leaving the attachment disk is composed of single threads which later join and wind to form the dragline. Single silk threads leaving an attachment disk would be expected to damp transients produced along the line more readily than a complete dragline entering an attachment disk. If this were the case, dragline-following toward the pole with the higher resonant frequency would constitute movement in the direction the silk was laid (Tietjen, unpub. data). Such a system would require that males immobilize a portion of the dragline, perhaps with a palp, while plucking on either side of the fixed portion. Male spiders encountering a female line often wipe the dorsal surface of each palp alternately over the silk and often pluck at the silk with the first legs as they swivel their bodies along a short length of the trail. This behavior may represent both a sampling for female pheromone and a testing for differential mechanical properties of the line related to the direction in which it was laid.

Unprimed male *L. rabida* did not exhibit a polarity in dragline-following, but a positive correlation between courtship latency and total distance followed was observed. The above correlation indicates that unprimed males probably have a lower threshold for chemical cues than do primed males. If unprimed males are attending more to chemical cues, they would be less likely to follow a dragline in a preferential direction if directional cues were dependent on the mechanical properties of the line.

SUMMARY

The dragline-following behavior of male wolf spiders was observed in response to male, female and imitation draglines. Male *L. rabida* followed female draglines suspended above the substratum but not those laid directly on the substratum. These males followed male silk and imitation lines if laid contiguously with female draglines, suggesting that they depend on tactile cues during dragline-following. On the other hand, male *L. punctulata* followed both aerial lines and ground lines laid by females but did not follow imitation or male lines. This suggests that male *L. punctulata* are more sensitive to tactile and/or chemical cues than are male *L. rabida*. Microhabitat preferences of the two species may explain the above differences. Data also suggest that males of both species are able to extract directional information from the dragline, perhaps by tensional cues.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to Dr. J. S. Rovner for his support, valuable discussions and assistance in the preparation of the manuscript. Thanks are also due Dr. W. D. Hummon, Dr. C. P. Spirito and Dr. G. E. Svendsen for their helpful criticism of this work. Anne Tietjen assisted in the preparation of the manuscript.

LITERATURE CITED

BRISTOWE, W. S. AND G. H. LOCKET
1926. The courtship of British lycosid spiders and its probable significance. Proc. Zool. Soc. **22:** 317–347.

CONOVER, W. J.
1971. *Practical Nonparametric Statistics.* New York: John Wiley and Sons, Inc. 492 pp.

DIJKSTRA, H.
1970. Comparative research of the courtship behaviour on the genus *Pardosa* (Arach. Araneae) III. Agnostic behaviour in *Pardosa amentata.* Bull. Mus. Nat. Hist. Natur. **41:** 91–97.

DONDALE, C. D. AND B. M. HEGDEKAR
1973. The contact sex pheromone of *Pardosa lapidicina.* Emerton (Araneida; Lycosidae). Canad. J. Zool. **51:** 400–401.

EASON, R. AND W. H. WHITCOMB

1965. Life history of the dotted wolf spider. *Lycosa punctulata* Hentz (Araneida; Lycosidae). Arkansas Acad. Sci. Proc. **19:** 11–20.

ENGELHARDT, W.

1964. Die mitteleuropischen Arten der Gattung *Trochosa* C. L. Koch, 1848. Z. Morph. Tiere. **54:** 219–393.

FITZGERALD, T. D.

1976. Trail marking by larvae of the eastern tent caterpillar. Science **194:** 961–963.

HALLANDER, H.

1967a. Courtship display and habitat selection in *Pardosa chelata* (O. F. Muller). Oikos **18:** 145–150.

1967b. Range and movements of the wolf spiders *Pardosa chelata* (O. F. Muller) and *P. pullata* (Clerck). Oikos **18:** 360–364.

HEGDEKAR, B. M. AND C. D. DONDALE

1969. A contact sex pheromone and some response parameters in lycosid spiders. Canad. J. Zool. **47:** 1–4.

HOLLANDER, J. DEN.

1972. Differential use of the habitat by *Pardosa pullata* (Clerck) and *Pardosa prativaga* (L. Koch) in a mixed population (Araneae, Lycosidae). Tijd. Joor. Entomol. **115:** 205–215.

KASTON, B. J.

1936. The senses involved in the courtship of some vagabond spiders. Entomol. Amer. **16:** 97–169.

KUENZLER, E. J.

1958. Niche relations of three species of lycosid spiders. Ecology **39:** 494–500.

MUMA, M. H.

1973. Comparison of ground surface spiders in four central Florida ecosystems. Florida Entomol. **56:** 173–196.

PLATNICK, N.

1971. The evolution of courtship behaviour in spiders. Bull. Brit. Arach. Soc. **2:** 40–47.

RICHTER, C. J. J.

1970a. Morphology and function of the spinning apparatus of the wolf spider *Pardosa amentata* (Cl.) (Araneae, Lycosidae). Z. Morph. Tiere. **68:** 37–68.

1970b. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa,* Araneae, Lycosidae). Oecologia **5:** 200–214.

RICHTER, C. J. J. AND J. DEN HOLLANDER

1971. Differences in breeding and motility between *Pardosa pullata* (Clerck) and *Pardosa prativaga* (L. Koch) (Lycosidae, Araneae) in relation to habitat. Oecologia **6:** 318–327.

ROBINSON, M. H.

1969. Predatory behaviour of *Argiope argentata* (Fabricus). Amer. Zool. **9:** 161–174.

ROVNER, J. S. AND S. J. KNOST

1974. Post-immobilization wrapping of prey by lycosid spiders of the herbaceous stratum. Psyche **8:** 398–415.

SOKAL, R. R. AND F. J. ROHLF
1969. *Biometry.* San Francisco: W. H. Freeman. 766 pp.
WALCOTT, C.
1969. A spider's vibration receptor: its anatomy and physiology. Amer. Zool. **9:** 133–144.
WHITCOMB, W. H., H. EXLINE AND M. HITE
1963. Comparison of spider populations of ground stratum in Arkansas pasture and adjacent cultivated field. Arkansas Acad. Sci. Proc. **17:** 1–6.
WIGGLESWORTH, V. B.
1966. *The Life of Insects.* London: William Clowes and Sons, Ltd. 360 pp.
WILSON, E. O.
1971. *The Insect Societies.* Cambridge: Belknap. 548 pp.
WITT, P. N.
1975. The web as a means of communication. Biosci. Commun. **1:** 7–23.

THE BIOLOGY OF *PHANETA IMBRIDANA* (LEPIDOPTERA : TORTRICIDAE), A SEED PREDATOR OF *XANTHIUM STRUMARIUM* (COMPOSITAE)

By J. Daniel Hare

Department of Ecology and Evolution*
State University of New York
Stony Brook, New York 11794

Of the more than sixty North American species of *Phaneta,* host plants are known for less than one third. All of the known hosts are in the family Compositae, and most species feed only on the flowers or seeds of their host plant (Heinrich, 1923, Mackay, 1959). (Host plants are listed by these authors for the species of the genus, *Thiodia,* the North American members of which have been transferred to *Phaneta* (Obraztsov, 1952)). Although *Phaneta imbridana* (Fernald) has been known to taxonomists for years (Fernald, 1905, Miller, 1970), nothing is known of its biology or life history. I therefore report certain aspects of the ecology of *P. imbridana* and its relationship with a local host plant, *Xanthium strumarium,* unique among the Compositae by having relatively large fruits and seeds. This information was obtained as part of a larger study of the variation in susceptibility of populations of *X. strumarium* to seed predation by more than one species of seed predator along Long Island beaches.

A. Life Cycle

Adults emerge in late August and can be found until late September, with oviposition occurring throughout the adult period. Females oviposit directly on the surface of the full-sized but immature burrs of *X. strumarium.* Eggs soon hatch and the larvae bore through the burr wall and begin to feed on one of two seeds of the burr. If one seed is insufficient for complete larval development, larvae will attack the other seed within the same burr, or rarely, seeds of another burr on the same plant. Full larval development is completed by late September or early October, at which

---

*Present address: Department of Entomology, Connecticut Agricultural Experiment Station, Box 1106, New Haven, CT 06504.

Manuscript received by the editor October 1, 1977.

Table 1

Distribution of *Phaneta imbridana* among
Populations of *Xanthium strumarium*

Mean Proportion Seeds Attacked (1973–1975)

	Population Number									
	1	2	3	4	5	6	7	8	9	10
Upper Seed	.03	.12	.05	.09	.01	.05	.03	.07	.07	0.0
Lower Seed	.07	.20	.24	.20	.07	.15	.10	.22	.12	.05

time larvae leave the burr through a hole bored near its basal end. Since burrs reach full maturity and are easily dislodged and dispersed before larvae leave the burr, passive long-range dispersal of *P. imbridana* may occur in the larval stage.

Local populations of *P. imbridana* overwinter as last-instar larvae in the dry pithy stems of *X. strumarium*. It is unlikely that *P. imbridana* is limited to *X. strumarium* for overwintering. however, the other common herbaceous species associated with *X. strumarium* do not contain overwintering larvae. Pupation occurs in the stem fragments in the following summer. Mating behavior was not observed.

B. Role as a Seed Predator

Levels of seed predation were measured for ten populations of *X. strumarium* over a three-year period. Consistent, significant differences in the abundance of *P. imbridana* were observed among plant populations (Table 1), however, mean seed loss was less than 10%.

The two seeds within a burr of *X. strumarium* differ in size and germination requirements (e.g. Wareing and Foda, 1957). The lower seed is larger and germinates the spring following production, while the smaller, upper seed remains dormant for one year or more if its seed coat remains intact. *Phaneta imbridana* is more commonly found in the lower, non-dormant seed within a burr (p less than .001). Although one cannot exclude the possibility that larvae or ovipositing females may be choosing seeds on the basis of their dormancy properties, differential seed predation within burrs is best explained by burr asymmetry. Since the larger seed occupies more than half of the burr cavity, it is covered by more than half of the burr surface, and oviposition is more likely to occur on burr surface adjacent to lower than to upper seeds.

C. Interactions with Other Seed Predators

The tephritid fly, *Euaresta aequalis* Loew, is another common seed predator of *X. strumarium.* The abundance of *E. aequalis* also varies significantly among populations, and larvae are more frequent in lower than upper seeds. The oviposition periods of both insect species coincide. Most local populations of *X. strumarium* are not attacked by both insect species, however, in those plant populations which experience at least 5% seed predation by both species, the abundance of the two species on individual plants is significantly negatively correlated (r = –.42, p less than .01). An oviposition experiment was performed using plants from several populations grown under uniform conditions and then simultaneously exposed to both insect species. The number of burrs attacked by both species was much less than expected assuming that their oviposition behaviors were independent (Table 2), and the number of burrs containing one larva of *P. imbridana* and one undamaged seed was much greater than expected.

These results indicate that within populations, some plants may produce burrs more susceptible to one insect species than the other,

Table 2

Frequency of Attack of
Seeds Within Burrs

	Disposition					
	PP	UP	PE	EE	UE	UU
Observed	16	70	43	110	46	87
Expected	14.1	56.5	60.2	64.2	130.5	56.5
Difference	1.9	13.5	–17.2	45.8	–74.5	30.5

G-test Statistic = 110.024, p less than .005

PP = Both seeds containing *P. imbridana.*
UP = One seed containing *P. imbridana* and the other undamaged.
PE = One seed containing *P. imbridana* and the other containing *E. aequalis.*
EE = Both seeds containing *E. aequalis.*
UE = One seed containing *E. aequalis* and the other undamaged.
UU = Both seeds undamaged.

and also that within plants, *P. imbridana* may avoid ovipositing on burrs previously attacked by others of its own or different species. Further investigations are in progress to determine which particular aspects of burr morphology and chemistry most strongly influence susceptibility of burrs to each insect species.

ACKNOWLEDGEMENTS

I thank William E. Miller and a reviewer for their information concerning the taxonomy and ecology of the genus *Phaneta.* Specimens were kindly identified by D. R. Davis of the U. S. National Museum. Contribution #226 from the program of Ecology and Evolution at the State University of New York at Stony Brook.

REFERENCES

FERNALD, C. H.
1905. North American Tortricidae. Can. Ent. **37:** 399–400.
HEINRICH, C.
1923. Revision of the North American Moths of the Subfamily Eucosminae of the Family Olethreutidae. Bull. U. S. Nat. Mus. #123. 298 pp.
MACKAY, M. R.
1959. Larvae of the North American Olethreutidae (Lepidoptera). Can. Ent. Suppl. #10. 338 pp.
MILLER, W. E.
1970. Fernald Types of North American Olethreutinae (Lepidoptera: Tortricidae). Proc. Ent. Soc. Wash. **72:** 288–294.
OBRAZTSOV, N.
1952. *Thiodia* Hb. as not a North American Genus (Lepidoptera, Tortricidae). Ent. News **63:** 145–149.
WAREING, P. F., AND H. A. FODA
1957. Growth Inhibitors and Dormancy in *Xanthium* seed. Phys. Plant. **10:** 266–280.

EVIDENCE FOR OBLIGATE MONOPHENISM IN *RELIQUIA SANTAMARTA*, A NEOTROPICAL-ALPINE PIERINE BUTTERFLY (LEPIDOPTERA:PIERIDAE)

By Arthur M. Shapiro[1]
Department of Zoology
University of California
Davis, California 95616, U.S.A.

Introduction

The phenomenon of seasonal polyphenism under photoperiodic control is now well established in a variety of butterflies, especially members of the family Pieridae (Shapiro, 1976a). Although it is expressed in nature primarily by multivoltine populations at low to middle altitudes in strongly seasonal mid-latitude climates, polyphenism has been found in a latent form in univoltine species which are ordinarily monophenic. These include species coevolved with vernal-ephemeral host plants (*Pieris virginiensis* Edwards, Shapiro, 1971; *P. napi microstriata* Comstock, Shapiro, 1975a) or facing short growing seasons due to altitude (*Pieris occidentalis "calyce"* Edwards, Shapiro, 1974) or latitude (*P.o. nelsoni* Edwards, Shapiro, 1975b). To date no population of either the *Pieris callidice* Hübner or *P. napi* Linnaeus complexes has been found to be obligately monophenic, although some *P. napi* (Yukon Territory and central New Mexico, Shapiro, 1976a) produce only more-or-less heavily dark-veined phenotypes. The ability of univoltine Pierines to produce phenotypes analogous to normal seasonal ones produced by their multivoltine relatives, when reared in photoperiod-temperature regimes which do not occur in their natural habitat, has been interpreted (Shapiro, 1976a) as evidence for the derivation of univoltinism/monophenism from multivoltinism/polyphenism in the course of adaptation to new or changing climates.

---

[1] This work was made possible by grants from the National Geographic Society (USA) and the National Science Foundation (USA) and with the help of Colombian friends too numerous to mention. Special thanks go to Ms Adrienne R. Shapiro and Dr. Arthur S. Weston for their companionship and constant help afield in the Sierra Nevada.

Manuscript received by the editor December 15, 1977.

Reliquia santamarta Ackery is an unusual Pierine of uncertain affinities which is known only from above 3500 m in the Sierra Nevada de Santa Marta of northeastern Colombia. It was discovered in 1971 and described four years later (Ackery, 1975). Phenotypically, the adult closely resembles high-altitude and -latitude members of the Holarctic *Pieris callidice* complex (figs. 1, 2) and is unlike the distinctive Andean montane and alpine Pierines (*Tatochila, Phulia, Piercolias*). In those genera the submarginal black chevrons on the hindwing above and below point outward in the interspaces. In Holarctic *Pieris* and in *R. santamarta* they point inward. Morphologically *R. santamarta* is also close to *Pieris,* and indeed would be included therein under the traditional broad concept of the genus, which is beginning to break down (Kudrna, 1974). These facts suggest that *R. santamarta* might represent a relict of a Holarctic stock of the *P. callidice* complex which invaded northern South America during a cold period, presumably in the Pleistocene. The Sierra Nevada de Santa Marta, although only 62 km from the Serrania de Valledupar which connects to the northern Andes, shows a very high degree of faunal and floral endemism. The entomologist who knows it best, Michael Adams, is convinced (1973, 1975, and personal communications) that its butterfly fauna had not begun differentiating before the eastern Andean orogeny — thus precisely contradicting the hypothesis of Todd and Carriker (1922) of an eastern Andean origin for the Sierran alpine avifauna — and that certain groups speciated and underwent character- and altitudinal displacement in the Pleistocene. A.S. Weston (personal communication) has noted a floristic connection between the Sierran páramos and those of Costa Rica. At least one butterfly, *Nathalis iole* Boisduval (Pieridae, Coliadinae) is perhaps a Nearctic relict in the Sierra Nevada de Santa Marta.

R. santamarta has been recorded from both dry seasons, the "verano" ("summer"; actually trade-wind season) in December-March and the shorter and less reliable "veranillo" in July — these being the only times of the year when weather conditions in the high Sierra would make butterfly collecting feasible. No phenotypic differences are apparent among the putative broods. This is perhaps not surprising. Pierines in middle latitudes respond phenotypically to daylength, but the Sierra lies at a latitude of 10°44′ N, and the longest and shortest days of the year there differ in length by only about 70 minutes. The literature is devoid of photoperiodic studies of circumequatorial insects, except for one paper by McLeod (1968) who excluded photoperiod as a factor in the seasonal polyphenism of an African Nymphalid. If, however, *Reliquia santamarta* were a Pleistocene derivative of the *Pieris callidice* complex, it might be expected to show a latent polyphenism when reared under a laboratory regime that induces light phenotypes in that group. Long days, particularly continuous light, coupled with high temperatures are very effective in this regard (Shapiro, 1976a).

MATERIALS AND METHODS

Eight females of *R. santamarta* were collected January 18–22, 1977 at and near the type locality (headwaters of the Río Cambirumeina and south slope of Cerro Icachui, 3950–4400 m). They were induced to oviposit in camp by confining them in sunlight in cylindrical tins 9.5 × 10.5 cm, covered outside with white glazed paper and topped with gauze, containing fresh sprigs of local Crucifers as oviposition substrates and Composite flowers as nectar sources. One female was a virgin, but all the others laid at least a few eggs. Eggs were placed on the plants, the gauze, and the tins. They were transported by ground to Valledupar, Department of Cesar, on January 26 and thence by air to Cali, Department of Valle del Cauca, the next day, where the first hatch occurred in the afternoon. Rearing was carried out in Cali on continuous light from a 60w bulb in plastic Petri dishes 18 cm × 3 cm on fresh sprigs of the Crucifer *Lepidium virginicum* L. collected from a vacant lot; this common weed has often been used in experiments with Pierines and is a frequent wild host of North American members of the *callidice* group. The rearing temperature was 26.5° ± 2° C. These conditions would induce light phenotypes in any Nearctic member of the *callidice* group which has been tested.

Due to electricity rationing in Colombia, it was necessary to substitute a powerful candle for the lamp from 1800 to 1900 hours daily throughout the rearing period. My impression, based on previous work with Pierines, is that this was read as "day" by the animals. Even if it was read as "night," a 23-hour photophase has always been read as a "long day" by Nearctic species.

R. santamarta proved difficult to rear under the experimental conditions in Cali. The culture started well, but about half the larvae died in the penultimate and ultimate instars of apparent

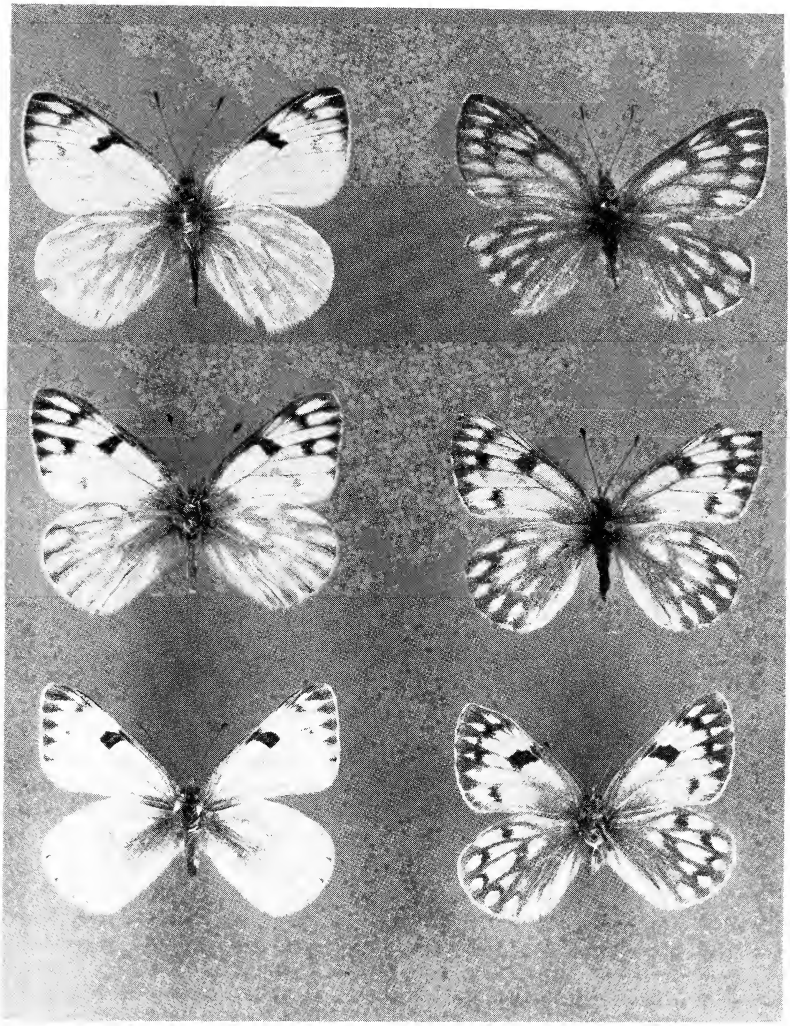


Figure 1. Dorsal surfaces of three Pierines from extreme climates, males at left. Top row: *Reliquia santamarta,* 4200 m, Sierra Nevada de Santa Marta, Colombia, 10°44′ N. Centre: *Pieris occidentalis "calyce,"* 3640 m, Colorado front range, USA, 40°01′ N. Bottom: *Pieris occidentalis nelsoni,* Fairbanks, Alaska, 64°51′ N.

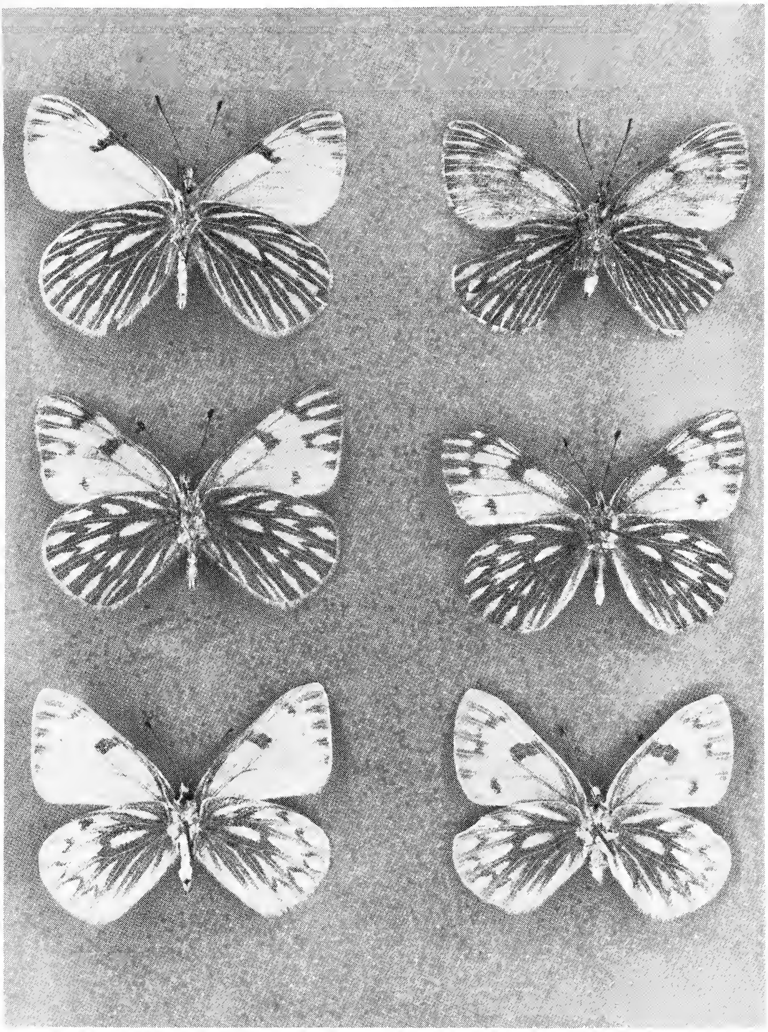


Figure 2. Same as figure 1, ventral surfaces.

bacterial septicemia, despite stringent sanitation and daily replacement of the host plant. Ultimately 16 pupae were obtained, but 9 of these died without showing development. The remaining 7 pupae proceeded rapidly to the pharate adult, but failed to eclose. On February 15 they were all dissected to determine the phenotypes of the pharate adults — an easy and reliable procedure. Examples of the early stages were preserved and the life-history will be described elsewhere.

RESULTS AND CONCLUSIONS

All of the pharate adults (5 males, 2 females) were in good enough condition for the ventral hindwing phenotype to be determined (one female had to be degreased). All were completely normal, with the dark ventral pattern precisely as it occurs on wild specimens from the mountains.

Despite the small sample size, the use of the candle, and the overall logistical difficulty of the experiment, this is a definitive result since the phenotypes were so consistent and because no known Nearctic Pierine reared under the same conditions would have given the same result. Obviously we cannot exclude the possibility of a latent polyphenism, but it is made much less probable by the demonstration that it cannot be exposed under the most effective rearing regime known for that purpose. Since no Nearctic species yet tested has so canalized its phenotype, the likelihood that *R. santamarta* is a close relative of the species it most resembles is diminished.

Why lose the potential for polyphenism? There is no obvious selective advantage in doing so. In Holarctic populations it is merely submerged when selection for an appropriate phenology alters photoperiodic thresholds. This is especially easy in taxa in which phenotype is somehow coupled to pupal diapause, since all diapaused pupae will yield dark adults. We do not know if *R. santamarta* is capable of diapause; certainly it would make sense during the wettest months (October and November), but we do not know what the environmental cues might be. At any rate, the animals collected in January 1977 were in very mixed condition, suggesting overlapping broods during the "verano." As noted before no sign of seasonal phenotypes has been detected even though some of these adults would have been from diapause pupae if there are any such. We know from the experiment what non-diapause animals look like.

The dark-veined phenotype is undoubtedly optimal at all seasons at Cambirumeina. In the two dry seasons the normal weather is clear in the morning and foggy in the afternoon. Night temperatures drop below freezing; before the fog asserts itself the temperature may climb to 18° C, but then it drops to 5–7° C and remains there until after nightfall, when clearing occurs. During my stay fog set in from 1000 to 1400 hours on different days, i.e. from 2 to 6 hours after the initiation of flight activity. This was at the sunniest time of the year; during the rainy seasons the temperature probably hovers between 2° and 6° C most of the time, and sunshine occurs only fleetingly. The *R. santamarta* phenotype is of a sort known to be thermoregulatorily used by Nearctic Pierines (Shapiro, 1975c, 1976a) and the behavior of *R. santamarta* afield precisely matches theirs (Shapiro, 1977). *Pieris occidentalis "calyce"* Edwards in the Colorado front range has the same kind of weather during its flight season in August and matches *R. santamarta* in pattern, almost scale for scale. However, it retains a latent polyphenism (Shapiro, 1974, 1976b).

It is, of course, possible that the phenotype of *R. santamarta* is merely convergent to *Pieris,* and that no polyphenism has ever existed in its ancestry. If this is the case, the phylogeny of the Pierini is more confused than ever, and *R. santamarta* has no known close relatives.

SUMMARY

Reliquia santamarta is a multivoltine Pierine butterfly from above 3500 m in the Sierra Nevada de Santa Marta, Colombia, latitude 10°44′ N. Its single natural phenotype is extremely similar to the high-altitude and -latitude members of the Holarctic *Pieris callidice* complex. When reared on continuous light at 26.5° ± 2° C, *R. santamarta* produced only its usual dark-veined, presumably thermoregulatory phenotype. In this regard it differs from all previously tested, Holarctic Pierines, which display latent polyphenism attributable to their evolution from multivoltine, phenotypically plastic ancestors. The seeming lack of a latent polyphenism in *R. santamarta* casts doubt on the close affinity of that animal to the *P. callidice* complex. Its relationships remain important for understanding the biogeography of the unusual endemic group of Andean Pierini.

REFERENCES

ACKERY, P. R.

1975. A new Pierine genus and species with notes on the genus *Tatochila* (Lepidoptera: Pieridae). *Bull. Allyn Mus. 30:* 1–9.

ADAMS, M.

1973. Ecological zonation and the butterflies of the Sierra Nevada de Santa Marta, Colombia. *J. Nat. Hist. 7:* 699–718.

1975. Full report of the third "North Colombia Butterflies Expedition 1974/75". Mimeograph, 42 pp.

KUDRNA, O.

1974. *Artogeia* Verity 1947 gen. rev. for *Papilio napi* Linnaeus (Lep., Pieridae). *Entomol. Gaz. 25:* 9–12.

MCLEOD, L.

1968. Controlled environment experiments with *Precis octavia* Cramer (Nymphalidae). *J. Res. Lepid. 7:* 1–18.

SHAPIRO, A. M.

1971. Occurrence of a latent polyphenism in *Pieris virginiensis* (Lepidoptera: Pieridae). *Entomol. News 82:* 13–16.

1974. Ecotypic variation in montane butterflies. *Wasmann J. Biol. 32:* 267–280.

1975a. Developmental and phenotypic responses to photoperiod in uni- and bivoltine *Pieris napi* in California. *Trans. R. ent. Soc. Lond. 127:* 65–71.

1975b. Photoperiodic control of development and phenotype in a subarctic population of *Pieris occidentalis* (Lepidoptera: Pieridae). *Can. Entomol. 107:* 775–779.

1975c. Ecological and behavioral aspects of coexistence in six Crucifer-feeding Pierid butterflies in the central Sierra Nevada. *Amer. Midl. Nat. 93:* 424–433.

1976a. Seasonal polyphenism. *in* M. K. Hecht, W. C. Steere, and B. Wallace, eds., *Evolutionary Biology,* vol. 9, pp. 259–333. Plenum Press, New York and London.

1976b. Photoperiodic responses of phenologically aberrant populations of Pierid butterflies (Lepidoptera). *Great Basin Nat. 35:* 310–316.

1977. Notes on the behavior and ecology of *Reliquia santamarta,* an alpine butterfly (Lepidoptera: Pieridae) from the Sierra Nevada de Santa Marta, Colombia, with comparisons to Nearctic alpine Pierini. *Studies in the Neotrop. Fauna Envt.,* in press.

TODD, W. E. C. AND M. A. CARRIKER, JR.

1922. The birds of the Santa Marta region of Colombia: a study in altitudinal distribution. *Ann. Carneg. Mus. 14:* 3–611.

SEXUAL BEHAVIOR OF *MURGANTIA HISTRIONICA* (HEMIPTERA:PENTATOMIDAE)

BY PATRICK J. LANIGAN[1] AND EDWARD M. BARROWS[2]

INTRODUCTION

Murgantia histrionica (Hahn) is an economically important pest of brassiaceous crops in Central and Southern United States. Aspects of its biology have been studied by Paddock (1918), Chittenden (1920), White and Brannon (1933), and Canerday (1965); however, its sexual behavior has not been studied in detail. Therefore, we studied courtship, copulation, polygyny, and polyandry in this bug. Fish and Alcock (1973) and Gamboa and Alcock (1973) have reviewed the literature on pentatomid courtship and copulation.

MATERIALS AND METHODS

In July and August, 1976, nymphs and adults of *M. histrionica* were collected in Washington, D. C. from cabbage, *Brassica oleracea capitata* L.; broccoli, *B. o. cymosa* L.; and radish, *Raphanus sativa* L. Groups of four to seven adult or nymphal bugs were maintained in petri dishes in the laboratory. The laboratory was illuminated with flourescent light and indirect sunlight, and temperatures varied from 24 to 38° C. Bugs were fed pieces of leaves of *B. o. capitata* or *R. sativa* that were changed about daily. When conspicuous mold appeared on bug feces in petri dishes, bugs were transferred to clean dishes to reduce mortality.

Only virgin adults were used in the study of courtship and copulation to reduce possible behavioral variability due to learned sexual behavior. In each trial of the experiment a male was removed from his dish with forceps and placed in a dish with a female. The female's dish was placed on white paper to provide a good background for observation. Food was removed from a female's cham-

---

[1] Department of Biology, Georgetown University, Washington, D.C., 20057.

[2] Department of Biology, Georgetown University, Washington, D.C., 20057, and The University of Michigan Biological Station, Pellston, Michigan, 49769. Send reprint requests to E. M. Barrows at Georgetown University.

Manuscript received by the editor November 10, 1977.

ber prior to introduction of a male. Males were marked on their scutella with dots of fast-drying, enamel paint so that they could be readily distinguished from females.

In November, 1976, *M. histrionica* were collected from the field for a study of polygamy. Twenty pairs were used, and the bugs may or may not have been virgins. One male and one female were placed with food in each of 20 petri dishes. After a pair copulated, the female was transferred to a dish with a different male. A sample mean is denoted by $\overline{X}$; median, M; and size, N.

RESULTS

Fourteen of 20 courtships of *M. histrionica* led to copulation (Fig. 1 and 2). Durations from introduction of a male to copulation initiation ranged from 8.5 to 47.3 min ($\overline{X} = 26.8$, $M = 24.5$). Main steps in this bug's sexual behavior are as follows:

(1) The male approaches the female with his antennae waving while she is mobile or immobile. She may become motionless and "crouch down" on the substrate if she is approached when moving, or she may escape and crawl away from the male.

(2) The male antennates the female while she is motionless. If his approach is from her front, he antennates her antennae and then her scutellum. If his approach is from behind, he antennates her posterior abdominal segments and posterior portions of her folded wings. Eighteen antennations lasted from 3 to 15 sec ($\overline{X} =$ 7.0, $M = 8.5$).

(3) After vigorous male antennation, the female rapidly and violently jerks her body sideways for approximately 3 sec. If the male approaches her from behind, he moves in front of her and antennates her antennae, and then the female shows jerking movements. Females may escape from males during this step in sexual behavior.

(4) The male moves to the female's side, stops, and antennates her side in different places. Antennating males frequently orient approximately 60, 90, 120° with respect to the female longitudinal axis. (Zero degrees is considered to be when the bugs are head to head.) Eleven males used all three orientations and stopped to antennate for from 3 to 5 sec before moving to female posteriors. Females respond to antennation by violent sideways jerking.

(5) When the male reaches the female posterior, he antennates and she shows sideways jerking for from 2 to 5 sec. He strokes the

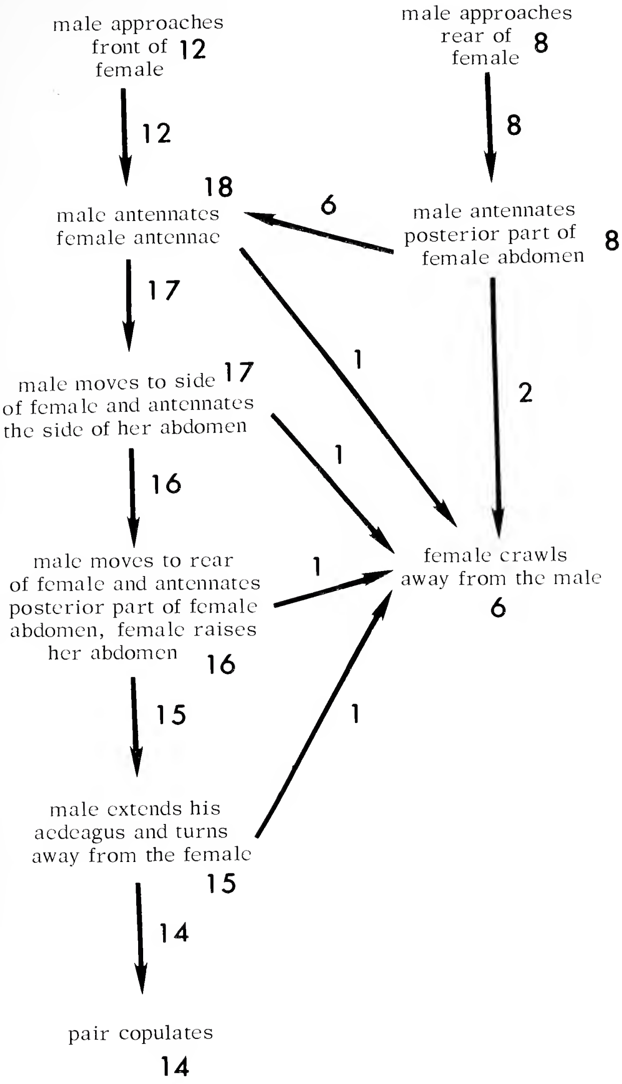


Figure 1. Behavioral sequence in courtship involving 20 pairs of *Murgantia histrionica.* See the text for further explanation.

female venter alternately with his left and right antennae, and then the female raises her abdomen to approximately 30° above the substrate. Females may escape during this step.

(6) With his aedeagus extended, the male makes a 180° turn which maneuvers him into a position from which he initiates linear copulation. Unreceptive females may also escape at this time.

(7) The male elevates his abdomen and backs directly against the female, and he initiates copulation.

(8) Once the pair starts copulating, they use their middle and hindlegs to jerk their bodies up and down. In 14 observations, jerking lasted from 10 to 185 sec ($\overline{X} = 52$, $M = 48$). This behavior also occurred from 5 min to 6 hr after copulation initiation.

(9) The male rapidly strokes up and down the sides of the female abdomen with both his hindlegs, This occurs during and after body jerking. Male leg stroking of the female lasted from 4 to 27 sec ($\overline{X} = 13$, $M = 11$, $N = 14$).

(10) The pair crawls in the petri dish with the female, which is usually larger, pulling the male in most cases. In 71 observation periods, copulating pairs remained motionless from 5 to 1260 sec ($\overline{X} = 453$, $M = 315$). When food was placed in the chamber after several hours of its absence, bugs often fed while *in copula*. Copulation duration ranged from 5.4 to at least 8.3 hr. The termination of copulation was not observed in most pairs.

In petri dishes, a common female escape behavior was quick-crawling to dish sides with the male in pursuit. Females on dish sides continued at steady paces and males followed them with quick-crawling bouts interspersed with rests. Males waved antennae as they approached females. If males reached females, or if females stopped, courtship was hindered because females often escaped when males tried to move in front of them. Females also escaped while males antennated their sides, venters, and when males made 180° turns before aedeagal insertions. Males that were on dish tops or bottoms courted females which were on dish sides, but males did not crawl on dish sides to attain typical positions that occur during copulation initiation. In other situations, two females raised their wings as males approached, and they crawled away as males attempted to court them.

Murgantia histrionica was polygynous and polyandrous in the laboratory. In the polygamy experiment, two males copulated with four different females; four males, with three females; and

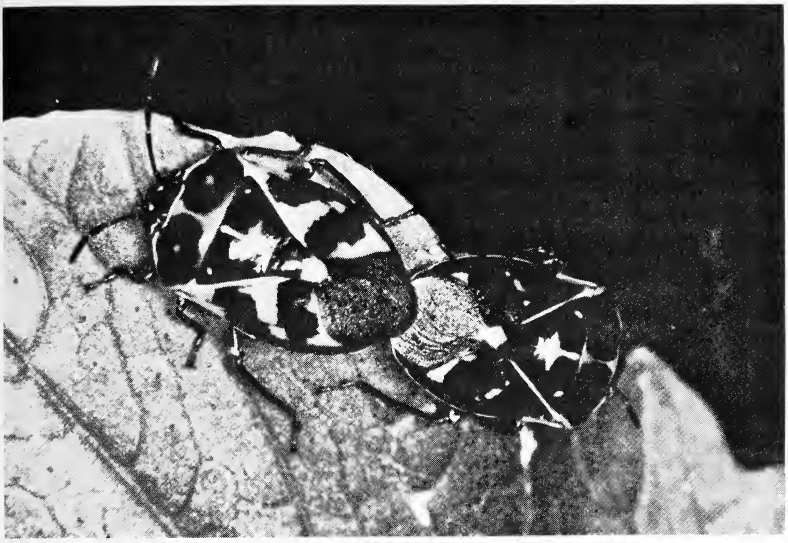


Figure 2. *Murgantia histrionica in copula* on radish foliage. The male faces to the right and lacks part of his right antenna.

two males, with two females. One male copulated once, and 11 other males did not copulate. Two females copulated with three different males; six females, with two males; seven females, with one male; and five females did not copulate.

DISCUSSION

Gamboa and Alcock (1973) reported three major methods by which pentatomids initiate copulation, one of which involves males and females facing in opposite directions, which we found in *M. histrionica*. Fish and Alcock (1973) noted that other species which employ this method have similar courtship behaviors. They listed four main behaviors shared by species of this group: (i) male antennation of the female, (ii) male attempt to lift the female abdomen with his head, (iii) abdominal elevation by receptive females, and (iv) male antennal and aedeagal stimulation of female abdomens. Fish and Alcock conclude that males attempt to induce females to assume positions that facilitate aedeagal insertion. Members of at least six other genera of pentatomids, besides *Murgantia,* are known to initiate copulation when males and females face opposite directions (Olsen, 1910; Esselbaugh, 1948; Mitchell and Mau, 1969; Alcock, 1971; Fish and Alcock, 1973; and Gamboa and Alcock, 1973).

In *M. histrionica,* male antennation of the female abdomen is followed by female abdominal-raising. Male *M. histrionica* did not attempt to raise female abdomens with their heads as do other males of genera in which bugs initiate copulation while facing opposite directions (Gamboa and Alcock, 1973). In this species, male antennation might be a more derived behavior than male use of heads to raise female abdomens as displayed in other species.

John Alcock (pers. comm.) observed about 25 courting pairs of *M. histrionica* on *Cleome jonesii* (MacBride) Tibestrom (Capparidaceae) on which they also fed, in Patagonia, Arizona, in July 1976. Bug courtship in Arizona was similar to that which we observed, but in addition, males used their abdominal tips to push at and lift female abdomens. Alcock saw many pairs *in copula;* however, none of the observed courtships led to copulation.

As noted above, *Murgantica histrionica* was polyandrous and polygynous in our laboratory study. These behaviors also occur in *Podisus modestus* (Dallas) (Tostowaryk, 1971) and in *Nezara viridula* (L.) (Mitchell and Mau, 1969).

ACKNOWLEDGEMENTS

Jon Herring (USDA, Washington, D. C.) made available his pentatomid literature file for this study. John Alcock (Arizona State University) and Lawrence S. Oliver (Georgetown University) offered important suggestions regarding a draft of this note.

LITERATURE CITED

ALCOCK, J.
1971. The behavior of a stink bug, *Euschistus conspersus* Uhler (Hemiptera: Pentatomidae). Psyche **78:** 218–228.
CANERDAY, T.
1965. On the biology of the harlequin bug, *Murgantia histrionica* (Hemiptera: Pentatomidae). Ann. Entomol. Soc. Amer. **58:** 931–932.
CHITTENDEN, F. H.
1920. Harlequin cabbage bug and its control. U. S. Dept. Agr. Farmers Bull. 1061.

ESSELBAUGH, C. O.
1948. Notes on the bionomics of some midwestern Pentatomidae. Entomol. Americana **28:** 1–73.
FISH, J. AND J. ALCOCK.
1973. The behavior of *Chlorochroa ligata* (Say) and *Cosmopepla bimaculata* (Thomas) (Hemiptera: Pentatomidae). Entomol. News **84:** 260–268.
GAMBOA, G. AND J. ALCOCK.
1973. The mating behavior of *Brochymena quadrapustulata* (Fabricius). Psyche **80:** 265–270.
MITCHELL, W. C. AND R. F. L. MAU.
1969. Sexual activity and longevity of the southern green stinkbug, *Nezara viridula.* Ann. Entomol. Soc. Amer. **62:** 1246–1247.
OLSEN, C. E.
1910. Notes on breeding Hemiptera. J. N. Y. Entomol. Soc. **18:** 39–42.
PADDOCK, M. S.
1918. Studies on the harlequin bug. Texas Agr. Exp. Sta. Bull. 227.
TOSTOWARYK, W.
1971. Life history and behavior of *Podisus modestus* (Hemiptera: Pentatomidae) in a boreal forest in Quebec. Can. Entomol. **103:** 662–674.
WHITE, W. H. AND L. W. BRANNON.
1933. The harlequin bug and its control. U. S. Dept. Agr. Farmers Bull. 1712.

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 Ave., 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.

ISSN 0033-2615

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 84 September-December, 1977 No. 3-4

CONTENTS

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1977–1978

President	GARY D. ALPERT
Vice-President	JOHN A. SHETTERLY
Secretary	ROBERT ROBBINS
Treasurer	FRANK M. CARPENTER
Executive Committee	MARTHA FISHER KATHERINE HORTON

EDITORIAL BOARD OF PSYCHE

PSYCHE is published quaterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: $8.00 for United States and Canada, $9.50 for other countries. Single copies, $2.50.

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 $23.50 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 June, 1977, Psyche (Vol. 84, No. 2) was mailed March 28, 1978

THE LEXINGTON PRESS, INC., LEXINGTON, MASSACHUSETTS

PSYCHE

Vol. 84 September-December, 1977 No. 3–4

DISPERSAL BEHAVIOR OF HONEY BEE SWARMS*

BY THOMAS D. SEELEY AND ROGER A. MORSE

Museum of Comparative Zoology
Harvard University, Cambridge, Massachusetts 02138
and Department of Entomology
Cornell University, Ithaca, New York 14853

INTRODUCTION

Food shortages were probably a major ecological force upon the European races of honey bees (*Apis mellifera*) in their natural habitat of temperate deciduous forest. And many features of honey bee biology are reasonably interpreted as techniques of competition for food. For example, the demographic properties of descendant honey bee colonies in North America, such as low reproductive rate and infrequent but expensive offspring, probably reflect selection for competitive ability rather than productivity (Seeley 1978). Also the honey bee's sophisticated recruitment system involving dance language and olfactory recruitment (von Frisch 1967, Gould 1975) seems ideal for a "scramble" type competitive device involving rapid discovery and exploitation of food sources. Furthermore bees from different colonies will fight at feeding dishes when the food is in short supply (Kalmus 1941) and will reduce each others' foraging range (Levin 1961, Levin and Glowska-Konopacka 1963, Gary *et al.* 1972, 1973, 1975). Thus honey bee colonies can apparently also compete for food sources using techniques of "contest" competition.

**Manuscript received by the editor March 15, 1978.*

Behaviors promoting colony spacing are another line of adaptations to limited food supplies and are widespread among the social insects (Brian 1965, Wilson 1971). For honey bees these behaviors fall logically into two classes: (1) attack by established colonies upon adjacent colonies, and (2) avoidance of established colonies by swarms when selecting nest sites. Behavior of the first category is apparently of minor importance with honey bees since bee colonies can be crowded into peaceful apiaries. However strong colonies occasionally plunder nearby weak colonies. Regarding the second category, Lindauer (1955) provides evidence suggesting that honey bee swarms avoid their parent colonies by selecting new nest sites at least a few hundred meters from the original nest. Given the importance of understanding colony spacing to a clear understanding of honey bee ecology, especially intraspecific foraging competition, we decided to investigate the dispersal behavior of honey bee swarms.

MATERIALS AND METHODS

The honey bees used in this study came from the Dyce Honey Bee Laboratory, Cornell University, and were hybrids of the European races of honey bees imported for American apiculture. These races include primarily *Apis mellifera ligustica* Spinola, *A. m. caucasica* Gorbatschew, *A. m. carnica* Pollmann and *A. m. mellifera* L. (Ruttner 1975). The study of swarm dispersal distance was conducted during the summers of 1976 and 1977 on Mount Pleasant, a large area of mature forest near Ithaca, New York. The test of swarms' preferred dispersal distance was performed during December, 1977 and January, 1978 at the Archbold Biological Station, Lake Placid, Florida. There the study area consisted of a sandy plain which extends for many kilometers and which is primarily covered by scrubby vegetation. The widely dispersed pine trees in this area offer very few, if any, natural nest sites for honey bees. Additional methodological details will be given with the descriptions of the individual experiments.

EXPERIMENTS AND RESULTS

Distribution of Swarm Dispersal Distances

Upon departing its parent colony, a honey bee swarm flies only a few tens of meters before assembling to form a hanging swarm cluster (Ambrose 1974). Scout bees fly from this cluster in search of a nest site and later recruit other scouts to newly discovered nest sites using the dance language (Lindauer 1955). These communication dances are conspicuously performed on the surface of the swarm. Thus one can measure approximately how far swarms move between parent and new colony sites by reading the recruitment dances of the scout bees on swarms.

We used artificial swarms of honey bees which were prepared as follows. First, worker bees were shaken off frames of a beehive into a swarm cage (15 × 25 × 35 cm) of wood and wire screen sides using a large funnel. Then the swarm's queen was removed from the beehive and confined in a standard queen mailing cage (3.2 × 10 × 1.6 cm) which was suspended amidst the worker bees in the larger swarm cage. The bees were kept confined and liberally fed with a 50% sucrose solution for at least 24 hours. Bees treated in this way behave like a natural swarm. If placed near their parent hive, they do not return to it but instead search for a new nest site. We controlled swarm size by weighing the workers shaken into the swarm cage. The swarms all weighed approximately 2 kg (about 15,000 bees), a typical size for natural swarms (Fell *et al.* 1977).

Each swarm was placed on a wood cross (120 cm high with a 46 cm long cross member) in the study area by tying the caged queen to the cross. The worker bees, upon being shaken from the swarm cage, would cluster about the caged queen. A 1-liter, gravity feeder jar provided sugar syrup continuously for each swarm. We positioned the swarms in a small clearing surrounded by forest for at least 1 km and generally 2 or more km. Thus the swarms were surrounded at both small and large distances by a presumably random distribution of natural nest sites. The swarms were run one at a time, except for three swarms which we observed simultaneously. The three concurrently run swarms were positioned at least 30 m from each other.

We followed each swarm's selection of a nest site from start to finish by reading the scout bees' dances to determine the distances and directions to the nesting sites they had discovered. The calibration curves of von Frisch (1967) and Lindauer (1971) for *Apis mellifera ligustica* were used to translate dance tempos into distances to the advertised nest sites. The dances representing the site finally selected by each swarm were easily recognized by the frenzy with which they were performed and by their heavy preponderance

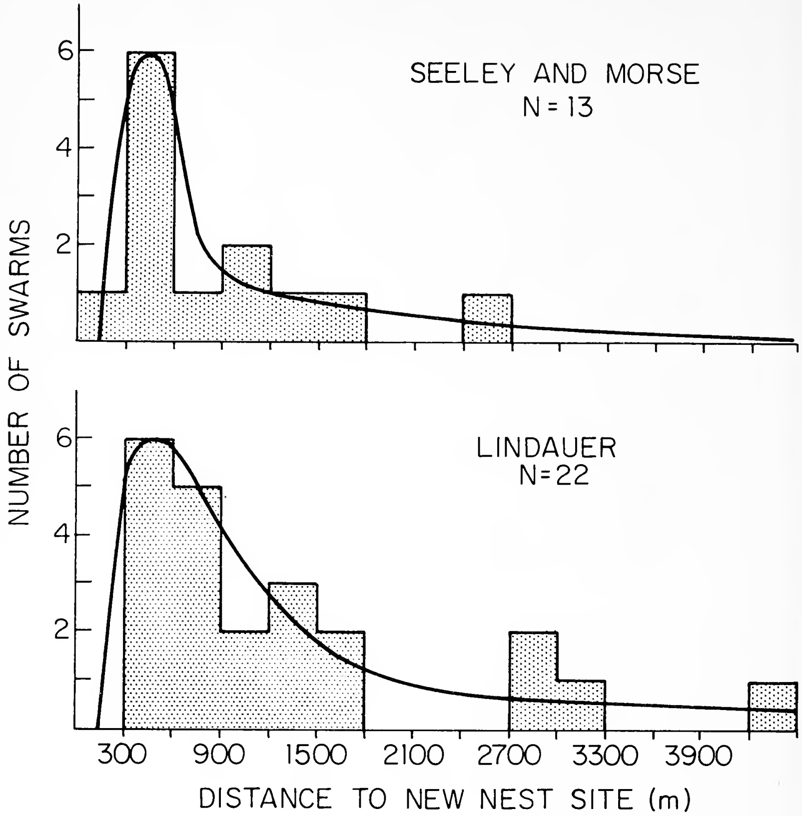


Fig. 1. Distributions of distances from swarm cluster sites to new nest sites, as calculated from the recruitment dances of scout bees on swarms. The curves are least-squares fits to points centered in the top of the histogram bars. Upper figure is original data; lower figure is after Table 1 in Lindauer (1955).

over all other dances just before each swarm lifted off to fly to its chosen site.

The results from observing 13 swarms are shown in Fig. 1. This figure also includes data gathered in similar fashion by Lindauer (1955) who observed swarms inside Munich and in various rural locations in West Germany. The curves in Fig. 1 were fitted to the histograms as described in Seeley and Morse (1978). The striking features of the two distributions are (1) their similarity despite widely separated study areas, and (2) the low frequency of swarms travelling less than 300 m to a new nest site. This pattern may simply reflect the smaller number of nest sites within a small radius area relative to a large radius area. But it could also represent a preference by swarms for nest sites beyond 300 meters from their cluster sites. Since swarms generally travel only a few tens of meters from the parent colony before settling at an interim cluster site, a preference for nest sites far beyond the cluster site would promote the dispersion of parent and daughter colonies. The following section reports a test for this preference.

Test of Preference for Distant Nest Sites

To test whether swarms prefer distant nest sites, we offered swarms a choice between two nestboxes which were constructed and positioned as identically as possible, but with one 20 and the other 400 m from each swarm's cluster site. These distances correspond to the low end tails and the modes of the distributions in Fig. 1. Lindauer (1955) performed a similar experiment with nestboxes 30 and 250 m from a swarm. His swarm chose the 250 m site. However, the lack of repetitions and of controls for differences in nest site exposure, to which bees are highly sensitive, make this experiment's result suggestive rather than conclusive.

The nestboxes for our experiment were nailed onto two very similar sand pines 380 m apart. Each nestbox was cube-shaped, 40 liters in volume, and had a 3 cm diameter entrance hole positioned midway across the front, 8 cm up from the nestbox floor. A nail driven horizontally across the entrance prevented occupation by birds. The nestboxes were constructed of 1.5 cm thick plywood and were painted dark green on the outside. Nestbox floors were removable to permit interior inspections. The seam between the floor and the walls of each nestbox was sealed with opaque photographic tape. The entrance of both nestboxes faced south and was 3.75 m above the ground. The wind, sun and rain exposures of both nestboxes were carefully matched by trimming off branches about the nestboxes and by nailing a shade board (56×100 cm) atop each nestbox.

Each trial of the test was started by introducing a colony of bees into the study area, positioning it 30 m from one of the nestboxes as shown in Fig. 2. We left each colony undisturbed for at least two days of good weather to provide time for the colony's orientation to its new home range. On the third day or later an artificial

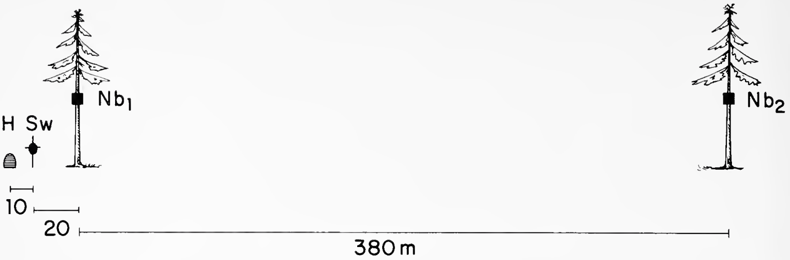


Fig. 2. Experimental array for testing preference in swarm dispersal distance. *H*, hive; *Sw*, swarm on wooden cross; *Nb*, nestbox. In the five trials of the test, the hive and swarm were alternately positioned near nestbox 1 or nestbox 2, always maintaining the distance relationships shown. All distances are in meters. The objects in this figure and the spacings between objects are not drawn to the same scale.

swarm was prepared from the hive as described above, but with the difference that each swarm was confined and fed in the swarm cage for only one hour. Following this brief confinement each swarm was placed on a wooden cross located between the parent hive and the nearby nestbox, 10 m from the former and 20 m from the latter. Thus a swarm cluster was established a natural distance from its parent colony and 20 and 400 m from two otherwise closely matched nest sites, as shown in Fig. 2. The parent hive and swarm were placed at opposite ends of the nestbox array on alternate trials. This provided control for possible differences between the nestboxes besides distance from the swarm.

We monitored each swarm's selection of a nest site by reading the recruitment dances as described above. But besides following the dances *on the swarm,* we periodically (at least hourly) measured the number of scout bees visible *at each nestbox* by making 10 counts, each count 15 seconds apart, while standing directly in front of a nestbox. Both near and far nestboxes were always rapidly discovered by the scout bees. Each morning, before the bees started flying, we inspected the interior of both nestboxes. Often 2 to 10 ants were found in the nestboxes and were promptly removed and killed. One morning during the second trial a complete ant colony (queen, workers and brood) was discovered in the far nestbox. This nestbox was quickly sealed with the ants inside, removed and replaced with a new nestbox. This was the only nestbox change performed during the experiment.

Table 1. Outcomes of five choices by honey bee swarms between near and far nestboxes.

Trial	Nestbox Near Swarm	Nestbox Chosen	Distance to Selected Nestbox (m)
1	1	1	20
2	2	2	20
3	1	1	20
4	2	2	20
5	1	2	400

We prevented swarms from occupying the nestboxes by keeping each swarm's queen caged on the wooden cross in a standard queen mailing cage. Every swarm's attempt to move to a nestbox ended with its return to the caged queen. But even though swarms never occupied the nestboxes, their nestbox preferences were always clearly indicated by large differences in the number of dances for and scouts at the two nestboxes.

The outcomes of five swarms' selections of a nest site are shown in Table 1. Apparently the nestboxes 1 and 2 were well matched, because with 2 and 3 selections respectively, no significant preference for either nestbox was shown. More important was the pattern of choice between near and far nestboxes: 4 to 1, respectively. The estimated probability of a swarm choosing the near nestbox is 0.80 and the 95% confidence limits on this probability are 0.48 and 0.95. Thus these results do not support the hypothesis that swarms prefer distant nest sites. Instead, they suggest that swarms prefer nearby nest sites. Unfortunately, because of lack of time, we were unable to perform further trials of this experiment.

The one selection of the distant nest site may not even be a valid test result. For in the fifth trial the swarm's choice between the nestboxes proceeded differently than with the previous four swarms. As is shown in Fig. 3, this swarm's preference developed initially in favor of the near nestbox and reached a point at which we expected the swarm to lift off and attempt moving to the near nestbox. Then suddenly the situation reversed. The scouts decreased at the near nestbox and increased at the far nestbox. Finally the swarm lifted off and flew past the near nestbox en route to the far nestbox. In the previous four trials, each swarm's preference between nestboxes

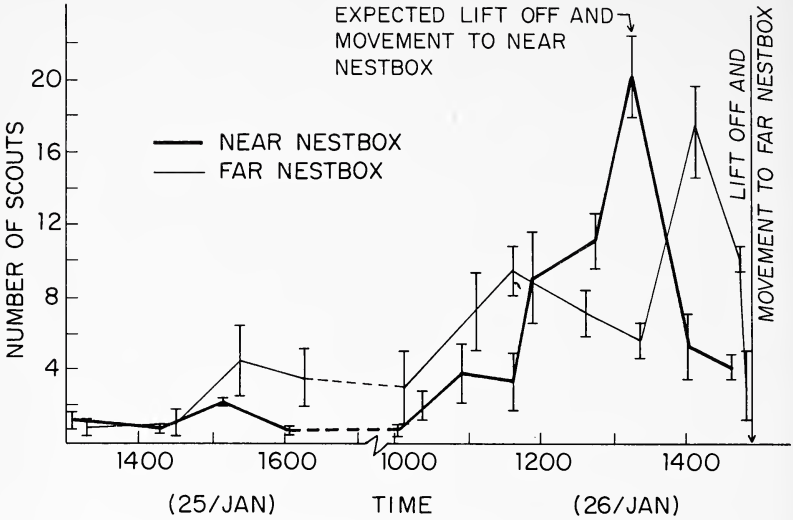


Fig. 3. Record from the fifth trial of a swarm's selection between near and far nestboxes, as monitored by counting the scouts visible at each nestbox. Vertical bars denote plus and minus one standard deviation for 10 counts at 15 second intervals.

developed smoothly and steadily in favor of the nestbox which was ultimately chosen. Moreover, when we inspected both nestboxes shortly after the lift-off in the fifth trial, we found the far nestbox empty inside except for a few scout bees, but we discovered four ants in the near nestbox. Similar nestbox inspections in the previous four trials had not disclosed any ants in either nestbox. These observations suggest that ants interfered in the fifth trial by entering the near nestbox. If so, then this may have created a difference in the nestboxes' qualities which outweighed any quality difference based upon the nestboxes' different distances from the swarm.

Discussion

The two experiments reported here appear to give conflicting results concerning the dispersal behavior of honey bee swarms. In the first experiment we observed swarms generally travelling a large distance, at least 300 meters, to new home sites. But in the second experiment, wherein we provided nest sites at 20 and 400 meters, the swarms showed no preference for the more distant nest site. This difference in dispersal behavior probably does not reflect differences between the bees used in the experiments. In both experiments the bees came from the same source, the apiaries of Dyce Laboratory, and in both experiments the bees were prepared as artificial swarms using nearly identical techniques. We suspect the disparity in experimental outcomes simply reflects a lack of nearby nest sites in the first experiment which forced the swarms to choose distant nest sites. If so, then our findings suggest that in nature the spacing out of feral honey bee colonies is based more upon the dispersion of suitable nest sites than upon programmed dispersal behavior in honey bee swarms.

Our findings also suggest that swarms prefer moving only a short distance to a new home site. Minimizing dispersal distance may be advantageous to swarms in reducing the hazard of losing poor flying queens. It might also help keep the daughter colony near the closely related, and thus perhaps minimally aggressive, mother colony. Robbing and foraging range restriction are probably the most common forms of aggression between bee colonies. Furthermore, because the honey bee's flying ability enables it to forage over very large areas, colony dispersal may not significantly reduce the competition, if any, between colonies for food.

We close this report by stating a possible weakness of this study: use of artificial swarms. Because this study's experiments required many repetitions, they would have proceeded exceedingly slowly had we used only swarms emerging naturally from colonies placed at the study sites. Thus we used the readily available artificial swarms. And these swarms appear to behave normally while selecting a nest site. They form a quiet cluster, dispatch scouts which discover and select the new home site, and finally fly to the chosen site. However, if a swarm's dispersal behavior is stimulated by its scouts' close familiarity with the surrounding region or is dependent upon the natural process of swarm formation, then our artificial swarms would have shown abnormal dispersal behavior.

ACKNOWLEDGMENTS

We thank Richard Nowogrodzki for field assistance and the Archbold Biological Station for the use of their research facilities. Bert Hölldobler critically reviewed the manuscript. Supported by the National Science Foundation (Grant No. BMS 76–15008), and the Anderson Fund and the Parker Fellowship, both of Harvard University.

SUMMARY

Insofar as normal honey bee behavior was observed in these studies with artificial swarms, our results indicate that swarms frequently move at least 300 meters from their parent colony to a new nest site, but that they do not prefer nest sites far from their parent colonies. Instead, swarms may prefer a nest site which is near the parent colony. Therefore the spacing of suitable nest sites appears to be a major determinant of the spacing of feral honey bee colonies, and behaviors promoting colony spacing to reduce foraging competition may not exist in the European races of honey bees.

REFERENCES

AMBROSE, J. T.
1975. A study of honey bee (*Apis mellifera* L.) swarms while in transit to a new homesite. Ph.D. thesis, Cornell Univ., Ithaca, N. Y.

BRIAN, M. V.
1965. *Social insect populations.* Academic Press, London and New York, 135 pp.

FELL, R. D., J. T. AMBROSE, D. M. BURGETT, D. DEJONG, 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.

GARY, N. E., P. C. WITHERELL AND J. MARSTON
1972. Foraging range and distribution of honey bees used for carrot and onion population. Environ. Entomol. **1,** 71–78.

GARY, N. E., P. C. WITHERELL AND J. M. MARSTON
1973. Distribution of foraging bees used to pollinate alfalfa. Environ. Entomol. **2,** 573–578.

GARY, N. E., P. C. WITHERELL AND J. M. MARSTON
1975. The distribution of foraging honey bees from colonies used for honeydew melon pollination. Environ. Entomol. **4,** 277–281.

GOULD, J. L.
1975. Honey bee recruitment: the dance-language controversy. Science **189,** 685–693.

KALMUS, H.
1941. Defence of source of food by bees. Nature **148,** 228.

LEVIN, M. D.
1961. Interactions among foraging honeybees from different apiaries in the same field. Insectes sociaux **8,** 195–201.

LEVIN, M. D. AND S. GLOWSKA-KONOPACKA
1963. Responses of foraging honeybees in alfalfa to increasing competition from other colonies. J. apic. Res. **2,** 33–42.

LINDAUER, M.
1955. Schwarmbienen auf Wohnungssuche. Z. vergl. Physiol. **37**, 263–324.

LINDAUER, M.
1971. *Communication among social bees.* Harvard University Press, Cambridge, Mass., 161 pp.

RUTTNER, F.
1975. Races of bees, pp. 19–38 *In* Dadant and Sons (Eds.), *The hive and the honey bee.* Dadant, Hamilton, Ill., 740 pp.

SEELEY, T. D.
1978. Life history strategy of the honey bee, *Apis mellifera.* Oecologia. **32,** 109–118.

SEELEY, T. D. AND R. A. MORSE
1978. Nest site selection by the honey bee, *Apis mellifera.* Insectes sociaux. In press.

WILSON, E. O.
1971. *The insect societies.* Belknap Press of Harvard University Press, Cambridge, Mass., 548 pp.

SEASONALITY AND THE FLIGHT OF PAUSSIDS (COLEOPTERA) IN WEST AFRICA

By Dennis Leston*
Biological Sciences Group
University of Connecticut
Storrs, CT 06268

Introduction

The paussids of this paper are the brown to black beetles, less than 8mm in length, with aberrant antennae, variously regarded as a superfamily, family or subfamily within Carabidae, or of even lower taxonomic rank (Darlington, 1950): all are myrmecophiles. That these insects come to light is well known; that the emission of adults is seasonal rests, as far as I am aware, unreported.

In West Africa almost all insects are markedly seasonal in breeding, dispersal, population growth or other life history phenomena. The insect periodicities can be tied to underlying events at the primary producer and/or decomposer levels and it has been demonstrated that these are associated with periodicities delimited by a combination of rainfall and sunshine (not daylength) factors (Gibbs & Leston, 1970; Leston, 1972, 1978; Leston & Gibbs, 1971).

This paper presents the evidence for seasonality in Ghana, attempting to place the ultimate factors within the framework of West African phenology.

Material and Method

The material was named using the collection of the British Museum (Nat. Hist.), London, where voucher specimens have been deposited. Taxonomists have clearly oversplit and the polytypic concept is not used by them.

Paussus cilipes Westwood — represented in West Africa by a subspecies other than the nominate.

---

*Present address: Department of Biology, University of Miami, Coral Gables, Florida 33124.

Manuscript received by the editor February 28, 1978.

Paussus klugi Westwood — I suspect this and *P. latreillei* Westwood are conspecific, with the West African subspecies distinct from the nominate.

Paussus setosus Westwood.

Paussus sphaerocerus Afzel — outside of the sampling area this is abundant in the forest zone of Ghana.

Paussus spinicoxis Westwood — again, the West African form differs at the subspecies level from the nominate one.

Paussus sp 4 — this is not in the British Museum collection.

Platyrhopalopsis laevifrons (Westwood) — not found in my samples and known to me only from a specimen from Tumu, Upper Region (P. M. Room).

The seven listed comprise all the Paussina (Darlington's subtribe) found in Ghana.

A 125 watt Robinson ultraviolet light-trap was run for 400 days on the campus of the University of Ghana, Legon, Accra District, Ghana. The catches were grouped into 20-day classes, a method found of value in previous investigations (Gibbs & Leston, 1970; Leston, 1973a). Sudden rain caused breakdowns on 14 nights: the figures were corrected by dividing the total for each species, for the relevant 20-day period, by the number of days actually sampled and adding this result for each missing sample — however, the overall results would have been the same even uncorrected. The original data sheets are deposited in the library of the Royal Entomological Society of London.

Legon, 5°40′N, was once forested but is now an area of derived savanna at the edge of the dry Dahomey Gap. Food-farms, gardens and buildings cover the region but once shade has been artificially reestablished forest zone crops such as cocoa and robusta coffee can be grown successfully.

Results

Numbers caught were

1. *Paussus spinicoxis*	758
2. *P. sphaerocerus*	165
3. *P. cilipes*	67
4. *P. setosus*	54
5. *P. klugi*	13
6. *P.* sp 4	6
Total	1063

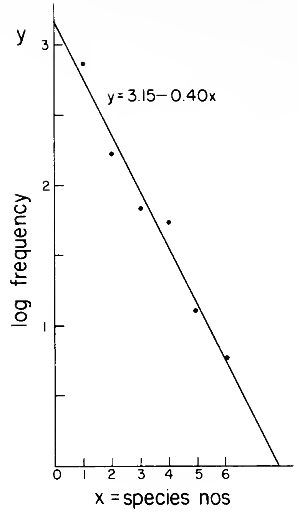


Fig. 1. Log frequency distribution and regression for the six paussid species trapped.

The log frequency was plotted, together with the calculated regression (Fig. 1). That the six species have a logarithmic distribution pattern can be seen by inspection.

The total catch (all species) for each sampling period is shown, together with the catches of the three most frequent species (Fig. 2). It would appear *spinicoxis, sphaerocerus* and *cilipes* frequencies are varying in parallel. The figures for these three species and the next most abundant, *setosus,* were tested for the significance of this apparent correlation by Kendall's coefficient of concordance (Siegel, 1956). The results:

n (number of sampling classes) = 20
K (number of species) = 4
W = 0.66
$\chi^2 = 50.22$
df = 19
$p < 0.001$

There is a highly significant correlation in the periodic trends in the four species, these accounting for 98.2 percent of the material caught (W was calculated uncorrected for ties; with a correction

Table 1. Days of sampling and numbers sampled to give an additional species.

Sampling day	Cumulative total sampled	Species added	Total species
1	0	0	0
4	1	1	1
7	4	2	3
44	52	1	4
47	56	1	5
116	220	1	6
400	1063	0	6

the value of χ^2 would have been even larger). We can therefore analyse the total paussids with some confidence as reflecting the trends in each.

It is usual in tropical phenology to attempt to tie phenomena to the rainfall pattern (Karr, 1976). The major peak (Fig. 3) occurred in April-May, when the rains were building up to their maximum, but the minor peak of January-February occurred in the dry period when the rains, although increasing, did not reach the effective level, 10cms/month. The August trough coincided with the so-called "little dry season" but no simple correlation of paussid frequency with rainfall amounts was detected.

Table 1 gives the arrival day and cumulative total for the capture of the i^{th} species.

Discussion

It is likely the six species trapped represented all of the group present in the locality; extrapolation from the figures of Table 1 suggests an additional species should have been found, if present, before the 1000th individual was trapped.

The lognormal species distribution parallels that found in samples from Ghana of birds, ants, snakes and several other taxa (Leston, 1972): no explanation is offered here (but see Williams, 1964).

Paussids are emerging throughout the year but with marked fluctuations in frequency. The four most frequent species show parallel trends in their respective frequencies, indicative of the same set of factors influencing all. The peak corresponds closely

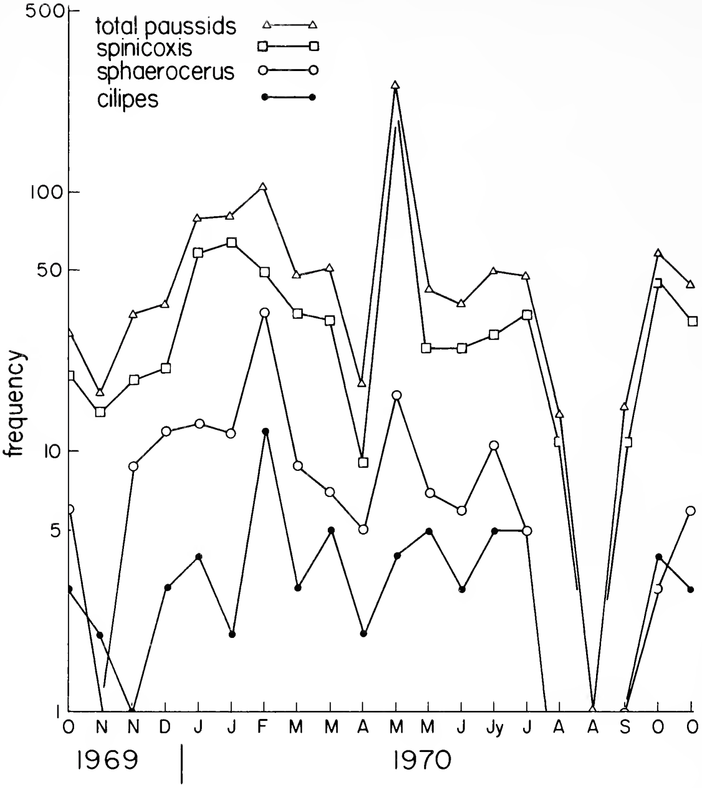


Fig. 2. Frequencies of all species together and the three most abundant species, in 20-day classes. Logarithmic.

to that found at Legon in the flight of male doryline ants (Leston, 1978), falling within the first wet sunny season (Gibbs & Leston, 1970). It coincides too with that of alate sewing-ants, *Oecophylla longinoda* (Latreille), in the forest zone: again a wet sunny season event (Leston & Gibbs, 1971).

But the apparent trimodality of the paussids does not fit just into the two wet sunny seasons of the forest zone although the October peak falls within the second of these. Were it not that a similar trimodality has been detected elsewhere it might have been dismissed as a peculiarity of the particular period sampled but a range of mantids sampled at Tafo, 35 miles north of Legon and in the forest zone, had a similar pattern (Leston, 1972).

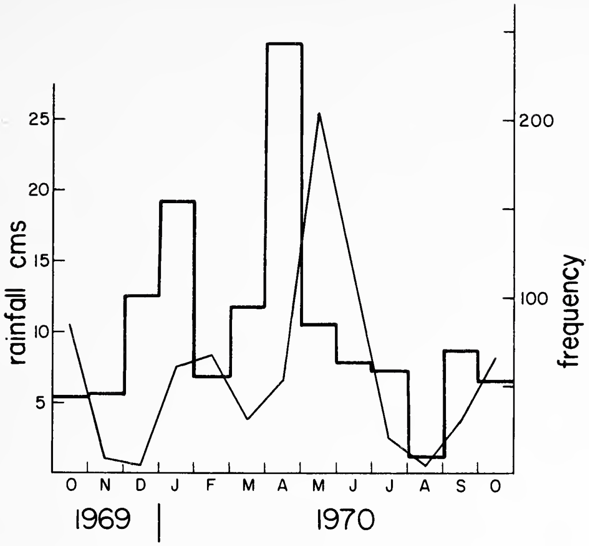


Fig. 3. Total paussids trapped (histogram) and rainfall, in monthly classes.

Paussids are entirely dependent for food upon ants (LeMasne, 1961). Ants in the West African forest zone are essentially predatory. Prey abundance there is more or less trimodal. There is a major peak in the first wet sunny season, around April, tied to the new flush and essentially comprising foliage feeders (augmented by decomposers). A second, less obvious, peak occurs in October-November, the second wet sunny season, and is again made up of foliage feeders, augmented this time by the fungivores. A third peak occurs around January, its date less reliable because of the variability in the intensity of the dry period from year to year: it sees a peak in insects associated with fruit or seeds (Gibbs & Leston, 1970; Leston, 1972).

It is suggested that the ultimate factors concerned in the production of paussids are directly tied to the seasonal availability of prey to their host ants, just as in Mantodea the ultimate factors are available prey. Elsewhere (Leston, 1978) it is indicated the seasonal production of alate male doryline ants, as with paussids reaching a peak in the first wet sunny season, is geared to the optimal availability of prey to the workers of the species involved. Once again it has been found that the seasonal pattern in a tropical insect taxon cannot be explained by a simple wet season/dry season cycle: the biological periodicities — the true seasons — are those which follow from periodicities in rainfall and sunshine taken together (Gibbs & Leston, 1970).

It is likely that the majority of the paussid species trapped at Legon came from the forest zone but nothing is known as to their host ants in West Africa. In view of their absence from the wide range of colonies of dominant, arboreal, ants sampled in Ghana (Leston, 1973b) it is probable their hosts are for the most part ground-nesting species.

ACKNOWLEDGEMENTS

My research has been supported by the Ghana Cocoa Growers' Research Association, the Cocoa, Chocolate and Confectionery Alliance (U.K.), the University of Ghana and the Research Foundation of the University of Connecticut.

CONCLUSIONS

1. Six paussid species were taken in an ultraviolet light-trap run for 400 days at Legon, Ghana, the catch totalling 1063.
2. The frequencies of the trapped species had a lognormal distribution.
3. The frequencies showed parallel periodic changes between the species.
4. Peak emissions occur in the 1st wet sunny period, lesser maxima in the 2nd wet sunny and the dry sunny periods of the Gibbs-Leston model.
5. The ultimate factor, it is suggested, is prey availability to the host ants.

REFERENCES

DARLINGTON, P. J. (1950) Paussid beetles. Transactions of the American Entomological Society **76:** 47–142.

GIBBS, D. G. & LESTON, D. (1970) Insect phenology in a forest cocoa-farm locality in West Africa. Journal of applied Eclogy **7:** 519–548.

KARR, J. R. (1976) Seasonality, resource availability, and community diversity in tropical bird communities. The American Naturalist **110:** 973–994.

LEMASNE, G. (1961) Recherches, sur la biologie des animaux myrmécophiles: observations sur le régime alimentaire de *Paussus favieri* Fairm., hôte de la fourmi *Pheidole pallidula* Nyl. C. R. Acad. Sci. Paris **253:** 1356–1357.

LESTON, D. (1972) Insect interrelations in cocoa: a contribution to tropical ecology. Ph.D. thesis, University of Ghana.

LESTON, D. (1973a) The flight behaviour of cocoa capsids (Hem., Miridae). Entomologia experimentalis et applicata **16:** 91–100.

LESTON, D. (1973b) The ant mosaic, tropical tree crops and the limiting of pests and diseases. PANS, London **19:** 311–341.

LESTON, D. (1978) Dispersal by male doryline ants in West Africa. Ecology (in press).

LESTON, D. & GIBBS, D. G. (1971) Phenology of cocoa and some associated insects in Ghana. Proceedings of the 3rd international Cocoa Research Conference, Accra, **1969:** 197–204.

SIEGEL, S. (1956) Nonparametric statistics for the behavioral sciences. McGraw-Hill; New York.

WILLIAMS, C. B. (1964) Patterns in the balance of nature. Academic Press; London.

AN ABERRANT NEW GENUS OF MYRMICINE ANT FROM MADAGASCAR[1]

By William L. Brown, Jr.
Department of Entomology
Cornell University
Ithaca, New York 14853

During a research trip to the Old World tropics during January to April 1977, I was allowed by M. A. Peyrieras, of the Institut de Recherche Scientifique of the Malagasy Republic in Tananarive, to sort through some berlesates of humus and leaf litter collected by him in various parts of Madagascar. Among these samples, I discovered a single worker example of an extraordinary new genus and species of Myrmicinae. M. Peyrieras has my thanks for these and many other interesting samples, including several undescribed species of ants. Among these are the first recorded representatives of *Discothyrea* and *Amblyopone* found on Madagascar, to be described in a separate publication. The new genus is described next below.

Pilotrochus new genus

Worker: Subfamily Myrmicinae, tribe unknown. Integument thick and rigid. Head subpyriform, slightly depressed but convex, broadest behind, without posteromedian excision; frontal carinae far apart, at sides of head, produced laterad angularly above antennal insertions, continuous posteriad with the sharp upper margins of deep and broad antennal scrobes occupying about 2/3 of length of sides of head; eyes small, situated on ventral borders of scrobes near their posterior ends, slightly posterior to midlength of head. Antennae 8-merous, scapes short and thick, much narrowed basad; club distinctly 2-merous, slightly longer than remainder of funiculus, apical segment about twice as long as

---

[1] Hymenoptera: Formicidae. A report of research from the Cornell University Agricultural Experiment Station. Research supported by National Science Foundation Grant DEB 75-22427.

Manuscript received by the editor February 3, 1978.

penultimate; funicular (ring) segments II–V small, subequal in length, broader than long; funicular segment I (pedicel) about equal in length to the next 2 to 3 (ring) segments.

Clypeus broad, shield-shaped, narrowed sharply laterad on each side, its surface gently convex; anterior margin broadly arcuate, with a complex median notch.

Mandibles triangular, convex, with opposable, serially-toothed mesial margins (teeth coarse, sharp, 7 in number on each mandible); these margins arcuate in side view and finally directed ventrad at apex. In the vee between each of the larger teeth is a minute piligerous denticle. Labrum thick, linguiform and narrowly rounded at apex, but appearing truncate in side view; its dorsal surface bearing a narrow pencil of fine white setae that arches forward to extend beyond the mandibular apices, probably serving as a "rangefinder" trigger hair. Palpi not visible and undoubtedly short, but segmentation not determined.

Trunk compact, its dorsal outline forming one continuous arc from base of pronotal cervix to petiolar insertion, dominated by pronotum. which makes up about half its length and is wider than the rest (a little more than half as wide as head). Promesonotal suture marked by a faint curved transverse line paralleled by a costa on the dorsum, but completely fused here, though complete on the pleura. Pronotum with blunt, barely suggested humeral angles as seen from above, but not distinctly marginate in front or on the sides; upper sides bulging and overhanging lower sides; ventral margins each forming a curved, cultrate, projecting flange or lamella. Metanotal groove obsolete, its position perhaps marked by a transverse carina at the top of what appears to be the propodeal declivity, but the true declivity probably is confined to the lower part of this slope, beneath a lower and weaker transverse carina or costula.

Mesopleura narrow and impressed, but their lower central parts (mesepisterna) are occupied on each side by a peculiar organ consisting of a large subcircular pit filled with a silvery-white, convex pad of fine, radially-arranged hairs. The anterior edge of this structure forms the posterior side of the ventral invagination between pro- and mesonotum, but a broad piece of mesokatepisternal cuticle separates the organ from the mesocoxa. This organ appears to be the external part of an exocrine gland or glands, though the gland openings, if any, are hidden by the pad of fine hairs.

The (probably) true propodeal declivity small, flat, steep, unarmed, bounded by an inverted U-shaped carina, flanked on each side by the large, circular openings of the propodeal spiracles, which are directed caudad. Inferior propodeal plates low and rounded.

Petiole curved-clavate, with a long, subcylindrical anterior peduncle, a long, low, rounded node, and poorly-defined posterior peduncle, or collar. Postpetiole rounded above and on the sides, broader behind than in front, and about as broad as long; sternum boxlike, with inwardly sloping sides and a flat, subrectangular ventral face limited on all 4 sides by sharp carinae; broadly attached to gaster behind, but with a moderate constriction between the 2 tagmata.

Gaster rounded at base to the basal constriction, which has a few short longitudinal costulae hidden within it. Basal segment extending over about 2/3 length of gaster, the remaining 3 visible segments curving to a pointed apex; terminal external (seventh) sternite (hypopygium) acutely pointed; sting with acute tip exserted, some of the rest of the shaft visible through transparent cuticle.

Legs moderately long. Femur robust, its flexor surface sulcate apicad to receive the folded tibia; tibia claviform, thickest near apical third, lacking spurs on middle and hind legs; tarsus slender, cylindrical; claws small, slender, simple.

Sculpture mostly shining; head both above and below (except clypeus and antennal scrobes) covered with a coarse reticulum of costulae forming large, shallow-polygonal fossae, each of which bears a long, fine, curved hair arising from an inconspicuous puncture, usually near the margin of the fossa. Similar sculpture on truncal dorsum, though here 10–11 longitudinal costae predominate. A broad median strip is nearly smooth, forming a very shallow median sulcus, which has a modest costa or carina in the middle. (The median posterior vertex is feebly subsulcate in much the same way.) Propodeum (sloping dorsum and declivity) nearly or quite smooth. Sides of trunk smooth and shining, but the posterior half with 5 strong costae radiating outward from the mesopleural organ. Petiolar and postpetiolar nodes loosely longitudinally rugose, with broad, shining interspaces; peduncles and sides of these segments becoming finely and densely punctate-reticulate and more opaque; ventral rectangle of postpetiole smooth and shining. Gaster smooth and shining, except posterolateral margins of segments, which are delicately reticulate-striolate, but still shining. Mandibles densely and finely punctulate, opaque (teeth infuscate and shining), lateral surfaces finely longitudinally costulate basad. Antennal scapes and legs shining, finely longitudinally rugulose to smooth; antennal funiculi densely punctulate, pubescent and opaque. Antennal scrobes basically smooth and shining, but each is crossed by 7–9 vermiculate transverse rugulae.

Pilosity consisting of long, fine, flexuous erect to decumbent hairs distributed widely over dorsal surfaces of body, and on scapes and legs, sparser on underside of head and gaster. Mandibles, antennal funiculi, and flexor surfaces of tibiae and tarsi with fine, appressed to decumbent pubescence.

Color light ferruginous red; antennae and legs more yellowish.

Queen, male and larva still unknown.

Type species: *Pilotrochus besmerus,* new species, described below.

Distribution as far as known limited to Madagascar.

Pilotrochus besmerus new species

Figs. 1, 2.

Holotype worker: Total length (TL) 2.9, head length (HL) 0.68, head width (HW) 0.60, mandibles extend beyond median clypeal free margin (ML) 0.11 mm; when head is tilted back a little from full-face view, mandibles may extend beyond clypeus as much as 0.18 mm; trunk length (WL) 0.64, scape L (excluding radicle) 0.32, greatest length of eye 0.07 mm. Petiole length (chord of arc) 0.45, hind femur length 0.43, hind tibia length 0.34, hind tarsus length 0.60 mm, of which metatarsus is half.

Details of form and sculpture are well shown in the figures. As seen in dorsal view, eyes hidden in full-face view, barely visible when head is tilted back slightly, as in fig. 1. Pronotum slightly broader than long (width 0.38 mm), rounded in front, excised behind; mesonotum subquadratic, about 0.20 mm wide, with feebly convex borders on all four sides. Petiolar node 0.17 mm wide, postpetiolar node with rounded sides, slightly wider behind (width 0.21 mm, length 0.20 mm).

Pronotum smooth and shining, with about 10 costulae running longitudinally at different lengths; mesonotum with 5 longitudinal costulae on rugulae. About 5 longitudinal rugules each on petiolar and postpetiolar nodes, but weaker on the postpetiole, so that its disc is primarily smooth and shining like the gaster.

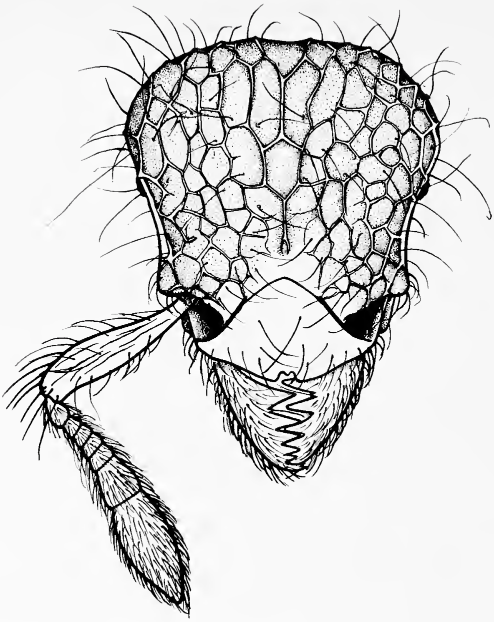


Fig. 1, *Pilotrochus besmerus,* new genus and species, holotype worker, head in dorsal view, tilted back slightly from the full-face position so as to show the mandibular dentition better, ×67. Drawing by Susan Poulakis.

Hairs mostly a little less than 0.1 mm long on anterior head and scapes, a little more than 0.1 mm on posterior vertex; 0.15–0.25 on trunk, petiole, postpetiole and gaster, becoming shorter again at gastric apex; about 0.1 to about 0.3 mm on legs; flagelliform, many with tips reflexed or even looped back.

Holotype (Museum of Comparative Zoology at Harvard University) a unique worker taken in a Berlese sample of forest humus and litter from along the road to Anosibé, 33 km south of Moramanga, in east central Madagascar, 4–12 April 1975 (A. Peyrieras).

The relationships of *Pilotrochus* are obscure. The shape of the head, with its broad and deep scrobes and small ventrolateral eyes, recalls that of *Dacetinops,* or the *Codiomyrmex* group of Dacetini, or even *Tatuidris,* but *Pilotrochus* differs strongly from all of these in its 8-segmented antennae, in the form of its mandibles and their teeth, and in the form of its trunk and petiole. The lateral "hair-

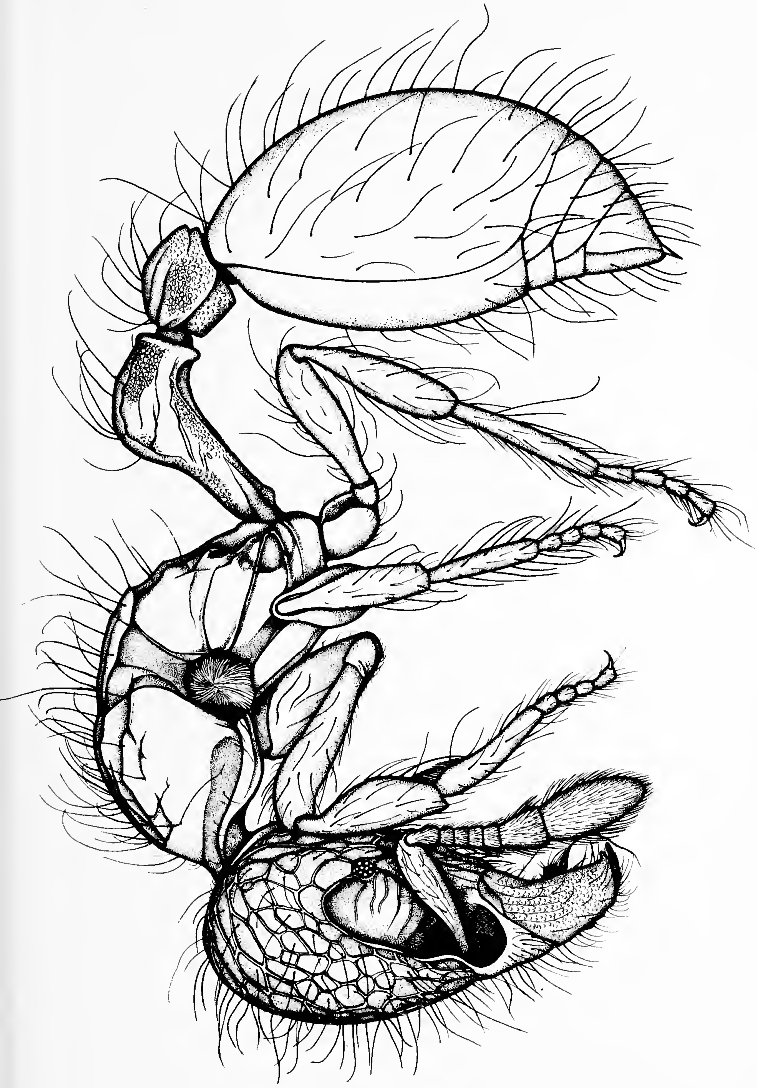


Fig. 2, *Pilotrochus besmerus*, new genus and species, holotype worker in side view, ×67. Drawing by Susan Poulakis.

wheel" organs are also striking, and so far as I am aware are unmatched among the ants, although the region of the ventral furrow between pro- and mesothorax is sometimes modified and apparently glandular in some dacetines and a few other myrmicines.

The 2-segmented antennal club, together with some points of habitus (especially coarse sculpture and long, flexuous pilosity, plus the antennal scrobes), recalls the neotropical genus *Lachnomyrmex,* but the shape of the trunk in *Pilotrochus* is completely different, the propodeal teeth so prominent in *Lachnomyrmex* are completely absent, and the mandibles in the two genera are very different.

At the moment, all one can say without seeing the winged forms and larvae of *Pilotrochus,* and without knowing something of its lifeway, is that it is a member of subfamily Myrmicinae, but one not belonging to any of the well-circumscribed "higher" tribes (Crematogastrini, Dacetini, Basicerotini, Cataulacini, Attini, etc.). Thus, it falls among the mass of generic complexes related to *Myrmica, Pheidole, Myrmecina, Rogeria,* etc., among which tribal boundaries are impossible to define for the present, or at least are in dispute.

Considering the revisionary work that must be done before we have a rational tribal classification of Myrmicinae, it seems to me that nothing would be gained by erecting a new tribe for *Pilotrochus,* even though for the time being I am able to fit it comfortably into any existing myrmicine tribe.

The generic name is derived from the Greek 'pilos' (hair) + 'trochos' (wheel), while the specific name *besmerus* combines the Latin 'bes' (eight of twelve) with the Greek 'meros' (part), in reference to the 8-segmented antennae as compared to the primitive myrmicine (and formicid) 12-merous condition.

SYMBIOSES BETWEEN INSECTS AND SPIDERS: AN ASSOCIATION BETWEEN LEPIDOPTERAN LARVAE AND THE SOCIAL SPIDER *ANELOSIMUS EXIMIUS* (ARANEAE: THERIDIIDAE)*

By Michael H. Robinson
Smithsonian Tropical Research Institute
P.O. Box 2072, Balboa, Canal Zone, Panama

Introduction

There are many instances of relationships between insects and spiders that are not simply relationships between predators and prey. Bristowe (1941) cites numerous examples either from his own extensive experience or from a broad review of the diverse literature. Moths have been reported to associate with spiders' webs both as adults and larvae. Thus Pocock (1903) reported a case of commensalism between the gregarious spider *Stegodyphus* sp. (Erisidae) and the moth *Batrachedra stegodyphobius* Walsingham. The unnamed species of *Stegodyphus* from South Africa had small lepidopteran larvae crawling about within the communal web. These fed upon "the carcases of the flies or other insects which, with infinite labour and patience, the spiders hauled up as near their nest as possible. . . ." Pocock states that pupation occurred within the nest (= web) and that, after emergence, adult moths moved about the web walking, leaping and fluttering. Reportedly the moths did not get caught in the sticky (cribellate) silk "being gifted apparently, like the spiders themselves, with some safeguard against the stickiness of the threads, which proved so fatal to other insects" (1903: 169). Brach (1977) reports that the webs of *Anelosimus studiosus,* in Florida are shared by a host of other arthropods including pyralid "webworms." He comments that the majority "are found in the periphery of senescent webs and may be physically isolated from contact with colony members by their own silken retreats" (1977:155). Robinson and Robinson (1976:12–16) report on a pyralid moth that, as an adult, rests on

---

**Manuscript received by the editor April 27, 1978*

the silk lines of araneid webs. They conclude that the moth gains protection by the association. In this paper I describe the association between larvae of the noctuid moth *Neopalthis madates* Druce and the colonial spider *Anelosimus eximius* Simon. In addition, three other instances of associations between lepidopteran larvae and web-building spiders are briefly reported. These involve the araneid *Cyrtophora nympha* Simon, an undetermined diplurid and an undetermined social theridiid in Papua New Guinea. The relationship between *Neopalthis* larvae and *A. eximius* is a symbiosis that primarily involves scavenging but may occasionally involve the loss to the spider of usable food resources. Thus the symbiosis is probably commensal for the most part but sometimes (or potentially) deleterious. The terminology of symbioses for such "borderline" cases is in a currently unsatisfactory state.

THE *NEOPALTHIS*/*ANELOSIMUS* SYMBIOSIS

The nature of the symbiosis can only be understood if some details of the biology of *Anelosimus eximius* are given. There have been a number of notes on aspects of the biology of this species (e.g., Levi, 1955; Brach, 1975) and it is currently under study at the Smithsonian Tropical Research Institute (by Dr. F. Vollrath). The following notes are based on my own studies and those of Vollrath (pers. comm.). *Anelosimus eximius* webs are built and occupied by a variable number of spiders, from less than a hundred to at least several thousand. They may persist in one place for many years. One on Barro Colorado Island, Canal Zone, was in the same tree from 1965 to 1971. Colonies may reach striking proportions, occupying many cubic meters of space. Essentially all webs have a simple basic structure. The lower web consists of a continuous sheet of silk that is concave and often basin-like, being raised at its periphery. Above this and partly attached to it is an aerial snare of threads that are preponderantly oriented more or less perpendicular to the sheet. This is the part that is the effective prey-capture structure. The spiders attack prey within the aerial snare and on the basal sheet. Since the basic web is persistent for long periods, it acquires a litter of plant debris and prey remains. (In captivity the spiders seem to indulge in occasional web-cleaning bouts and carry prey remains to the edge of the web where they are tipped out.)

I found the first caterpillars in an *Anelosimus* colony in January 1976. A small colony of less than one hundred individuals was collected from Cerro Galera, Canal Zone, Panama, and taken into the laboratory for behavioral studies. The collection was made by bagging the entire colony on the branch of a tree and then cutting off the branch. This was then set up in a cage. The colony was thus collected intact and complete with all spiders, debris, and inquilines. After some period of observations on the spiders, the caterpillars were seen. There appeared to be several of these; at least two were seen at one time, and eventually four pupae were recovered from the web. When not actively feeding, the caterpillars rested beneath the plant debris in the web or stretched out in stick-like postures. Feeding on insect remains was seen both by day and by night. Movement within the web seemed to be purposively towards prey remains rather than exploratory, but this proved difficult to quantify since the caterpillars had to weave their bodies in and out of the maze-like strands of the snare. In an attempt to investigate the possible cues used by the caterpillars in finding their food, I excised a section of the web away from a spider aggregation and put two caterpillars in this. (Cutting sections of spider web is easy, a hot soldering iron or glowing tip of a lighted cigarette cuts the silk with little pressure.) In this spider-free web I placed a freshly killed tettigoniid (Orthoptera) of about 100 mg weight. The caterpillars made no immediate move towards the katydid, but some hours later both were feeding on it and one was almost inside the body of the dead insect. Figure 1 shows a caterpillar in action. Clearly the caterpillars could feed on an entire insect as well as on exoskeletal fragments. They may well do this in the natural situation. Both caterpillars pupated the morning following this massive meal and this ended the investigation. Caterpillars have been found in other *Anelosimus eximius* colonies by me and by F. Vollrath (pers. comm.). Vollrath raised *Neopalthis madates* from his caterpillars and also another moth species that was clearly not a noctuid. This species has not been determined. It is entirely possible that still other species of lepidoptera could be involved in this kind of symbiosis with *Anelosimus eximius;* this matter is discussed later. Further investigation of the relationship awaits a situation where infested colonies are abundant and can be subjected to traumatic or destructive experimentation.

Figure 1. Two larvae of *Neopalthis madates* feeding on a katydid (see text). One larva is in profile; the other, arrowed, is facing the camera and only the head is visible.

Figure 2. Larva (unidentified) feeding on a moth within the web of *Cyrtophora nympha.* The characteristic fine mesh of the *Cyrtophora* web is visible in the background.

OTHER MOTH CATERPILLAR/SPIDER SYMBIOSES

The following observations are fragmentary but are worth recording to alert workers in this field to the possibility of widespread symbioses between web-building spiders and lepidopterans. The most excitingly suggestive observation is the discovery, during my brief visit to Wau Ecology Institute, Papua New Guinea, in May 1977, of caterpillars living in colonies of a social theridiid there. The theridiid has not yet been determined and its relationship to the Neotropical *Anelosimus eximius* is thus unknown. Despite this, it is reasonable to assume that the symbiotic caterpillars represent a case of convergent evolution. I would guess that they were not noctuid caterpillars, but none were collected.

In Panama a web of the araneid spider *Cyrtophora nympha* Simon, collected in July 1976 on the Navy Pipeline Road, Gamboa, Canal Zone, contained a single caterpillar moving about in the web in the same way as the larvae in the *Anelosimus* colonies. This was collected together with the web and the host. The caterpillar is shown in Figure 2. It disappeared without trace.

Finally, F. Vollrath reports (pers. comm.) that he found a caterpillar living in the web of a diplurid and feeding on prey remains; it also apparently fed on the web silk, where it made "dime-sized holes." Neither the diplurid nor the moth have been determined.

DISCUSSION

So far all the associations between lepidopteran larvae and spiders occur where the hosts build webs that persist for long periods at the same site. This is certainly true of *Stegodyphus* and *Anelosimus* colonies and also true of *Cyrtophora nympha.* The webs of the latter are presumably high investment structures like those of *C. moluccensis* (see Lubin, 1973, 1974); they are solitary and become littered with leaves and debris and often look defunct. An indication of the persistence of *C. nympha* webs is given by the fact that colonies of *Uloborus republicanus* often establish themselves in the upper snare (personal observations). In Panama, ground-living diplurids build their sheet webs at one site for long periods and have a wide range of arthropod commensals, kleptoparasites and other symbionts (Vollrath, Kirkendall, pers. comm.). The correlation between persistent webs, or persistent utilization of web sites, and the occurrence of lepidopteran symbionts suggests that the webs of other perennial (or long-term) web-site occupiers should be examined for caterpillar cohabitants. The various gregarious *Cyrtophora* species are clear candidates for such studies.

Another factor is necessary to provide a niche (within a web) for scavenging cohabitants: clearly there must be an accumulation of prey-remains. If prey-remains were rapidly ejected from the web, there would be no resource for a scavenger to exploit; kleptoparasitism or commensalism would be the only feeding niches available to symbionts.

The evolution of finely adjusted interspecific relationships must have involved innumerable adaptive steps that are almost inconceivable in their probable complexity. Lepidopteran larvae (and other spiders) may be, as producers and manipulators of silk, somewhat preadapted to evolve symbioses with web-building spiders. Adult butterflies and moths are probably less endangered by sticky spider silk than are most other insects (Eisner, Ettershank and Alsop, 1964) and this could reduce *some* of the dangers involved in evolving symbioses with spiders. Nonetheless, the caterpillars had to solve two major problems. They had to in some way suppress the predatory responses of the spiders to objects moving on the web and also develop a system of detecting their own food within the web. From my own observations I would conclude that both *Stegodyphus* sp. and *Anelosimus eximius* are much less responsive to gently moving objects in their webs than are many orb-weavers. It may have thus been slightly less dangerous for moving caterpillars to invade these webs in the first place, but I strongly suspect that the present immunity to spider attacks depends on something more than the caterpillars "walking softly."

ACKNOWLEDGMENTS

I am extremely grateful to Dr. E. L. Todd, Systematic Entomology Laboratory, IIBII Institute, U.S. Department of Agriculture, for identifying the moths. My thanks to Dr. F. Vollrath of STRI for access to unpublished observations and for helpful comments.

REFERENCES

BRACH, V.

1975. The biology of the social spider *Anelosimus eximius* (Araneae: Theridiidae). Bull. So. Calif. Acad. Sci. **74:** 37–41.

1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasi-sociality in theridiid spiders. Evolution **31:** 154–161.

BRISTOWE, W. S.

1941. The Comity of Spiders. Vol. II. Roy. Soc. London.

EISNER, T., R. ALSOP AND ETTERSHANK, G.

1964. Adhesiveness of spider silk. Science **146:** 1058–1061.

LEVI, H. W.

1955. The spider genera *Neottiura* and *Anelosimus* in America (Araneae: Theridiidae). Trans. Amer. Microscop. Soc. **75:** 407–422.

LUBIN, Y. D.

1973. Web structure and function: the non-adhesive orb-web of *Cyrtophora moluccensis* (Doleschall) (Araneae: Araneidae). Forma et Functio **6:** 337–338.

1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zool. J. Linn. Soc. **54:** 321–339.

POCOCK, R. I.

1903. Notes on the commensalism subsisting between a gregarious spider *Stegodyphus* sp. and the moth *Batrachedra stegodyphobius* Wlsm. Ent. Mon. Mag. **39:** 167–170.

ROBINSON, M. H. AND B. ROBINSON

1976. The ecology and behavior of *Nephila maculata:* a supplement. Smithson. Contrib. Zool. **218:** 1–22.

POPULATION STRUCTURE AND POLYMORPHISM IN THE SLAVE-MAKING ANT *HARPAGOXENUS AMERICANUS* (EMERY) (HYMENOPTERA: FORMICIDAE)

By Alfred Buschinger[1] and Thomas M. Alloway[2]
Fachbereich Biologie, Institut für Zoologie,
der Technischen Hochschule, D6100 Darmstadt, Schnittspahnstr. 3;
and Erindale College, University of Toronto,
Mississauga, Ontario, L5L 1C6, Canada

Introduction

The biology of the slave-making ant, *Harpagoxenus americanus,* has been studied by several previous investigators. Creighton (1927, 1929) described slave raids and performed some experiments on colony foundation. Wesson (1939) provided a classic account of numerous aspects of the natural history of *H. americanus* including its distribution, colony demography, hibernation, brood development, and its colony-foundation, mating, and slave-raiding behaviours. Alloway (in press) provides a detailed account of its raiding behaviour in comparison to that of the closely related, but more primitive, species *Leptothorax duloticus.*

Wesson (1939) found that, in addition to a rather small proportion of "normal" queenright colonies, there are many queenless "branch colonies" which sometimes contained apparently fertile "gynecoid" workers. Moreover, he observed the formation of such "branch colonies" as a consequence of slave raids which occurred late in the raiding season. Previously, Sturtevant (1927) had dissected *americanus* workers and found that they typically have 6 ovarioles and "a sac arising from the anterior end of the common oviduct" which he interpreted as being a seminal receptacle. Sturtevant also found some workerlike individuals with rudimentary ocelli and presumed that *H. americanus,* like the European *H. sublaevis,* has ergatoid queens. However, Wesson (1939) wrote that he had

---

[1] Supported by a grant from the Deutsche Forschungsgemeinschaft.
[2] Supported by Grant A0301 from the National Research Council of Canada.
Manuscript received by the editor April 27, 1978.

failed to note any "ergatoids such as occur with European *H. sublaevis.*" Nevertheless, Creighton (1950, p. 281), comparing *H. americanus* with *H. canadensis* and *H. sublaevis,* stated that in *americanus* "the ergatoid female is rarely produced."

In a recent study (Buschinger & Alloway, in press), we demonstrated that in all probability there are no ergatoid queens at all in *H. canadensis.* In contrast, although "normal" full queens occur occasionally in *H. sublaevis,* the usual reproductive female in this species is an ergatoid form which closely resembles the worker caste in its external morphology. Moreover, polymorphism among reproductive females is genetically mediated in *H. sublaevis* (Buschinger, 1975, 1978, in press). Thus, the main objective of the present study was to determine whether ergatoid queens analogous to those found in *H. sublaevis* occur in *H. americanus* and, if so, what role they play. We especially wondered whether they might be the usual reproductives in the numerous "branch colonies" that lack a dealate full queen.

MATERIAL AND METHODS

Colonies of *H. americanus* were collected from various localities in the regional municipalities of Halton and Peel in southern Ontario, Canada. A few additional colonies were found near Cleveland and Ashtabula, Ohio, in the United States. Most of the colonies were nesting in old hollow acorns and hickory nuts lying on the ground. The colonies were removed from their nests using an aspirator either immediately in the field or later in the laboratory. Colonies whose broods consisted only of larvae and prepupae at the time of collection were kept alive in the laboratory for a few weeks to determine the sex and caste of the *Harpagoxenus* pupae that were produced. Some of the *Harpagoxenus* queens, all intermorphs, and most of the *Harpagoxenus* workers were dissected using a method which we have described fully elsewhere (Buschinger & Alloway, in press).

RESULTS

1. *Population data.*

No effort was made to determine the ratio of *Harpagoxenus* to host-species colonies or the number of colonies per unit of area. Both variables fluctuate widely and depend upon a large number

Table I. Occurrence of *Lepothorax longispinosus* and *L. ambiguus* as host species in colonies of *H. americanus.*

H. americanus colonies	with slave species *L. longispinosus*	*L. ambiguus*	*L. Long.* + *L. amb.*
incipient	2	—	1
queenright	12	—	1
queenless	13	4	6

of factors such as the type of vegetation, surface drainage, the distribution of habitable nesting sites, *etc.* Sturtevant (1927) recorded an infestation rate of 13% for *H. americanus* (i.e. 17 *americanus* colonies to 132 colonies of one of its three host species, *Leptothorax curvispinosus* Mayr). In the areas where we collected our material, the host species were *Leptothorax ambiguus* Emery and *L. longispinosus* Roger. Although *ambiguus* was generally the more abundant of the two host species in acorn and hickory-nut nests, *longispinosus* was more frequently enslaved (Table I). These data suggest that colony-founding *Harpagoxenus* queens preferentially seek out *longispinosus* colonies but that established *Harpagoxenus* colonies, especially the so-called "branch colonies," raid the nests of both hosts.

Our material consisted of a total of 41 *Harpagoxenus* colonies or "branch colonies" in the sense of Wesson (1939). Thirteen "primary colonies" contained a dealate full *Harpagoxenus* queen and from 1 to 8 *Harpagoxenus* workers. The average number of *Harpagoxenus* workers in these colonies was 3.0. Three incipient colonies contained only a *Harpagoxenus* queen, several host-speices workers, and a brood which consisted of *Harpagoxenus* worker pupae or larvae which developed into *Harpagoxenus* worker pupae. The 25 "branch colonies" lacked a dealate full queen but contained from 1 to 9 *Harpagoxenus* workers (with an average of 2.8), a variable number of host-species workers, and a brood. Six of these "branch colonies" produced only male pupae of the parasite species; but the rest yielded female, worker, and male pupae of the parasite species. In one acorn which contained no adult *Harpagoxenus* when it was collected, there were nevertheless *Harpagoxenus* male, female, and worker pupae which were being attended by several *longispinosus* workers. Apparently, the *Harpagoxenus* adults had either died or were away for some reason (perhaps on a raid) when their nest was collected. Finally, we made one quite peculiar observation. We found a dealate *Harpagoxenus* queen crawling around on the outside of an acorn which contained 3 *Harpagoxenus* workers, several *longispinosus* slaves, and a brood. After collecting the queen and the "colony" together in a vial, the *Harpagoxenus* queen was heavily mutilated by the *Harpagoxenus* workers, thus indicating that the queen and the workers did not belong together. Dissection revealed that the queen was an inseminated, egg-laying individual and that all 3 of the workers in the nest were completely sterile. In all probability this collection represents a newly founded *Harpagoxenus* colony that had been raided by workers of another *Harpagoxenus* colony.

2. *Dissections*

Dealate queens: The only dealate females from 8 colonies and both dealate females from a single colony which contained 2 such individuals were dissected. All 10 females had 6 ovarioles and a spermatheca. One of the females from the two-queen colony had short ovarioles that contained no developing eggs, and an empty spermatheca. However, the other 9 individuals were functional colony queens, individuals with receptacula filled with sperm and ovarioles which were about their total body length and which contained eggs in different stages of growth and corpora lutea.

Intermorphs: In 6 different colonies (2 queenright colonies and 4 "branch colonies"), we found a total of 6 individuals that were morphologically intermediate between worker and full queens and which could thus be regarded as intermorphs. These individuals had more or less well developed ocelli on their heads and several distinct sclerites on the alitrunk. Workers lack these structures. All of these intermorphs except one had 6 short, empty ovarioles like those of a virgin queen. None of them had a spermatheca. One individual had ovarioles which were about as long as the gaster and which contained developing oocytes and corpora lutea. These data indicate that *H. americanus* intermorphs have a reproductive function which cannot be distinguished from that of ordinary workers. Although they cannot be inseminated, they do sometimes become egg-layers.

Workers: We dissected a total of 91 workers, 28 from 8 queenright colonies and 63 from 22 "branch colonies" which contained

Table II: Numbers of fertile and sterile workers in queenright and queenless colonies.

Colony no.	queen	workers and intermorphs (I)			Harpagoxenus ♂♀☿ produced +)	date of collection
		sterile	with growing oocytes	with grow.ooc. and corpora lutea		
1	1	-	3	1	♂ ♀ ☿	VI-12-77
2	1	1	2	-	♂ ♀ ☿	VI-12-77
3	1	3	-	-	♂ ♀ ☿	VI-12-77
4	1	8	-	-	☿	VI-13-77
5	1	1	-	-	☿	VI-24-77
6	1	2	-	-	2♀ 4☿	VI-16-77
7	1	4	-	-	☿	VII-17-77
8	-	1	-	-	4♂ 4♀ 2☿	VI-12-77
9	-	1(I)	1	-	2♂ 2♀ 2☿	VI-12-77
10	-	1	-	-	17☿	VI-24-77
11	-	2	1	-	1♂ 1♀ 7☿	VI-16-77
12	-	2	1	-	♂ ♀ ☿	VI-22-77
13	-	-	-	1	♂ ☿	VII-1-77
14	-	-	4	4+1(I)	11♂ 1♀ 8☿	VI-12-77
15	-	-	-	1	5♂ 4☿	VI-14-77
16	-	2	-	3	7♂	VI-14-77
17	-	-	3	1	10♂ 1☿	VI-22-77
18	-	-	-	1	4☿	VI-24-77
19	-	-	1	1	34♂ 1♀	VI-27-77
20	-	3	-	1	10♂ 2☿	VII-1-77
21	-	-	2	1(I)	15♂	VI-16-77
22	-	-	-	1	11♂	VI-22-77
23	-	-	-	1	♂	VI-27-77
24	-	1	3	5	10♂	VII-1-77
25	-	2	-	2	52♂	VII-1-77

+) Numbers are indicated where the production could be completely recorded

no dealate queen. None of the workers had a spermatheca, but most of them had a rather large number of ovarioles. More specifically, we found 2 workers with 2 ovarioles, 1 with 3, 6 with 5, 81 with 6, and 1 with 7. Thus, most workers have the same number of ovarioles as queens. About half (45) the workers had short, thin ovarioles that contained no developing oocytes. These individuals were completely sterile. However, the other 46 workers manifested varying degrees of fertility. A total of 22 individuals possessed ovarioles containing white oocytes (a fact indicating that yolk has been deposited in the growing eggs); and 24 workers had actually begun to lay eggs, as indicated by the fact that there were corpora lutea in the bases of their ovarioles. The numbers of workers manifesting different degrees of fertility are shown in Table II for a selection of 25 typical colonies.

An examination of Table II reveals two facts which are especially noteworthy. First, workers with growing oocytes in their ovarioles and workers that have actually begun to lay eggs sometimes occur in queenright colonies (cf. Colonies 1 and 2 in Table II). One is tempted to speculate that these fertile workers are especially likely to found "branch colonies." However, no firm conclusion in this regard can be reached. Fertile workers also occur occasionally in queenright colonies of *H. sublaevis* (Buschinger & Winter, 1978) and *H. canadensis* (Buschinger & Alloway, in press), even though neither of these latter species appears to produce "branch colonies" of the kind seen in *H. americanus*. Second, some "branch colonies" which lacked a fully fertile worker (cf. Colonies 8, 9, 11, and 12 in Table II) nevertheless produced *Harpagoxenus* males, queens, and workers. This latter fact, the fact that workers never possess a spermatheca, and the fact that most of the "branch colonies" which contained fertile workers produced only (cf. Colonies 16, 21, 22, 23, 24, 25 in Table II) or preferably (cf. Colonies 13, 14, 15, 17, 19, 20 in Table II) males of the parasite species combine to suggest that the queens and workers produced in "branch colonies" may never be the offspring of egg-laying workers. Thus, instead of assuming that *H. americanus* workers possess the highly unusual ability to produce female offspring parthenogenically (an assumption made by Wesson, 1939), we speculate that all workers and queens produced in branch colonies may be derived from female larvae which are carried over to the "branch colony" nest at the time of its initial occupation by *H. americanus* workers. In this connection, we stress that our data regarding the frequency of production of males, queens, and workers in branch colonies agree closely with those of Wesson (1939).

DISCUSSION

The main result of the present study is our failure to confirm the assumption (Sturtevant, 1927; Creighton, 1950) that *H. americanus* produces true ergatoid queens (workerlike individuals which possess a spermatheca, can be inseminated, and thus can lay fertilized eggs and function as colony queens). We suspect that the organ which Sturtevant interpreted as being the spermatheca in the *H. americanus* workers that he dissected was in fact the Dufour's gland. Thus, in *H. americanus* as in *H. canadensis* (Buschinger & Alloway, in press), only the initially alate full queens possess a spermatheca and are capable of being inseminated. In this respect, both North American species differ radically from the European *H. sublaevis* in which true ergatoid queens are very common (Buschinger, 1975, 1978, in press).

H. americanus populations consist of both monogynous, queenright "primary colonies" and queenless "branch colonies." In most locations, the "branch colonies" outnumber the "primary colonies" by a ratio of approximately 2 : 1. In accordance with the observations of Wesson (1939), we assume that the "primary colonies" are founded by single, newly fecundated *H. americanus* queens which penetrate small host-species colonies, usurp the place of the host queens, and begin to lay eggs. A first brood of *americanus* workers is then reared with the assistance of host workers. Subsequently, the supply of host workers is augmented by slave raids in which both the *americanus* workers and their slaves participate (Wesson, 1939; Alloway, in press). Late in the summer, some of these raids terminate in the formation of "branch colonies" by some of the *americanus* workers and their slaves (Wesson, 1939). However, despite Wesson's failure to observe the phenomenon in the laboratory, we suggest that, in the process of forming "branch colonies," the *americanus* workers and their slaves carry across a certain number of *americanus* larvae from the "primary colony" to their new nest. Most of these larvae mature to become workers, alate queens, and males the next summer. At the same time, one or more of the "branch colony" workers become fertile and begin laying eggs which develop into males during subsequent years. However, a few of the female larvae from the "primary colony" may undergo an additional hibernation before maturing to become queens or workers, a process which would explain Wesson's (1939) observation that "branch colonies" occasionally produce small numbers of queens and workers even in the second year in the laboratory. Such double hibernations are known to occur in *Harpagoxenus sublaevis* and its host species (Buschinger, 1973). Although we cannot definitely rule out the parthenogenic production of females in *H. americanus,* our supposition that the phenomenon does not occur affords (in addition to the advantage of simplicity) an explanation of our observations that (a) workers and queens are produced most abundantly in "branch colonies" which possess no fully functional egg-laying worker at all and (b) "branch colonies" that possess one or more egg-laying workers produce only or preferably males.

The functional significance of "branch colonies" in *H. americanus* remains uncertain. As Wesson (1939) demonstrated experimentally, they do not result from mere mechanical crowding in the "primary colonies." Moreover, our observations confirm those of previous investigators in indicating that queenright *americanus* colonies tend to be quite small, The branch colonies do serve as a source of surplus males which might be essential to insure the insemination of all *americanus* queens. However, this possibility seems unlikely since "primary colonies" produce large numbers of males and since both *H. canadensis* and *H. sublaevis* appear to get along without "branch colonies." Indeed, since "branch colonies" often occur within less than a meter of queenright colonies from which they may well have arisen, it is hard to understand why raiding competition between a "primary colony" and its "branches" would not interfere with "primary colony's" capacity to exploit host-species resources. However, such competition might be minimized by the fact that *americanus* raiders kill very few host-species adults in their raids and the tendency of *americanus* colonies to rear host-species queens and males in their nests and then apparently to permit these individuals to go out on nuptial flights (Alloway, in press). These relatively nondestructive characteristics may permit dense *americanus* populations to survive without depleting host-species resources.

However, perhaps the best hypothesis regarding a possible adaptive advantage for the "branch colony" system in *americanus* arises if we suppose that the raiding range of each *americanus* nest is quite restricted. Thus, the formation of "branch colonies" at the periphery of the range of a "primary colony" may greatly expand the range of action of a "primary colony" and its "branches."

However, these interpretations are highly speculative. Further detailed field work is needed to work out the spatial relationship between *americanus* "primary colonies" and their "branches." In addition, a combined set of laboratory and field studies is needed to determine the means by which branch colonies are formed and to test our hypothesis that all *Harpagoxenus* queens and workers produced in "branch colonies" are derived from larvae taken from "primary colonies."

SUMMARY

During the summer of 1977, we collected numerous colonies of the slave-making ant *Harpagoxenus americanus* in southern Ontario and northern Ohio. The numbers of dealate *Harpagoxenus* queens, intermorphs, and workers were recorded; and the production of young *Harpagoxenus* workers and sexuals were observed in 41 colonies. Some of the *Harpagoxenus* queens, all the intermorphs, and most of the *Harpagoxenus* workers were dissected to determine the structure and function of their reproductive organs. The queens, intermorphs, and most of the workers have 6 ovarioles. However, since only alate and dealate full queens have a spermatheca, they are the only individuals that can be inseminated. Thus, no true ergatoid queens exist in *H. americanus.* Nevertheless, many workers have functional ovaries and lay eggs, sometimes even in queenright colonies. We found 3 incipient colonies, 13 queenright colonies, and 23 "branch colonies" that lacked a dealate queen but contained one or more fully or partially fertile workers. Younger "branch colonies" produce males, queens and workers, supposedly from larvae of their "mother colony," older "branch colonies" only yield males. The significance of this population structure is discussed.

LITERATURE CITED

ALLOWAY, T. M.

[1978] Raiding behaviour of two species of slave-making ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* Wesson (Hymenoptera: Formicidae). Animal Behaviour, in press.

BUSCHINGER, A.

1973. The role of daily temperature rhythms in brood development of ants of the tribe Leptothoracini (Hymenoptera: Formicidae). In: Effects of Temperature on Ectothermic Organisms. Ed. W. Wieser, Springer Berlin-Heidelberg-New York, pp. 229–232.

1975. Eine genetische Komponente im Polymorphismus der dulotischen Ameise *Harpagoxenus sublaevis.* Die Naturwissenschaften **62:** 239.

[1978] Genetisch bedingte Entstehung geflügelter Weibchen bei der sklavenhaltenden Ameise *Harpagoxenus sublaevis* (Nyl.) (Hym., Form.). Ins. soc., in press.

BUSCHINGER, A. AND T. M. ALLOWAY
[1978] On caste polymorphism of *Harpagoxenus canadensis* M. R. Smith. Ins. soc., in press.

BUSCHINGER, A. AND U. WINTER
1978. Echte Arbeiterinnen, fertile Arbeiterinnen under sterile Wirtsweibchen in Völkern der dulotischen Ameise *Harpagoxenus sublaevis* (Nyl.) (Hym., Form.). Ins. soc. **25:** 63–78.

CREIGHTON, W. S.
1927. The slave raids of *Harpagoxenus americanus*. Psyche **34:** 11–29.
1929. Further notes on the habits of *Harpagoxenus americanus*. Psyche **36:** 48–50.
1950. The ants of North America. Bull. Mus. Comp. Zool., Harvard, **104:** 1–585.

STURTEVANT, A. H.
1927. The social parasitism of the ant *Harpagoxenus americanus*. Psyche **34:** 1–9.

WESSON, L. G.
1939. Contributions to the natural history of *Harpagoxenus americanus* Emery (Hymenoptera: Formicidae). Amer. Ent. Soc. **65:** 97–122.

NEW RECORDS AND SPECIES OF LEIODINAE AND CATOPINAE (COLEOPTERA: LEIODIDAE) FROM JAMAICA AND PUERTO RICO, WITH A DISCUSSION OF WING DIMORPHISM*

By Stewart B. Peck
Department of Biology, Carleton University
Ottawa, Ontario, K1S 5B6, Canada

Since my earlier reports on the Leiodidae of Jamaica and Puerto Rico (Peck, 1970, 1972), I have had the opportunity to spend an additional 13 weeks in field work on these islands. In Jamaica this was from mid-December to mid-January, 1972–1973, and from late July to early September, 1974. In Puerto Rico it was from early to late May, 1973, and a week in June, 1974. This has resulted in new data on the leiodids of these islands, which are presented here. Additional data and information on forest habitat sites may be found in Peck and Kukalova-Peck (1975), and on cave sites in Peck (1974, 1975).

Methods and materials are similar to those utilized for my earlier papers. Collections were primarily made in forests with pitfall traps baited with carrion and human dung (Newton and Peck, 1975); by Berlese-Tullgren funnel extraction of arthropods from sifted forest litter, and from bat guano accumulations in caves. In this work, 259 kg (770 liters) of sifted forest litter were processed for Jamaica and 93 kg (171 liters) for Puerto Rico, in addition to many other extractions from samples of bat guano. Most of the arthropod residues from these collections are deposited with the Field Museum (Chicago). Some beetles are deposited in the Museum of Comparative Zoology (Harvard University), and the Canadian National Collection of Insects (Agriculture Canada, Ottawa).

In this paper I report only on new collections of 393 specimens of *Dissochaetus jamaicensis,* 460 specimens of *Aglyptinus puertoricensis,* 10 specimens of *Aglyptinus jamaicensis,* 1032 specimens of *Aglyptinus dimorphicus,* and on four new species of *Aphelo-*

**Manuscript received by the editor December 22, 1977*

plastus. Type specimens will be placed in the Canadian National Collection, Ottawa. The rest will be held in the author's collection, with some distributed to the Field Museum and Museum of Comparative Zoology.

Subfamily Catopinae

Dissochaetus jamaicensis Peck, 1972

New Records. Jamaica. Portland Parish. 1 mi W Ecclesdown (John Crow Mts.), 1500 feet, August, 1974, 14 males in traps. St. Thomas Parish. Portland Gap, 5500 feet, January, 1973, 2 in traps; August, 1974, 2 in dung traps; below Portland Gap at 4500 feet, August, 1974, 37 in traps. Whitfield Hall, 4250 feet, August, 1974, 13 females and 51 males in traps in forested ravine; 5 from guano in abandoned mine. Corn Puss Gap (4 mi N Bath), 2100 feet, August, 1974, 37 in dung trap. St. Andrew Parish. Hardwar Gap, 4200 feet, January, 1973, 215 in traps. Hermitage Dam, 1750 feet, August, 1974, 17 in traps.

Proptomaphaginus puertoricensis Peck, 1970

New Records. Puerto Rico. Aguas Buenas Cave (near town of Aguas Buenas), 15 mi S San Juan, 250 m elev., May, 1973, several hundred on guano. No specimens of this beetle were taken in traps in the well-preserved forest outside of this cave.

We can conclude that this genus is absent from Jamaica in the light of the failure of extensive collecting to take it there. It is otherwise known to occur only in Cuba and Mexico (Peck, 1977).

Subfamily Leiodinae

Correction. I earlier indicated (1972) that the tarsal formula for the genus *Aglyptinus* was 3–3–3 in females and 4–3–3 in males. Dr. Alfred F. Newton and Mr. Quentin Wheeler have brought it to my attention that it is really 3–3–3 in both sexes. I have reexamined my material and have found them to be correct.

Aglyptinus puertoricensis Peck, 1972

New Records. Puerto Rico. Aguas Buenas Cave (near town of Aguas Buenas, 15 mi S San Juan), 250 m elev., May, 1973, 3 females and 1 male in forest malt traps; 422 from forest litter Berlese;

20 males and 12 females from wet guano in cave. Cueva del Humo (part of Rio Camuy Cave System at Bayaney), May, 1974, Forest Miller leg., 2 on guano.

No tendency for eye reduction or wing dimorphism has been noted in forest or cave populations of this species.

Aglyptinus jamaicensis Peck, 1972

New Records. Jamaica. St. Andrew Parish. Hardwar Gap, 4000 feet, January, 1973, 1 male and 3 females in Berlese of woody fungi; 1 male, 6 females in Berlese of fleshy fungi.

This species remains scarce, and the only detailed habitat data is its association with fungi. Previous examples came from forest litter samples and it is remarkable that no more appeared in the more extensive litter samples reported on in this paper. The species is now known from the center and eastern half of the island, and from 2000 to 4000 feet elevation.

Aglyptinus dimorphicus Peck, 1972

The dimorphic condition of the wings is reported below as LW (long winged) and SW (short winged). The long winged form seems to be fully functional in flight. It has two folds, with the extended wing exceeding two elytral lengths. There is a distinct gap between this condition and the short winged form, which at most has only one wing fold, and in length barely extends beyond the elytra. From this condition various degrees of reduction culminate in a thin and tiny paddle-shaped remnant. Individuals with the most reduced wings have partially fused elytra, and occur at higher elevations.

New Records. Jamaica. Clarendon Parish. Pedro River, outside Pedro Great Cave, 1750 feet, August, 1974, litter Berlese 284, LW females 5, SW females 15, LW males 5, SW males 14. Pedro Great Cave (inside), December, 1972, SW females 1, SW males 5.

Portland Parish. 1 mi W Ecclesdown, 1500 feet, August, 1974, litter Berlese 280 and 294, LW females 13, SW females 21, LW males 6, SW males 15. 0.5 mi NE Ecclesdown, 1250 feet, August, 1974, litter Berlese 296, LW females 9, SW females 1, LW males 0, SW males 2.

St. Andrew Parish. Hardwar Gap, 4–4500 feet, January, 1973, litter Berlese 256, LW females 1, SW females 14, LW males 0, SW males 12. Hermitage Dam, 1750 feet, August, 1974, bait trap, SW males 1; litter Berlese 295, LW females 29, SW females 3, LW males 25, SW males 3. Morces Gap, 5000 feet, January, 1973, litter Berlese 253, SW males 2.

St. Ann Parish. 1 mi S Claremont, 1500 feet, December, 1972, litter Berlese 249, LW females 4, SW females 8, LW males 6, SW males 10. Ken Connell Hole (cave), August, 1974, SW females 1, SW males 2. Mt. Diablo (S of Moneague), 2250 feet, December, 1972, litter Berlese 258, LW females 6, SW females 18, LW males 6, SW males 27. Moseley Hall Cave, December, 1972, SW females 69, SW males 95. Thatchfield Great Cave, October, 1973, R. Norton leg., SW females 10, SW males 15.

St. Catherine Parish. Swansea Cave, November, 1973, R. Norton leg., SW females 2, SW males 1.

St. Elizabeth Parish. Peru Cave (near Santa Cruz), December, 1972, LW females 1, LW males 1.

St. James Parish. Mocho Cave, October, 1973, R. Norton leg., LW females 5, SW females 1, LW males 5, SW males 0. Brandon Hill Cave (Montego Bay), September, 1974, SW females 1. Maldon School Cave, September, 1974, SW females 3, SW males 5.

St. Mary Parish. Goshen, 1500 feet, December, 1972, litter Berlese 257, SW females 0, SW females 16, LW males 2, SW males 16. Lucky Hill Farm Cave, December, 1972, SW females 2, SW males 6. Mt. Plenty Cave, March, 1973, R. Norton leg., SW females 7, SW males 17; August, 1974, SW females 14, SW males 15. Rock Springs Cave (near Pear Tree Grove), August, 1974, SW females 4, SW males 8.

St. Thomas Parish. Bath Fountain, 500 feet, August, 1974, litter Berlese 283, LW females 36, SW females 9, LW males 36, SW males 11. Blue Mountain Peak, 7400 feet, January, 1973, litter Berlese 252, SW male 1; August, 1974, dung bait traps, SW females 10. Corn Puss Gap, 2100 feet, August, 1974, litter Berlese 293, LW females 13, SW females 0, LW males 16, SW males 2. Portland Gap, 5500 feet, January, 1973, litter Berlese 254, SW females 28, SW males 23; on rocks at soil line under debris (in site shown in fig. 3 in Peck and Kukalova-Peck, 1975), SW females 8, SW males 16; dung traps, SW females 6, SW males 6; litter Berlese 291, August, 1974, SW females 26, SW males 37. Whitfield Hall, 4100 feet, January, 1973, litter Berlese 255, LW females 1, SW females 1, SW males 2.

Trelawny Parish. 5 mi N Alberttown, January, 1973, litter Berlese 250, LW females 3, LW males 8. Discovery Bay Marine Lab., 10 feet, September, 1974, dung trap LW males 1. Drip Cave, August, 1974, SW females 6, SW males 6. Windsor Great Cave, March, 1973. R. Norton leg., SW females 8, SW males 10; August, 1974, SW females 54, SW males 72. Windsor, 500 feet, August, 1974, litter Berlese 290, SW females 3, SW females 1, SW males 2, SW males 3.

These data show the species to be spread across the island in humid forests, from sea level to 7400 feet elevation.

Discussion. For purposes of analysis of wing dimorphism, the above data has been combined with that of this species in my 1972 paper. The data show that there is no particular relationship between wing condition and sex. The sex ratio is statistically distributed around an equal ratio of males to females, and the short wing form is not significantly more prevalent in either sex.

However, there is a relationship between wing condition and habitat. In all 15 caves known to be inhabited by the beetle (ranging from 200 feet to 1750 feet in elevation), the populations are almost exclusively short winged. The exceptions are two and 10 long winged specimens from Peru and Mocho Caves respectively. Otherwise, all the other 516 cave-collected specimens are short winged.

A second relationship exists between wing condition and forest habitat elevation. Generally, the short winged form is more prevalent at higher elevations. Combined data were analyzed to try to determine the existence of a quantitative relationship between wing reduction and elevation, but the scatter of the data points, even after an arc sin transformation, was too great to allow the calculation of a meaningful regression line. This is because many of the lower elevation samples are too small to significantly record wing condition in the population. Even large Berlese samples often yielded only one or two specimens. Another error source is that pitfall traps in the lowlands selectively sampled long winged individuals because they are more able to arrive at the traps by flight.

The increased occurrence of wing reduction at higher elevations has been noted and discussed by Darlington (1943, 1970) for temperate and tropical carabid beetles. The phenomenon has also been an important component in the unraveling of the Pleistocene and Recent distributional history of carabids in Scandinavia (Lindroth, 1969, 1970). In addition to wing reduction, high elevation litter beetles are often eyeless or microphthalmous, and less darkly pigmented. This generalization was strikingly demonstrated to me by the beetles in a litter sample from the highest point in Jamaica, forested Blue Mountain Peak at 7400 feet. The sample contained beetles with these characters in the families Histeridae, Tenebrionidae, Curculionidae, Cerylonidae, Pselaphidae, and Carabidae, as well as Leiodidae. Most of these beetles were absent or much less common at lower elevations. In *Aglyptinus dimorphicus* there was only a very slight indication of reduction in eye size at higher elevations or in cave populations.

An explanation for wing reduction in *A. dimorphicus* is not difficult to envision. Selective pressures must favor retention of long winged genotypes in the lowlands because the habitats are climatically more variable (with wet and dry seasons) and have feeding and reproduction resources that last for a short time (dung and fungi is consumed or decays quickly). The ability to disperse to new and more favorable sites is necessary for populations in such lowland circumstances. In contrast, selection for wings is relaxed in cave and montane forest populations because the dispersal function of flight is less important. The beetles live in a stable climate (with little or no seasonal variation in temperature and moisture, especially in deep litter), and feeding and reproduction resources are long lasting (guano piles and deep mats of slowly decomposing montane vegetation).

I would reason that the lowland caves were occupied in the past by long winged individuals. They could more easily arrive at the guano piles deep in the caves, through flight guided by olfaction. These winged colonizers also carried the short winged condition in their genome, perhaps in a simple recessive condition. Peru and Mocho caves now contain long winged members in their populations and may thus represent recent colonizations. The other 13 caves, with only short winged populations, must represent older colonizations from which selection has removed the long winged condition. This seems to represent an active selective force against wings, rather than just a relaxed selection which no longer encourages their genetic maintenance. I cannot identify the selective force that seems to work so well against the winged condition of these beetles in caves (but see Barr, 1968, and also Regal, 1977, for a discussion of the loss of "useless" features). I also cannot determine the amount of time that has been required for the selection of short wings, but I imagine that the process has been rapid and in the span of a few thousand years.

Creagrophorus jamaicensis Peck, 1972

My Jamaican field work yielded no collections of this poorly known genus and species. However, Dr. Newton has found another four specimens in the collections of the Museum of Comparative Zoology, from Port Antonio, Jamaica, collected by A.E. Wight, "12/14." The male protarsal segment number was previously not known for this species. Examination shows that the one male in the new material has three protarsal segments. Thus, the tarsal formula for both sexes of the species is 3–3–3. Since Matthews (1888) reported his species to have a formula of 4–4–3, they should be reexamined to confirm this and allow a more secure characterization for the genus. The unusual shape of the first abdominal sternite that Matthews mentioned is a longitudinal carina crossing the face of the segment, so that it superficially looks as if it were composed of two segments, of which the first is triangular and separated by the coxae. The characters of the longitudinal carina across the first abdominal segment and the 3–3–3 tarsal formulae of both sexes are shared with *Aglyptinus* and the Scotocryptini, eyeless inquilines in Meliponine bee nests. These characters unite all these beetles more than had been previously thought. The compact antennal club of *Creagrophorus* separates it from *Aglyptinus* and the Scotocryptini, with their longer and less compact clubs.

Apheloplastus Brown

Diagnosis (drawn from Brown, 1937, 1963). Shape rounded, strongly convex. Antennae with 10 segments, club composed only of last four enlarged segments, with no smaller segment between the seventh and eighth. Antennal grooves beneath head. Prosternum finely carinate before the coxae. Mesosternum carinate, vertical between coxae. Middle and posterior legs with tibiae very broad, and tarsi compressed. Male and female with tarsal formulae of 5–5–4. Six visible abdominal sternites.

The aedeagus is unusually small in relation to adult body size, ranging from 0.2 to 0.3 mm in different species.

The only other species presently recognized in the genus is *A. egenus* LeConte, distributed from Ontario to North Carolina (Brown, 1937). The presence of the following four new species in Jamaica and Puerto Rico strengthens Brown's suspicion that *Cyrtusa conicitarsus* Champion (1925) of St. Vincent in the Lesser Antilles is actually an *Apheloplastus*. We may also expect that other species described as *Cyrtusa* belong in *Apheloplastus*. In this context, Brown mentions species from New Zealand and Europe. The many species of *Cyrtusa* described in the past two decades by Hlisnikowski should also be reexamined with this in mind.

All members of the genus probably feed on fungi in decomposing forest litter. All specimens reported on in this paper were taken in litter Berlese samples only.

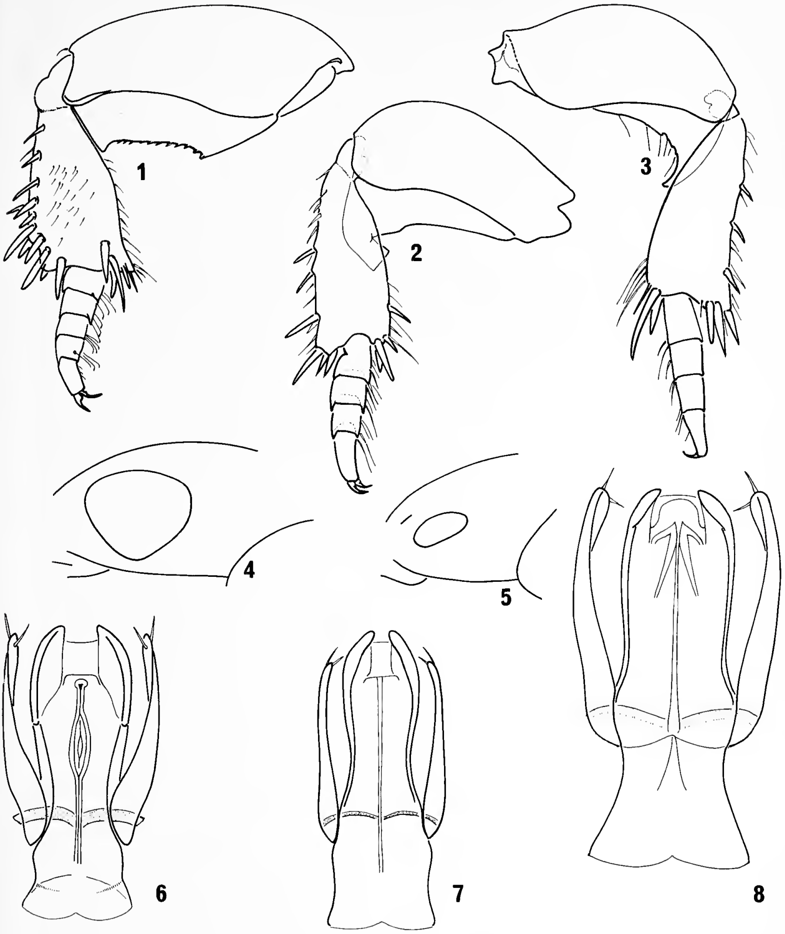
Apheloplastus jamaicensis new species

Figs. 1, 2, 4, 6.

Holotype male and allotype female in CNC. Locality and data. Jamaica. Trelawny Parish. Windsor, 500 feet, 25.VII.74, S. & J. Peck, litter Berlese 290. Paratypes: 2 females with same data. 5 mi N Alberttown, 1000 feet, 30.XII.72, S. & J. Peck, Berlese 250, 1 male. Portland Parish. 0.5 mi NE Ecclesdown, 1250 feet, 12.VIII. 74, S. & J. Peck, Berlese 296, 2 females. St. Andrew Parish. Hardwar Gap, 4–4500 feet, 6–7.I.73, S. & J. Peck, Berlese 256, 1 female. Morces Gap, 5000 feet, 8.I.73, S. & J. Peck, Berlese 253, 1 female. St. Ann Parish. 1 mi S Claremont, 1500 feet, 26.XII.72, S. & J. Peck, Berlese 249, 1 male.

Diagnosis. The species is distinguished by its restriction to Jamaica, its large eye size, functional flight wings, relatively uniform brown color, shape of male femora and tibiae, and aedeagus.

Description. Length 0.9–1.4 mm, width 0.7 to 0.9 mm. Color uniformly light to medium dark yellowish brown. Eye large (fig. 4), as wide as long. Head and pronotum lightly punctured, elytra with nine rows of punctate striae, the ninth marginal. Metasternum strongly punctured. Flight wings fully developed. Male mesofemur with partially serrated hind margin, mesotibia with many strong spines (fig. 1). Male metafemur with pronounced apical tooth (fig. 2). Aedeagus (fig. 6) with broad lobes at tip, parameres almost as long as median piece.



Figures 1–8. 1. Middle leg of *Apheloplastus jamaicensis*. 2. Hind leg of *A. jamaicensis*. 3. Hind leg of *A. puertoricensis*. 4. Side of head of *A. jamaicensis* showing relatively normal eye size. 5. Side of head of *A. microps* showing reduced eye size. 6. Dorsal view of aedeagus of *A. jamaicensis*. 7. Dorsal view of aedeagus of *A. microps*. 8. Dorsal view of aedeagus of *A. puertoricensis*. Figs. 1–5 all to same scale. Figs. 6–8 all to same scale.

Variation. Heterogonic development affects the male metafemoral tooth. It varies in shape from sharply pointed in smaller individuals to more broadly blunt in more developed individuals.

Collection data of the ten known specimens suggests that the species occurs throughout the island, at least from Windsor in the west to Ecclesdown in the east, and from the lowlands (500 feet at Windsor) to montane sites (5000 feet at Morces Gap).

Apheloplastus microps new species

Figs. 5, 7.

Holotype male in CNC. Locality and data. Jamaica. St. Andrew Parish. Morces Gap, 5000 feet, 8.I.73, S. & J. Peck, litter Berlese 258.

Diagnosis. The species is distinguished by its restriction to high elevation forests of Jamaica, its small eye, lack of elytral striae, strongly reduced wings, and aedeagus.

Description. Length 0.9 mm, width 0.7 mm. Color uniformly darker brown. Eye reduced in size, about twice as long as wide (fig. 5). Head and pronotum lightly punctured. Elytra with small, sparsely distributed hairs; with no trace of punctate striae. Metasternum without strong punctures. Flight wings reduced to tiny paddle-shaped rudiments. Male meso- and meta-femora with ventral flange extending over tibiae when reflexed, but apices broadly rounded, teeth not present. Aedeagus (fig. 7) with thin lobes at tip in dorsal view, parameres clearly shorter than median piece.

The species is known only from the holotype male. It was taken in a litter sample along with one female *A. jamaicensis* so the species are sympatric at this site. Slide preparations were not made of the legs of the unique, so they could not be illustrated.

Apheloplastus puertoricensis new species

Figs. 3, 8.

Holotype male in CNC. Type locality and data. Puerto Rico. Forest at Aguas Buenas Cave, 250 m elev. (near town of Aguas Buenas, about 15 mi S of San Juan), 7–17.V.73, S. Peck, Berlese 265.

Diagnosis. The species is distinguished by its restriction to Puerto Rico, and the shapes of the male hind femora and tibiae, and aedeagus.

Description. Length 1.3 mm, width 1.0 mm. Color uniformly light yellowish brown. Eye large. Head and pronotum lightly punctured. Elytra with nine rows of punctate striae. Metasternum strongly punctured. Flight wings fully developed. Male mesofemur with sharp, curved, distal-posterior tooth (fig. 3). Metatibia strongly spinose (but less so on inner margin than in *A. jamaicensis*). Aedeagus (fig. 8) more robust, with thin lobes at tip, two sclerotized "teeth" near orifice, at side of internal sac-stylet; parameres as long as median piece.

Apheloplastus bicolor new species

Holotype female in CNC. Type locality and data. Jamaica. St. Ann Parish. Goshen, 1500 feet, 25.XIII.73, S. & J. Peck, litter Berlese 257.

Diagnosis. The species is distinguished by its restriction to Jamaica, its distinctly bicolored body with dark blackish brown head and prothorax and lighter reddish brown elytra, and larger size.

Description. Length 1.7 mm, width 1.1 mm. Distinctly bi-colored; head and prothorax dark blackish brown, elytra lighter reddish brown. Antennae dark brown at base, club lighter brown. Eyes large. Head and pronotum regularly punctured. Elytra with nine rows of strongly punctured striae, intervals with two or three faint rows of very weak punctures. Metasternum strongly punctured. Posterior-ventral surface of female femora expanded to partially cover tibiae when reflexed; hind margin rounded, without teeth. Tibiae expanded to apex, strongly spinose. Male unknown.

ACKNOWLEDGEMENTS

Russell M. Norton provided some collections he made in Jamaica. Dr. G. Richard Proctor of the Institute of Jamaica was of great help in suggesting field sites in Jamaica. My wife, Jarmila, and our daughters, Olga and Hana, helped with the labor of litter sifting and of changing Berlese funnel samples. Jarmila also helped with the illustrations. Dr. George Carmody discussed statistical and genetical matters with me. Field work was partially supported by a Canadian National Research Council operating grant. Dr. Alfred F. Newton reviewed the manuscript, and shared his ideas and observations on leiodids.

LITERATURE CITED

BARR, T. C., JR.

1968. Cave ecology and the evolution of troglobites. Evol. Biol., **2:** 35–102. Dobzhansky, Th., M. K. Hecht, W. C. Steere, eds. Appleton-Century-Crofts, New York.

BROWN, W. J.

1937. Descriptions of some genera and species of Leiodidae (Coleoptera). Canadian Entomol., **69:** 158–165; 170–174; 193–203.

1963. Leiodidae, fasicle **20:** 343–347, *in* Arnett, R. H. The beetles of the United States (A manual for identification). Catholic University of America Press, Wash., D. C. 1112 pp.

DARLINGTON, P. J., JR.

1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. Ecol. Monog., **13:** 37–61.

1970. Carabidae on tropical islands, especially the West Indies. Biotropica, **2:** 7–15.

LINDROTH, CARL H.

1969. The theory of glacial refugia in Scandinavia: Comments on present opinions. Notulae Entomol., **49:** 178–192.

1970. Survival of animals and plants on ice-free refugia during the Pleistocene glaciations. Endeavour, **29:** 129–134.

MATTHEWS, A.

1888. Silphidae. Biologia Centrali-Americana. Coleoptera **2**(1): 72–101.

NEWTON, ALFRED F. AND S. B. PECK.

1975. Baited pitfall traps for beetles. Coleop. Bull., **29:** 45–46.

PECK, S. B.

1970. The Catopinae (Coleoptera; Leiodidae) of Puerto Rico. Psyche **77:** 237–242.

1972. Leiodinae and Catopinae (Coleoptera: Leiodidae) from Jamaica and Puerto Rico. Psyche, **79:** 49–57.

1974. The invertebrate fauna of tropical American caves, Part II: Puerto Rico, an ecological and zoogeographic analysis. Biotropica, **6:** 14–31.

1975. The invertebrate fauna of tropical American caves, Part III: Jamaica, an introduction. Int. J. Speleol., **7:** 303–326.

1977. The subterranean and epigean Catopinae of Mexico (Coleoptera; Leiodidae). Ass. Mexican Cave Studies, Bull, 8, in press.

PECK, S. B. AND J. KUKALOVA-PECK.

1975. A guide to natural history field localities in Jamaica. Studies on the Neotropical Fauna, **10:** 105–116.

REGAL, PHILIP J.

1977. Evolutionary loss of useless features: Is it molecular noise suppression? Amer. Natur., **111:** 123–133.

OBSERVATIONS ON THE NESTS AND PREY OF EUMENID WASPS (HYMENOPTERA, EUMENIDAE)*

By Howard E. Evans

Department of Zoology & Entomology
Colorado State University
Fort Collins, Colo. 80523

The recent development of the techniques of trap-nesting have added greatly to knowledge of the biology of twig-nesting Eumenidae (e.g. Cooper, 1953, 1955; Krombein, 1967; Fye, 1965). However, only scattered information is available on species that nest in the ground or make free mud nests. Recent papers describing the behavior of North American ground-nesters include two on species of *Stenodynerus* (Evans, 1970; Clement, 1972) and two on species of *Pterocheilus* (Grissell, 1975; Evans, 1977). The present paper includes notes on a ground-nesting *Pseudepipona* and an aerial-mud-nesting *Parancistrocerus* as well as on a mud nest built by a species of *Euodynerus* in a burrow dug by a sphecid wasp. This last example is described first.

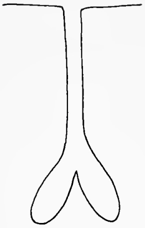
Euodynerus auranus (Cameron)

Several females of this species were seen in a large blow-out in a dune area near Roggen, Weld Co., Colorado, on 2 August 1977. This blow-out was a major nesting site for the sphecid wasps *Bembix pruinosa* Fox and *Philanthus albopilosus* Cresson, but it seemed an unusual habitat for a eumenid. When a female *Euodynerus auranus* was seen to plunge into an open hole in sloping sand carrying a small caterpillar in her mandibles, she was captured and the hole excavated.

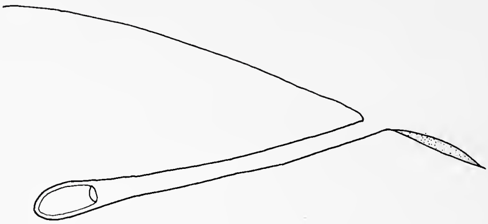
The burrow was apparently an abandoned, incipient nest of *Bembix pruinosa,* being of the form characteristic of that species and having a mound of sand on the down-slope side. The burrow terminated 15 cm from the entrance, at a depth of 5.5 cm from the surface directly above. In the bottom of the burrow was a single mud cell, open facing the burrow, measuring 9 mm in diameter

---

**Manuscript received by the editor January 26, 1978.*



1



2

Figure 1. Diagram of nest of *Pseudepipona herrichii*, near Moran, Wyoming.
Figure 2. Diagram of cell of *Euodynerus auranus* in abandoned burrow of *Bembix pruinosa*, near Roggen, Colorado.

and 16 mm in length (Fig. 2). It was extremely delicate, the walls measuring only 0.3 mm thick, smooth on the inside and slightly rough on the outside. The soil from which it was made was darker and more fine-grained than the surrounding sand, so had obviously been brought from some distance.

The cell contained 25 small, tightly coiled, paralyzed caterpillars of two species. These were identified as *Filatima* sp. (4) and near *Anacampsis* sp. (21) (both Gelechiidae). A wasp larva only 3.8 mm long was suspended by a short filament from the top wall of the cell 7 mm from its closed end. The larva was surely not more than a few hours old, but the fact that the female was still provisioning this nest demonstrates that this was an example of delayed provisioning, in the sense of Evans, 1966.

Bohart (1951) reported this species as making "clumps of five or six complete jug-shaped mud pots" in the ground (under the name *Rygchium boscii auranum*).

Pseudepipona herrichii (Saussure)

I observed 2 females of this Holarctic species nesting in the hard sandy loam of a path, 13–15 July 1977, in Grand Teton National Park, Wyoming, about 4 km WNW of the Moran Post Office. The path was in a meadow with sparse aspens and lodgepole pines, about 20 m from the banks of the Snake River. On the 13th, one of the females was digging her nest, flying obliquely upward with small lumps of earth to a height of about 0.3 m and dropping the earth 0.6–0.9 m away. Two days later she was seen

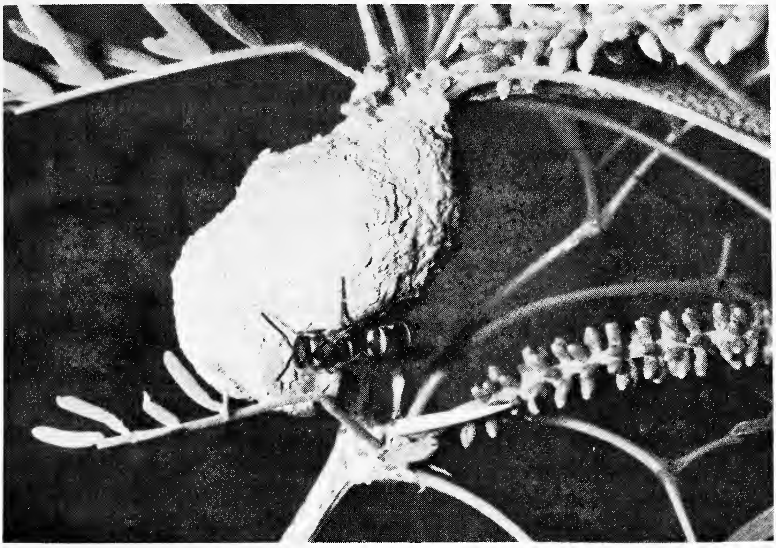


Figure 3. Nest of *Parancistrocerus vagus* on mesquite, Mescalero Sands, New Mexico.

provisioning the nest with small caterpillars carried in her mandibles. I captured her and excavated the nest, finding one cell with an egg and another with a rather large larva. Evidently the female had been digging the newer cell when first observed.

The burrow proved to be vertical, 6 mm in diameter, reaching a depth of only 5.5 cm. The two cells diverged 4 cm down, each measuring 10 mm in diameter and 15 mm long (Fig. 1). The larva had nearly consumed all the prey in one cell, which was closed by a thin barrier of soil. The other cell contained 17 small, paralyzed caterpillars, all one species of *Chionodes* (Gelechiidae). The egg of the wasp measured 0.6 × 2.3 mm and appeared to be loose toward the top of the cell, although I may have dislodged it during digging.

The second nest was only 7 cm away and was similar in dimensions except that there was only one cell. This cell had 5 caterpillars (*Chionodes* sp.) and presumable an egg, though I failed to find it. Caterpillars in both nests showed much movement but were unable to walk in a coordinated manner. Neither nest had any evidence of a turret at the entrance.

Parancistrocerus vagus (Saussure)

Some years ago I reported briefly on a mud nest of this species found on a willow branch in Kansas (Evans, 1956). I take this opportunity to include a photograph of a very similar nest found on 4 June 1974 at Mescalero Sands, east of Roswell, New Mexico (Fig. 3). The nest was on the branch of a mesquite bush (*Prosopis juliflora*) 0.6 m above the ground. The nest measured 3.4 × 1.9 cm and contained 6 cells, two of which were empty. Cells measured 6 × 13 mm. Two contained cocoons, one a large eumenid larva, and one nothing but dried, shriveled larvae of Microlepidoptera which were in too poor condition to be identified. The female wasp rested on the outside of the nest in a small hollow which would probably have formed the floor of a new cell.

The two cocoons both yielded cuckoo wasps, *Chrysis dugesi* Buysson, 2–3 weeks later.

DISCUSSION

These three examples reinforce the impression that certain aspects of nesting behavior are relatively fixed in Eumenidae (oviposition and type of prey) while others are diverse and not closely correlated with generic divisions based on structure (location and type of nest). Eumenidae are largely solitary nesters, and it may be some years before enough information has accumulated to clarify the patterns of evolution within the group. The occurrence of delayed provisioning in *Euodynerus auranus* is of interest. This occurs in certain other Eumenidae and is regarded as one of several preadaptations for social life in wasps (Evans, 1958). Oviposition in the empty cell and use of materials from sources other than the immediate substrate provide other preadaptations; some Eumenidae use plant materials in nest construction (Bohart & Stange, 1965). Species of *Montezumia* are evidently communal nesters and progressive provisioners (Evans, 1973). Thus there is every reason to regard the Eumenidae as providing the ancestral stock of the social Vespidae.

ACKNOWLEDGMENTS

I am indebted to R. M. Bohart for identifying the Eumenidae and Chrysididae and to D. M. Weisman for identifying the Lepidoptera larvae. These observations were a by-product of studies of philanthine wasps, supported by the National Science Foundation, grant BNS76–09319.

LITERATURE

BOHART, R. M.

1951. Subfamily Eumeninae. *In* Muesebeck, C. F. W., *et al.* Hymenoptera of America North of Mexico: Synoptic Catalog. U.S. Dept. Agri. Monogr. **2**, pp. 884–907.

BOHART, R. M. AND STANGE, L. A.

1965. A revision of the genus *Zethus* in the western hemisphere. Univ. Calif. Publ. Ent., **40:** 1–208.

CLEMENT, S. L.

1972. Notes on the biology and larval morphology of *Stenodynerus canus canus* (Hymenoptera: Eumenidae). Pan-Pac. Ent., **48:** 271–276.

COOPER, K. W.

1953, 1955. Biology of eumenine wasps. I, II. Trans. Amer. Ent. Soc., **79:** 13–35; **80:** 119–174.

EVANS, H. E.

1956. Notes on the biology of four species of ground-nesting Vespidae (Hymenoptera). Proc. Ent. Soc. Wash., **58:** 165–270.

1958. The evolution of social life in wasps. Proc. 10th Internat. Congress Ent., **2:** 449–457.

1966. The Comparative Ethology and Evolution of the Sand Wasps. Harvard Univ. Press, Cambridge, Mass. 526 pp.

1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. Bull. Mus. Comp. Zool. Harvard, **140:** 451–511.

1973. Notes on the nests of *Montezumia* (Hymenoptera, Eumenidae). Ent. News, **84:** 285–290.

1977. Notes on the nesting behavior and immature stages of two species of *Pterocheilus* (Hymenoptera: Eumenidae). Jour. Kansas Ent. Soc., **50:** 329–334.

FYE, R. E.

1965. The biology of the Vespidae, Pompilidae, and Sphecidae (Hymenoptera) from trap nests in northwestern Ontario. Canad. Ent., **97:** 716–744.

GRISSELL, E. E.

1975. Ethology and larva of *Pterocheilus texanus* (Hymenoptera: Eumenidae). Jour. Kansas Ent. Soc., **48:** 244–253.

KROMBEIN, K. V.

1967. Trap-nesting Wasps and Bees: Life Histories, Nests, and Associates. Smithsonian Press, Washington, D.C. 570 pp.

NEW NAME FOR A TRIASSIC MAYFLY FROM SOUTH AFRICA (EPHEMEROPTERA)*

BY MICHAEL D. HUBBARD[1] AND E. F. RIEK[2]

In a recent paper Riek (1976) described a new species of fossil Ephemeroptera from the Triassic of South Africa as *Xenophlebia optata.* This mayfly, of which only the wing is known, is sufficiently distinct from other known mayflies to be referrable to a separate superfamily (Xenophlebioidea) without recognizable close phyletic relationship to any other known Ephemeroptera.

Unfortunately, through a chain of circumstances, the fact that Demoulin (1968) had already used the generic name *Xenophlebia* for a genus of fossil Leptophlebiidae (Ephemeroptera) from the Baltic amber was not taken into consideration. Thus *Xenophlebia* Riek, 1976, must fall as a junior homonym of *Xenophlebia* Demoulin, 1968, and be replaced by a new name. The International Code of Zoological Nomenclature also requires that family-group names based on a genus name that is a junior homonym be replaced as invalid. We therefore propose the following new names.

Superfamily **Litophlebioidea:** new name for Xenophlebioidea Riek, 1976:149.

Family **Litophlebiidae:** new name for Xenophlebiidae Riek, 1976:150.

Genus **Litophlebia:** new name for *Xenophlebia* Riek, 1976: 150.

Entymology: Gr., *Litos,* meaning frugal, and *Phlebos,* meaning vein, in reference to the marked reduction in the cubito-anal field of the wing.

Type species: *Xenophlebia optata* Riek, 1976, by objective synonymy.

Species included: *Litophlebia optata* (Riek, 1976) new combination.

---

[1] Laboratory of Aquatic Entomology, Florida A&M University, Tallahassee, Florida 32307, USA.

[2] 19 Duffy St., Ainslie, Canberra, ACT 2602, Australia.

**Manuscript received by the editor January 26, 1978.*

We thank the Cooperative State Research Service, U.S.D.A., PL 89–106, for partial financial support.

LITERATURE CITED

DEMOULIN, G.
1968. Deuxième contribution à la connaissance des Éphéméroptères de l'ambre oligonène de la baltique. Dtsch. Entomol. A., N.F., **15:** 233–276.

RIEK, E. F.
1976. An unusual mayfly (Insecta:Ephemeroptera) from the Triassic of South Africa. Palaeontol. Afr. **19:** 149–151.

THE LARVA OF *ROTHIUM SONORENSIS* MOORE & LEGNER WITH A KEY TO THE KNOWN LARVAE OF THE GENERA OF THE MARINE BOLITOCHARINI (COLEOPTERA : STAPHYLINIDAE)[1]

By Ian Moore
Department of Entomology, University of California,
Riverside, California 92521

Larvae of Staphylinidae are difficult to associate with adults except in some specialized habitats where few species are present. In the intertidal habitat it has been possible to associate adults and larvae when they are present. The present larva is identified by its size, color and association with adults.

Rothium sonorensis Moore & Legner (1977) is a recently described genus and species of intertidal rove beetle from the Gulf of California belonging to the tribe Bolitocharini.

Larva of *Rothium sonorensis* Moore & Legner

Length 5.1 mm. Body elongate, slightly convex, parallel, sclerites pale brown with the center of tergite eight dark brown, appendages and intersegmental membranes cream with the ungues brown. Surface smooth and shining. Head subquadrate, a little longer than wide, with a small dark eye spot midway between the antennal fossa and the lateral margin; epicranial suture Y shaped. Clypeus narrowed and truncate in front, without teeth. Antennal fossa located at inner end of arm of epicranial suture. Antenna three-segmented; first segment a little longer than wide; second segment about one and one-half times as long as first and a little wider, widest near apex; apex bearing an "acorn seta" which is more than three times as wide and about as long as third segment; third segment about four times as long as wide, tapered to pointed apex which bears a short seta. Mandible arcuate, acute at tip, with a large central tooth internally. Maxillary palpus three-segmented with the first two segments subequal in length, the second a little narrower than first, third segment narrower and a little longer than second, narrowed gradually to pointed apex. Lacinia triangular, minutely

---

[1] *Manuscript received by the editor December 28, 1977.*

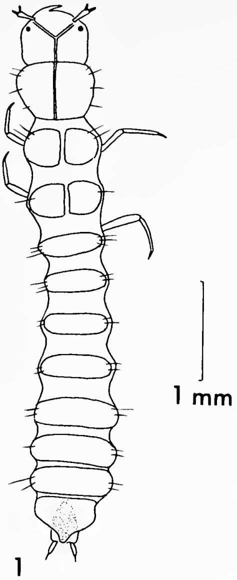
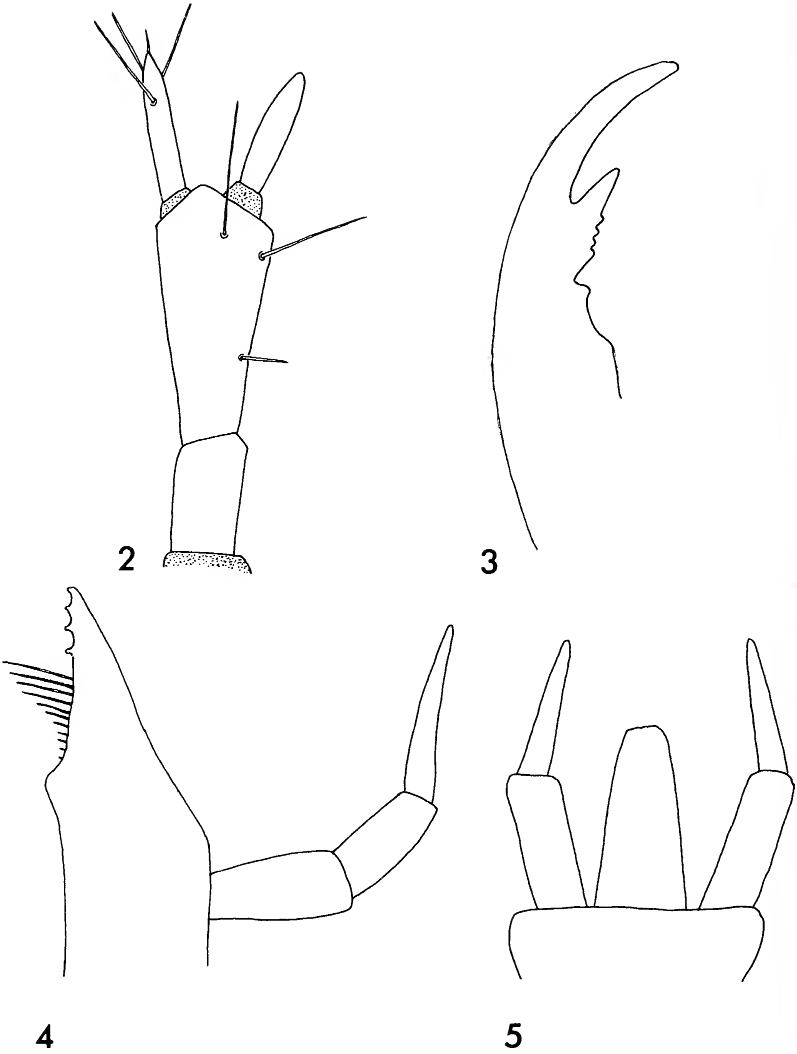


Figure 1. Larva of *Rothium sonorensis* Moore & Legner; dorsal aspect.

hooked and with a small tooth at apex and three other small teeth internally just below apex; with a row of long setae beginning at basal half and diminishing in length to base. Labial palpus two-segmented, first segment slightly more than twice as long as wide, parallel sided; second segment narrower but almost as long as first, tapered to apex. Ligula longer and wider than first segment of labial palpus, narrowed to truncate apex. Pronotum a little wider than long; quadrate; with the apex arcuate, apical angles broadly rounded, sides straight and somewhat converging to narrowly rounded basal angles; base almost straight; surface with scattered long setae. Mesonotum and metanotum of about equal size and shape; about as wide as pronotum and only half as long; each side with a row of five setae below the anterior margin, two discal setae, a row of three setae along the base and three setae in the lateral series. Tergites one through seven similar, with the first about as wide but not as long as metanotum, each succeeding very slightly wider and somewhat longer than the preceding so that tergite seven is wider than the metanotum and about as long; each with a discal



Figures 2–5. Larva of *Rothium sonorensis* Moore & Legner. Fig. 2, left antenna, dorsal aspect. Fig. 3, left mandible, ventral aspect. Fig. 4, right maxilla, ventral aspect. Fig. 5, labium.

row of ten setae, two setae laterally at the anterior margin and several other scattered lateral setae. Ninth tergite narrower than eighth, which is produced posteriorly in its central third in a narrowly rounded dark lobe that probably represents opercula for an osmeterium. Urogomphus one-segmented with a long seta at pointed apex. Pseudopod represented by a short narrow projection at the apex of a small broad triangular organ, the entire structure not more than half as long as the urogomphus, the cylindrical apical projection about one-third as wide as the urogomphus.

One specimen taken in company with five adults at Mexico, Sonora, Tide Pool Beach, 29.49–112.40, 20 March 1974, V. Roth and W. Brown, collectors. Another specimen was taken by V. Roth at Mexico, Sonora, Punta Cirio, 29.50–112.39, 12–20 January 1974, from intertidal rock crevice.

Among the marine Bolitocharini the larva of *Phytosus nigriventris* Chevrolat was described by Fauvel (1862), that of *Halmaeusa atriceps* (Waterhouse) by Paulian (1949) (as *Antarctophytosus*), those of *Liparocephalus cordicollis* LeConte and *Diaulota densissima* Casey by Saunders (128) and Chamberlin and Ferris (1929). These descriptions were reviewed by Moore (1956) who described the larvae of three more species of *Diaulota* and gave a key to the genera and the species of *Diaulota*.

KEY TO THE KNOWN LARVAE OF THE GENERA OF THE MARINE BOLITOCHARINI

1. Apex of ninth abdominal segment truncate .. *Phytosus* Curtis
   Apex of ninth abdominal segment produced in two appendages (urogomphi) 2
2. Urogomphus not segmented 3
   Urogomphus segmented 4
3. Antenna 3-segmented .... *Liparocephalus* Mäklin
   Antenna 2-segmented .... *Diaulota* Casey
4. Urogomphus one-segmented ..... *Rothium* Moore & Legner
   Urogomphus 2-segmented .... *Halmaeusa* Kiesenwetter

LITERATURE CITED

CHAMBERLIN, J. S. AND G. F. FERRIS
1929. On *Liparocephalus* and allied genera. Pan-Pac. Ent. **5:** 137–143, 153–162.

FAUVEL, ALBERT

1862. Notice sur quelques aléochariens nouveaux ou peu connus et description de larves de *Phytosus* et *Leptusa.* Ann. Soc. Ent. France, Ser. 4, **2:** 81–94.

MOORE, IAN

1956. Notes on some intertidal Coleoptera with descriptions of the early stages (Carabidae, Staphylinidae, Malachiidae). Trans. San Diego Soc. Nat. Hist. **12:** 207–230.

MOORE, IAN AND E. F. LEGNER

1977. A report on some intertidal Staphylinidae from Sonora, Mexico with four new genera (Coleoptera). Pac. Insects **17:** 459–471, 20 Figs.

PAULIAN, RENAUD

1941. Les premier états des Staphylinoidea. Études des morphology comparée. Mém. Mus. Nat. Hist. **15:** 1-361, 1367 Figs.

SAUNDERS, L. G.

1929. Some marine insects from the Pacific coast of Canada. Ann. Ent. Soc. Amer. **21:** 521–545.

COMPARATIVE STUDIES OF *DICTYNA* AND *MALLOS* (ARANEAE, DICTYNIDAE):
III. PREY AND PREDATORY BEHAVIOR

By Robert R. Jackson*
North Carolina Division of Mental Health Services
Research Section, P. O. Box 7532
Raleigh, N. C. 27611

Introduction

Although spiders are a major group of predaceous arthropods (see Turnbull, 1973), the types of prey consumed in their natural habitats are known for relatively few species. Some of the more noteworthy studies have employed daily monitoring of webs of araneids (Robinson and Robinson, 1970) and immunological techniques with lycosids (Greenstone, 1978); however, very little information is available for the dictynids. There is particular interest in the diet of dictynids because different species in this family live under a variety of types of social organization (Jackson, 1978). Discussions of the prime movers in the evolution of social phenomena frequently emphasize the type of prey taken by social predators (Wilson, 1975). An important factor for some species (e.g., army ants, canids, and killer whales) seems to be the ability of groups of individuals acting together to handle relatively large and dangerous prey. In order to evaluate the importance of this factor in the evolution of social phenomena in spiders, we need information concerning the diet and predatory behavior of species with differing types of social organization.

The species in this study belong to the closely related genera, *Mallos* and *Dictyna*. These are small cribellate spiders (body length usually 5 mm or less). Observations of actual feeding and other behavior related to predation were made in the western United States of America in June and July, and in south-central Mexico in September. Additional observations were made in the labora-

---

*Present address: Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.

Manuscript received by the editor January 15, 1978.

tory. Also, arthropod carcasses in webs were collected and identified. Data are given as means ± S.D.

Most dictynid species are solitary, each individual generally living alone in an individual web that does not touch other occupied webs. Communal, territorial species (*M. trivittatus* Banks, *D. albopilosa* Franganillo, *D. calcarata* Banks) live in web complexes, consisting of web units connected to each other by silk. *M. gregalis* Simon (communal, non-territorial) lives in communal webs not subdivided into web units. Aggressive and cannibalistic behavior are virtually non-existent in this species, and individuals routinely feed in groups on the same prey. The other species are aggressive and cannibalistic, and most often they feed one spider per prey. In this paper basic information concerning the feeding behavior and diet of varied species will be presented, and a specific hypothesis will be discussed: namely, is predation on relatively large and dangerous prey an important factor in *M. gregalis?* Other aspects of the feeding behavior of *M. gregalis* have been reported elsewhere (Burgess, 1975; Jackson, 1979a; Witt, *et al.,* 1978).

Data concerning *M. gregalis* were gathered in conjunction with another study (Jackson, 1979a) to which the reader should refer for a description of laboratory methods. "Large webs" were communal webs built on plants in the laboratory, each probably containing several hundred spiders (Jackson and Smith, 1979); and these were not enclosed. "Small webs" (built by four spiders each) and "single-female webs" were built inside plastic cages. Data concerning where the spider first grasped the fly came from all three types of webs; data concerning size and composition of feeding groups came from large webs only.

DIET

Diptera were the predominant prey upon which *Dictyna* and *Mallos* were observed feeding (Table 1), and these dominated the collection of carcasses (Table 2). The data in Table 2 should be viewed as a list of probable rather than certain prey of these species, since some were possibly not fed upon by the dictynids. Two small Diptera in webs of *M. niveus* and one small Diptera in a web of *D. tridentata* were still filled with hemolymph. Probably these were captured flies on which the spiders had not yet fed completely. this species came from spending many hours observing a particular

Table 1. Number of instances of dictynids feeding on different types of prey listed according to their estimated relative sizes (prey size/spider size). When more than one individual fed on the same prey item (*M. trivittatus*), relative prey size based on largest spider.

Species	Type of Prey	Number of Prey			Total
		Smaller than Spider	Same size as Spider	Larger than Spider	
Dictyna calcarata	Diptera	0	1	2	3
Dictyna completa	Diptera	0	2	1	3
Dictyna phylax	Diptera	2	0	0	2
Dictyna tridentata	Diptera	1	1	0	2
Mallos dugesi	Diptera	0	1	0	1
Mallos niveus	Diptera	2	0	0	2
Mallos trivittatus	Diptera[a]	25	12	15	52
	Lepidoptera[b]	0	0	4	4
	Conspecific Spider	0	2	0	2

[a] Tipulidae: 14
Other Diptera: 38

[b] Moths

My approach to the web may have disturbed the spider, causing it to depart from the prey. A living tipulid caught in a *M. trivittatus* web will be discussed later. All other carcasses in Table 2 were dry, hollow, and almost entirely intact, which is the usual condition of prey of these spiders after feeding has occurred. Spiders inject enzymes into their prey, and digestion takes place primarily outside the spider's body. The spiders ingest the prey's tissues in fluid form. Unlike some other spiders, no noticeable mastication of the prey occurs with dictynids. Since other species of spiders (salticids, tetragnathids, etc.) frequently were found inside or near webs containing dictynids, possibly some of the arthropod carcasses in Table 2 were prey of these species, but most were probably prey of the dictynids. Predation on conspecifics (cannibalism) is discussed elsewhere (Jackson, 1979b).

CIRCADIAN PATTERN OF FEEDING AND OTHER ACTIVITIES

Many more data are available concerning *M. trivittatus* than for the other species. Most of the observations of feeding (88%) for

Table 2. Number of arthropod carcasses ("prey remains") found in webs occupied by dictynids. Listed according to their estimated relative sizes (prey size/spider size). When more than one individual dictynid occupied the same web, relative prey size based on largest spider. Unidentified Dictyna: sp. no. 1, Querecho Plains, New Mexico, U.S.A.; sp. no. 2, Whiskey Mountain, Wyoming, U.S.A.; sp. no. 3, Lake Chapala, Jalisco and Michoacan, Mexico.

Species	Type of Prey	Number of Prey			
		Smaller than Spider	Same Size as Spider	Larger than Spider	Total
Dictyna albopilosa Franganillo	Diptera	8	5	2	15
Dictyna annexa Gertsch & Chamberlin	Diptera	30	16	1	47
	Coleoptera	0	1	0	1
Dictyna bellans Chamberlin	Diptera	2	2	0	4
	Lepidoptera[1]	0	0	1	1
Dictyna calcarata Banks	Diptera	55	16	4	75
	Coleoptera	0	2	2	4
	Homoptera[2]	2	0	0	2
	Hymenoptera[3]	0	2	0	2
	Lepidoptera[1]	0	0	1	1
Dictyna coloradensis Chamberlin	Diptera	21	1	2	24
	Hemiptera	0	0	1	1
Dictyna completa Chamberlin & Gertsch	Diptera	1	5	1	7
Dictyna tridentata Bishop & Rudeman	Diptera	42	46	37	125
	Coleoptera	0	0	1	1
	Hemiptera	0	0	1	1
Dictyna phylax Gertsch & Ivie	Diptera	9	3	0	12
Dictyna sp. no. 1	Diptera	26	7	0	33
	Hymenoptera[4]	0	0	1	1
	Lepidotera[1]	0	0	1	1
	Conspecific	1	0	0	1
Dictyna sp. no. 2	Diptera	0	4	4	8
	Hymenoptera[4]	0	0	1	1
Dictyna sp. no. 3	Diptera	7	8	6	21
	Homoptera[2]	1	0	0	1

Species	Type of Prey	Number of Prey Smaller than Spider	 Same Size as Spider	 Larger than Spider	 Total
Mallos dugesi Becker	Diptera	3	1	2	6
Mallos niveus O. P. Cambridge	Diptera	57	38	18	113
	Coleoptera	0	3	2	5
	Homoptera[2]	0	1	0	1
	Hymenoptera[4]	0	1	2	3
	Orthoptera[5]	0	0	1	1
	Thysanoptera	2	0	0	2
	Salticid spider	0	0	1	1
Mallos trivittatus Banks	Diptera[6]	163	20	38	221
	Coleoptera	1	0	0	1
	Homoptera[2]	3	0	0	3
	Hymenoptera[3]	1	0	0	1
	Lepidoptera	0	11	5	16
	Neuroptera	1	0	0	1
	Conspecific	2	3	0	5

[1] Moth
[2] Aphid
[3] Ant
[4] Wasp
[5] Grasshopper nymph
[6] Tipulidae: 33
Other Diptera: 188

web complex, located in a culvert through which a creek passed in the Chiracahua Mountains of Arizona. This large web complex was estimated to contain more than 10,000 individuals of *M. trivittatus* (Jackson and Smith, 1979). Since initial observations suggested that feeding occurred predominantly in the late afternoon and early evening (see below), one hour was spent inside the culvert on each of 12 evenings (5 in June; 7 in July); and records were kept for all observed cases of feeding. Diptera and other insects in the vicinity were especially active at this time of the day, and this was generally true in other habitats of *M. trivittatus* and the other dictynids.

Table 3. Temporal pattern of activity of spiders in their natural habitats. Time of day: early morning and early evening, within 2 hr before and after sunrise and sunset, respectively. Duration of observation estimated. Walking: without spinning and exclusive of intraspecific interactions. Intraspecific interactions described elsewhere. (Jackson, 1979b). *Dictyna phylax* and *Mallos dugesi* observed in day only.

Species	Time of Day	Duration of Observation (hr)	No of Spiders Feeding	No. of Spiders Walking	No. of Spiders Spinning	No. of Intraspecific Interactions
Dictyna calcarata	Early Morning	3	2	5	6	1
	Day	5	0	0	0	0
	Early Evening	2	1	0	0	0
Dictyna completa	Early Morning	2	1	0	0	0
	Day	4	2	0	0	0
	Early Evening	2	0	0	1	0
Dictyna phylax	Day	6	2	0	0	0
Dictyna tridentata	Early Morning	6	1	2	0	2
	Day	14	0	0	0	0
	Early Evening	4	1	0	0	0
Mallos dugesi	Day	7	1	0	0	0
Mallos niveus	Early Morning	5	0	0	0	0
	Day	14	2	0	0	0
	Early Evening	5	0	0	2	1
Mallos trivittatus	Early Morning	17	0	3	0	0
	Day	34	3	0	0	0
	Early Evening	19	53	18	3	9

With the exception of the evening observations in the culvert, the amount of time spent observing webs was recorded only approximately. These estimates were used for the calculations in Table 3. Based on these data, it seems that feeding and general activity of the dictynids in this study occur predominantly in the evening.

INITIAL CONTACT OF SPIDER WITH PREY

Certain spiders, such as some araneids and theridiids, wrap their prey either before and/or after biting; however, this does not occur in the Dictynidae. These spiders seem to simply rush out and bite the prey. If the prey is violently struggling, the spider may walk or stand in the vicinity until activity subsides.

Bristowe (1958) reported that dictynids invariably grasp their prey initially by a leg. The initiation of feeding was seen for one *M. niveus* and five *M. trivittatus.* In each case, the spider initially grasped a leg or antenna of the prey. Of the spiders already feeding when found, some were feeding on the head, thorax, or abdomen of the prey (Fig. 1), although data were not recorded. *M. gregalis, M. trivittatus, M. niveus,* and *D. calcarata* were maintained and fed in the laboratory, and it was noted that the spiders sometimes initially grasped the prey by its head or body rather than by an appendage. For *M. gregalis* in the laboratory, the location at which the spider first grasped the prey was recorded for 66 individuals: leg, 44%; head, 15%; abdomen, 14%; thorax, 11%; wing, 9%; antenna, 7%. All of these flies were active when contacted.

Once I saw an opilionid walk onto a web unit containing an adult female *M. trivittatus.* The spider rushed out of its nest and grasped a leg of the opilionid with its chelicerae. Immediately, the spider released the opilionid and returned to its nest, suggestive of opilionids being distasteful to dictynids (see Bristowe, 1941). Several minutes later, the opilionid escaped from the web.

EXTENSION LINES

Webs of *M. trivittatus* frequently contain long, heavy lines of silk (extension lines) that extend to objects some distance from the mesh (Jackson, 1978). Once in Utah I found an extension line fastened at one end to a mesh, with a female *M. trivittatus* inside the nest. On the other end, a tipulid fly was tethered by its thorax.

Fig. 1. Adult female *Mallos trivittatus* (body length: 7 mm) at East Turkey Creek (Chiracahua Mountains, Arizona) feeding on tipulid fly. Fly grasped at ventral thorax.

The tipulid flew in circles continuously for 10 min while I observed, after which I collected the fly and the spider. Of the set of *M. trivitattus* observed feeding in nature, 9% were on extension lines at the time; and 5% of the arthropod carcasses found in webs of *M. trivittatus* were found on extension lines. *M. gregalis* webs also have extension lines, and these spiders sometimes fed on flies caught on extension lines.

FEEDING GROUPS — SIZE AND COMPOSITION

The few cases in which more than one spider fed on the same prey in species other than *M. gregalis* are described elsewhere (Jackson, 1979b). In the laboratory, the size and composition of the group feeding on the fly was recorded 15 min after it contacted the web, and cases in which no spiders were feeding at the end of the 15 min are excluded. Group size was 4.8 ± 2.96 spiders (range: 1–15; n = 38). In the cases in which a single spider fed on the fly, three were females, two were immatures, and none were males. One of the immatures was a second instar; the other was almost adult size. In cases in which more than one spider fed on the fly, there were three groups consisting of females only; 4, immatures only; 21, females and immatures but no males; 2, males and immatures but no females; and 3, females, males, and immatures. In more casual observations, single males feeding on flies and groups consisting of females and males but no immatures were seen; but groups of more than one male but no females or immatures were not noticed. Groups of more than 20 individuals have been seen.

DISCUSSION

Based on arthropod carcasses found in webs and observations of actual feeding in nature, Diptera seem to constitute the major prey of the closely related species of *Dictyna* and *Mallos* in this study. Billaudelle (1957), Bristowe (1958), and Wiehle (1953) commented on dictynids preying on Diptera, ants, and lice. Unfortunately, only limited information is available concerning the natural prey of *M. gregalis,* the communal, non-territorial species. I was not able to find this species when I was in Mexico. Diguet (1909a, b, 1915) and Burgess (1976 and personal communication) noted that Diptera seem to be the primary prey of this species in nature, although wasps are also fed upon. The Diptera seem to be predominantly ones of body lengths of approximately 5 to 10 mm, such as the "domestic fly" (presumably *Musca domestica*), tabanids, and bot flies. Burgess collected a portion of a web in Mexico; and when examined in the laboratory, it contained a great number of carcasses, all of Diptera in the size range of 5 to 10 mm. In the laboratory, *M. gregalis* has thrived for several years on a diet of *M. domestica* almost exclusively. The natives of Michoacan have given this species the name *el mosquero.* During the rainy season, they take portions of communal webs from trees and place these in and around their homes, using them as fly traps (Berland, 1913; Diguet, 1909a, b, 1915; Gertsch, 1949).

Burgess (1975) has demonstrated that vibrations within a frequency range comparable to the wing beat frequency of *Musca domestica* is the most effective stimulus for eliciting predatory behavior from *M. gregalis.* Furthermore, the web transmits vibrations within this frequency range more readily than ones with other frequency characteristics. It seems that the web has characteristics that are particularly appropriate for the predominant prey species. The vibration transmission properties of webs of other species have not been investigated yet.

Some Diptera may be captured when they fly into *Dictyna* and *Mallos* webs. However, it was noticed that many Diptera tend to land on the stems and leaves of herbs and shrubs, on rock ledges, and on other objects on which dictynids tend to build their webs. Perhaps the majority of Diptera are captured when they inadvertently use a web as a perch. *Musca domestica* were frequently captured, seemingly in this manner, on webs of *M. gregalis* in the laboratory. These webs were kept in the open, on plants and other objects, in the laboratory. During routine feeding, house flies were thrown into the communal webs, but many inadvertently escaped into the room beforehand. Frequently these were seen subsequently landing on the webs and adhering to the silk. Thrown flies would seem more comparable to flying Diptera, and there is no evidence that the ratio of flies captured to ones that escaped differed for flies landing on the web compared to ones thrown into the web (Jackson, 1979a).

The extension lines in webs of *M. gregalis* and *M. trivittatus* may have a function related to predation. Diptera may find them to be particularly attractive perches and become trapped when they land on them. Another cribellate species, *Miagrammopes* (Uloboridae) has a single thread snare, and it reportedly captures Diptera that use the thread as a perch (Akerman, 1932).

Dictynid webs have nests, which are tubular structures of more densely woven silk; and the spiders tend to reside in their nests when not active. Spiders in various families (e.g., Agelenidae, Eresidae, Dysderidae) which have nests in their webs often transport prey to the nest before feeding(see Bristowe, 1958; Krafft, 1971). Araneid spiders tend to transport prey to the hub of the web before feeding (Robinson and Olazarri, 1971). Although data were not collected, it was noticed that arthropod carcasses tended to be concentrated near the nests of the solitary and the communal, territorial species; and many of the feeding dictynids were near their nests at the time. These observations suggest that dictynids transport prey to their nests, although actual transport has not been seen. Billaudelle (1957) noted that *D. civica* carries prey from the periphery to the center of the web.

Most dictynid webs tend to be 2-dimensional; i.e., most of the silk of the web is in a single plane. In contrast, the communal webs of *M. gregalis* tend to be 3-dimensional; and the nests are in the interior of the webs, beneath the surface sheet on which flies are captured. Although flies were occasionally pulled into the interior of webs by spiders, in the vast majority of cases the prey was fed upon at the capture site in communal webs in the laboratory.

Returning to the hypothesis proposed at the beginning of this paper, is the prey of *M. gregalis* relatively large and dangerous compared to that of other dictynids? Diptera are apparently the primary prey of most species. Since Diptera such as muscids, culicidids, etc. would not seem especially dangerous for dictynids, differences in the danger associated with different prey would not seem important. Adult females of *M. gregalis,* the largest sex/age class, tend to weigh 4 to 21 mg, adult *Musca domestica* tend to weigh 10 to 20 mg (Witt, *et al.,* 1978). If prey of *M. gregalis* is in this weight range, then prey tends to range from approximately equal in size to individual spiders to a few times larger. In the solitary and in the communal, territorial species, prey were often smaller than the spiders. However, the difference in relative prey size among species is not absolute. Many prey of solitary and communal, territorial species were equal to or larger in size than the spiders (see also Bristowe, 1958; Wiehle, 1953).

Since prey sizes overlap for different dictynids, we need quantitative data from which variances can be calculated for relative prey size. Data from the natural habitats of *M. gregalis* in Mexico are especially needed. It will be tentatively concluded that *M. gregalis* preys primarily on relatively large prey. However, the differences in relative prey size do not seem dramatic. In a sense, the social organization of *M. gregalis* seems very different from that of the other dictynids, with great numbers of spiders living and feeding together in the same communal webs. If diet is a major factor in the evolution of social phenomena in dictynid spiders, we might expect the diet of *M. gregalis* to differ greatly from that of other dictynids. Although differences in prey size seem to occur, perhaps the most interesting finding in this study is that there is considerable overlap in prey sizes of different dictynids. We need to consider the possibility that predation on relatively large and dangerous prey is only one among other equally or more important factors acting as prime movers in the evolution of social phenomena in the Dictynidae and perhaps for other groups as well.

SUMMARY

Based on arthropod carcasses in webs and observations of actual feeding, Diptera seems to be the major prey of *Dictyna* and *Mallos*. *M. gregalis,* a species that routinely feeds in groups, may tend to prey upon relatively large prey compared to the other species. However, relative prey sizes overlap for species of all types of social organization. No apparent differences occur in the degree to which prey are dangerous. These observations are not to be expected from the hypothesis that the prime mover in the evolution of social phenomena in spiders is the ability of predators acting as a group to handle relatively large and dangerous prey. Although legs of flies are frequently grasped first, *M. gregalis* may initially grasp almost any part of the fly. Size of feeding groups varies greatly, ranging from 1 to more than 20. The hypothesis is proposed that prey is captured by *Dictyna* and *Mallos* primarily when flies use webs as resting sites. Feeding and other activity occur especially in the early evening and early morning.

ACKNOWLEDGEMENTS

For valuable discussions and comments on the manuscript, I would like to thank P. N. Witt, M. C. Vick, S. E. Smith, and J. W. Burgess. Special thanks go to W. J. Gertsch for his assistance in the identification of spiders. C. E. Griswold, P. S. Jackson, and V. D. Roth are gratefully acknowledged for helping me locate spiders in the field. The assistance of the Southwestern Research Station of the American Museum of Natural History is gratefully acknowledged. Thanks go to R. B. Daniels for typing the manuscript. This work was supported in part by the North Carolina Division of Mental Health Services, Research Section and by N.S.F. grant number BMS 75-09915 to P. N. Witt.

REFERENCES

AKERMAN, C.
1932. On the spider *Miagrommopes* sp which constructs a single line snare. Ann. Natal Mus. **7:** 1-7.

BERLAND, L.
1913. Utilisation pour la capture des Mouches, des nids de l'Araignée mexicaine *Coenothele gregalis* E. Simon. Bull. Mus. hist. nat. **1913:** 432-433.

BILLAUDELLE, H.
1957. Zur Biologie der Mauerspinne *Dictyna civica* (H. Luc.) (Dictynidae, Araneida). Z. Angew. Entomol. **41:** 475-512.

BRISTOWE, W. S.
1941. The comity of spiders. Vol. II. London: Ray Society. 560 pp.
1958. The world of spiders. London: Collins. 304 pp.

BURGESS, J. W.
1975. The sheet web as a transducer, modifying vibration signals in social spider colonies of *Mallos gregalis*. Neurosci. Abstr.: 557.
1976. Social spiders. Sci. Amer. **234:** 100-106.

DIGUET, L.
1909a. Sur l'Araignée mosquero. C. R. Acad. Sci., Paris **148:** 735-736.
1909b. Le mosquero. Bull. Soc. Acclim. France **56:** 368-375.
1915. Nouvelles observations sur le mosquero ou nid d'Araignées sociales employé comme piège a mouches dans certaines localités du Mexique. Bull. Soc. Acclim. France **62:** 240-249.

GERTSCH, W. J.
1949. American spiders. Princeton: Van Nostrand. 285 pp.

GREENSTONE, M.
1978. Non-density-dependent predation and maintenance of a mixed diet in a field population of the wolf spider, *Pardosa ramulosa*. Symp. Zool. Soc. Lond. In press.

JACKSON, R. R.
1978. Comparative studies of *Dictyna* and *Mallos* (Araneae: Dictynidae): I. Social organization and web characteristics. Rev. Arachnol., in press.
1979a. Predatory behavior of the social spider *Mallos gregalis:* Is it cooperative? In prep.
1979b. Comparative studies of *Dictyna* and *Mallos* (Araneae: Dictynidae): II. The relationship between courtship, mating, aggression and cannibalism in species with differing types of social organization. In prep.

JACKSON, R. R. AND S. E. SMITH
1979. Aggregations of *Mallos* and *Dictyna* (Araneae, Dictynidae): Population characteristics. In prep.

KRAFFT, B.

1971. Contribution à la biologie et l'Ethologie d'*Agelena consociata* Denis (Araignée sociale du Gabon). Troisieme Partie. Etude expérimentale de certains phenomenes sociaux. Biol. Gabon. **7:** 3–56.

ROBINSON, M. H. AND J. OLAZARRI

1971. Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius): (Araneae: Araneidae). Smiths. Contrib. Zool. **65:** 1–36.

ROBINSON, M. H. AND B. ROBINSON

1970. Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. Zool. J. Linn. Soc. **49:** 345–357.

TURNBULL, A. L.

1973. Ecology of the true spiders (Araneomorphae). Ann. Rev. Entomol. **18:** 305–348.

WIEHLE, H.

1953. Spinnentiere oder Arachnoidea (Araneae) IX. Orthognatha-Cribellate-Haplogynae-Entelegynae (Pholcidae, Zodariidae, Oxyopidae, Mimetidae, Nesticidae). In: Die Tierwelt Deutschlands (F. Dahl, ed.) Jena: Fischer.

WILSON, E. O.

1975. Sociobiology. Cambridge, Massachusetts: Belknap. 697 pp.

WITT, P. N., M. B. SCARBORO, AND D. B. PEAKALL

1978. Comparative feeding data in three spider species of different sociality: *Araneus diadematus* Cl., *Mallos trivittatus* Banks and *Mallos gregalis* Simon. Symp. Zool. Soc. Lond. In press.

A SUPPLEMENT TO THE WORLD REVISION OF *ODONTOMACHUS* (HYMENOPTERA: FORMICIDAE)[1]

By William L. Brown, Jr.
Department of Entomology
Cornell University
Ithaca, New York 14853

In a recent publication (Brown, 1976, Studia Entomologica 19: 67–171) I reviewed the world fauna of the ponerine ant genus *Odontomachus*. While that contribution was in press, and since its appearance, some significant new *Odontomachus* material, and information about material, has come to my notice. It seems appropriate to supplement the revision now, while it is fresh, by offering the new information for incorporation.

The first and most important addition is the description of a new (twentieth) species in the *haematodus* group.

Odontomachus scalptus new species

Holotype, worker: TL 10.0, HL 2.66, HW (across vertex) 1.79, ML 1.40, scape L 2.52, eye L 0.42, WL 3.08 mm; CI 67, MI 53, SI 141.

Measurements for the 4 paratype workers range upward to the largest specimen, the antenna-less example from Oronoque R., Guyana: TL 11.0, HL 2.87, HW 2.05, ML 1.45, eye L 0.47, WL 3.40 mm; CI 71, MI 51.

Closely resembling continental samples of *O. bauri*, but differing sharply in sculpture of mesonotum and gaster:

(1) Mesonotum and metanotum longitudinally striate, the striae tending slightly to diverge cephalad on mesonotum. In outline from side view, the mesonotum is a little more strongly convex than in *bauri*.

(2) First 3 gastric terga finely but very distinctly striate-punctulate, the punctulae in single longitudinal rows (striae) separating the very fine ridges (costulae). The punctulae tend to be more

---

[1] A Report of Research from the Cornell University Agricultural Experiment Station, New York State College of Agriculture and Life Sciences. The research was supported by National Science Foundation Grant GB-31662.

Manuscript received by the editor February 27, 1978.

distinct anteriad on each segment, while the costulae predominate posteriad; this is especially true in the eastern (Surinam and Guyana) samples, in which the costulae become virtually obsolete on the anterior half of each tergum. The sculptured surface is opaque to sericeous-opaque, depending on magnification and lighting. The fourth gastric tergum, largely retracted, appears to be finely and superficially punctulate and subopaque. Underside of gaster shining, finely reticulate.

Other minor average differences from *O. bauri* are as follows: Costulae of the head and trunk a trifle more strongly shining (about 6–7 costulae per 0.1 mm square on each side of the vertexal midline). Striation of petiolar node finer than in most *bauri,* oblique. The node itself is a little less "dome-shaped", less convex in outline behind, and therefore more as in *O. haematodus,* but the metasternal process is low, and not produced into paired sharp teeth, as it is in *O. haematodus.*

Apical spine of petiole straight and only weakly back-tilted. Pilosity and pubescence copious and distributed much as in *O. bauri,* but on the average a trifle shorter and less dense; 4–8 standing hairs on pronotum; standing hairs of body about 0.2–0.45 mm long. Mesopleura obliquely striate, with a few coarse punctures in the mid-section; in the eastern samples, the mesopleural sculpture is effaced, smooth and shining in the mid-section, and the punctures here are smaller. Color black in Ecuadorean samples, with dark brown legs; antennal funiculi and tarsi yellowish-brown. Eastern samples dark reddish-brown to piceous (some possibly faded), funiculi and tarsi yellowish-brown. Palpi segmented 4,3.

In some specimens, the longitudinal striation of the metanotum even continues for a short distance onto the anterior part of the propodeum.

Queen and male unknown.

Holotype (Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts, USA) and one paratype worker from a rain forest litter berlesate taken 20 km south of Tena, Napo Prov., Ecuador, 11 July 1976, by S. and J. Peck, sample no. B-360. Two paratype workers from Surinam: [apparently near Paramaribo], "Sectie O," on forest floor, D. C. Geijskes, 15 July 1942. One paratype worker from southern Guyana: Oronoque River, 2°41′N, 25 July 1936, by N. A. Weber, no. 594. Paratypes in MCZ and U.S. National Museum of Natural History, Washington, D.C.

During work on the revision of *Odontomachus* (Brown, 1976, Stud. Ent. 19:67–171) I had in hand a single specimen of this new species, the paratype from Guyana listed above. The specimen lacked both antennae, and in a complex as difficult as the *haematodus* group, it was unwise to add yet another sibling species on the basis of a sample that might have been only a freak variant of *O. bauri.* Since the revision went to press, however, I have been able to study the 4 additional specimens from two widely separated hylaean localities, which convince me of the high probability that this phenon represents a distinct species.

In the key to neotropical *Odontomachus* species (Brown, 1976, *op. cit.,* p. 112), *O. scalptus* keys uneasily to couplet 3, first lug (*O. yucatecus*) — "uneasily" because some *O. scalptus* samples have striation fairly distinct, even if "mixed", over the anterior half of gastric tergum I. *O. scalptus* differs primarily from *O. yucatecus* in having the gastric dorsum distinctly and sharply, if finely, sculptured.

The only other species with both mesonotum and gastric dorsum longitudinally striate is the sympatric *O. caelatus,* but this species is larger, has the gastric dorsum regularly striate (not punctulate), with a few, large, blunt hairs, and virtually obsolete pubescence. The appressed and decumbent pubescence of *O. scalptus* is abundant and conspicuous by contrast.

Odontomachus turneri

Dr. R. W. Taylor informs me *in litt.* that his recent researches in northern Queensland indicate that the variant of *O. cephalotes* having a densely punctulate or striate gastric dorsum and numerous standing hairs on the pronotum is actually a separate and distinct species occurring in the area near the base of Cape York and westward to Arnhem Land and beyond, perhaps to the Kimberleys. He finds it only in savanna or savanna woodland areas, and I recall that a form answering this general description is common nesting in termite hills in northern Queensland. Taylor writes that he has been calling this form *O. turneri,* but that it might possibly have a prior name (*semicircularis* Mayr?). I have thought of this form as corresponding to Forel's var. *ajax,* but since it shows considerable geographical variation, the whole situation needs re-study in the light of the new material now gathered in the Australian National Insect Collection.

Odontomachus laticeps

In my discussion of this variable species in 1976 (p. 154 ff.), I found no South American records certainly attributable to it, but Dr. D. R. Smith has now called my attention to a small number of worker specimens in the U.S. National Museum from Bolivia that probably do belong to *O. laticeps.* These samples come from Covendo, Huachi and Cachuela Esperanza, all in Beni Province, and all were collected by W. M. Mann. These workers are brown in color, with legs usually lighter, and they all have the gastric dorsum predominantly finely but distinctly longitudinally striate and opaque; the bottoms of the striae are punctulate. The size is a little smaller than in Central American *laticeps* (HL 2.48, HW 1.67 mm in an average specimen from Huachi, Bolivia), but the cephalic index (67) is within the range of Central American *laticeps,* which have CI 66–73.

The main difference comes in the shape of the apical spine of the petiole: This is lower and thicker in side view in the Bolivian samples, but still sharply back-tilted: figure 14 (p. 156) in the 1976 rereview shows the slender spine of an average Central American specimen. The Bolivian population(s) could represent another sibling species of the *haematodus* group restricted to Bolivia (or even to the drainage of the Rio Beni), but the close relationship to *O. laticeps* is obvious, and I prefer to assign them to that species until we know more about the Bolivian *Odontomachus* in general. All previous records of *O. laticeps* from South America are based on *O. biumbonatus* or other species.

Odontomachus mormo

I described this giant species in the 1976 review (p. 161) from 3 specimens collected in transandean Ecuador. Now Stewart and Jarmila Peck have sent me more specimens, including a partial nest series with queen, from the Rio Palenque Research Station, 47 km SW of Santo Domingo de los Colorados, Pichincha Prov., Ecuador. The species remains known only from western Ecuador.

Odontomachus bradleyi

This species, also described in 1976 (p. 133) from Dept. Junin in central Peru, has now been rediscovered by the Pecks in eastern

Ecuador: 23 km NE of Baeza, Napo Prov., 4 March 1976, nest under log in pasture. This record is a long extension of range, and shows that the species is probably widely distributed along the eastern flank of the Andes in Amazonian-drainage valleys.

NEW OBSERVATIONS OF MATERNAL CARE EXHIBITED BY THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* HENTZ (ARANEIDA:OXYOPIDAE)[1]

BY JOHN B. RANDALL

Dept. of Entomology and Nematology
University of Florida
Gainesville, Florida 32611

INTRODUCTION

Maternal care of young is found in various families of spiders, most notably the lycosids (Whitcomb and Eason, 1964; Eason, 1964, 1969; Rovner, 1973). Whitcomb and Eason (1964) reported the duration of egg incubation in wolf spiders could be monitored easily in the egg sac because lycosids will mend egg sacs that have been opened for inspection.

An important facet of the maternal care by lycosid females is opening the egg sac to facilitate the emergence of young. The wolf spider rotates the egg sac with her legs and palps and cuts the seam of the egg sac with her chelicerae. Few wolf spider young have been observed to emerge from an egg sac without the aid of the female (Eason, 1964). Eason noted that female lycosids with young or with an egg sac from which spiderlings are due to emerge would "adopt" spiderlings of the same species from another egg sac. Unmated females with no egg sac were not as receptive to such spiderlings. Eason successfully exchanged egg sacs between females.

The Green Lynx Spider, *Peucetia viridans* Hentz, displays maternal care behavior (Whitcomb, *et al.,* 1966). The female Green Lynx, like the lycosids, aids the emerging young by opening the egg sac along a seam with her chelicerae. Whitcomb noted that, unlike the lycosids, spiderlings of *P. viridans* will emerge from the egg sac without maternal aid.

Descriptions of egg sac construction by *P. viridans* were reported by Whitcomb (1962) and Whitcomb, *et al.* (1966). The female usually constructs the first egg sac 21–28 days after mating. Egg sac

---

[1] Fla. Agricultural Experiment Station Journal Series No. *1036.*

Manuscript received by the editor March 8, 1978.

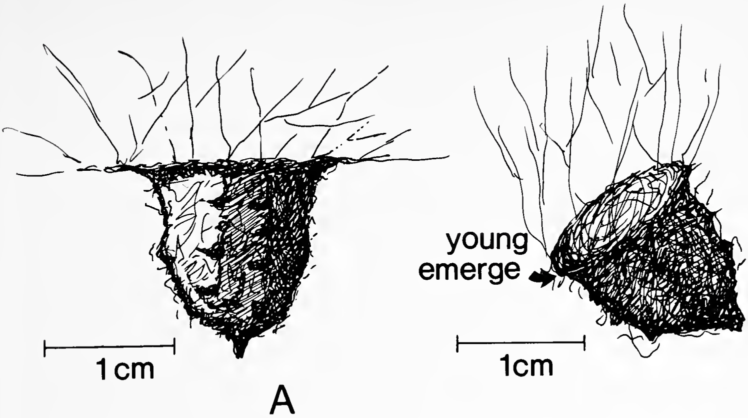


Figure 1. *Peucetia viridans*. A, newly formed egg sac. B, egg sac after opening and tilting by the female (arrow indicates lowest bowl/lid juncture).

construction is initiated by the spider spinning a silk disc under which a silk bowl with an opening in the bottom is formed. The egg sac is oriented in the upright position (Fig. 1A). The female forces eggs up into the bowl and seals the egg sac when oviposition is completed. The eggs hatch in 11–16 days depending on temperature and the spiderlings emerge from the egg sac 10–13 days after hatching.

METHODS

During early September 1974, 63 adult female *P. viridans* without egg sacs were collected. The spiders were maintained individually in the laboratory. The rearing containers were examined daily for the presence of egg sacs.

Egg sacs collected from the laboratory specimens were used to establish three distinct groups of egg sacs. The establishment of the experimental groups is described below.

GROUP I: Egg sacs without maternal care.

On 16 October 1974 10 female *P. viridans* constructed egg sacs. The egg sacs were removed in separate containers. Group I egg sacs went through development without an adult female ever being present.

GROUP II: Egg sacs with maternal care.

On 17 October 1974 seven females constructed egg sacs and on 19 October 1974 three more females constructed egg sacs. The Group II egg sacs were allowed to remain with the females until the emergence of young.

GROUP III: Egg sacs with "adopted" maternal care.

A 3rd group of 10 egg sacs was collected on 28 October 1974. These egg sacs were taken from the females who had made them. Each egg sac was then placed in a rearing container that housed one of the females that had been removed from the Group I egg sacs. The Group III egg sacs were now with females whose own young were due to emerge in approximately 12 days but the young of the Group III egg sacs were not due to emerge for approximately 24 days. Thus these females had adopted egg sacs that were 12 days behind the schedule of the female's own egg sacs.

Results and Discussion

The average duration of incubation and 1st stadia spent in the egg sac for the groups studied was: Group I — 25.25 days; Group II — 23.6 days and Group III — 22.6 days with ranges of 21–28, 22–29 and 20–26 days respectively; all falling within the time range as reported by Whitcomb, *et al.* (1966). Only two of the 30 egg sacs were found to contain dead 2nd instar spiderlings. I believe in handling those two egg sacs it was very possible that excess silk normally holding the egg sac in foliage held the lid to the bowl of the egg sac in such a way as to make emergence of young impossible.

The female Green Lynx Spider aids in emergence of young by tearing the egg sac shortly after the 1st deutova (1st instar — without tarsal claws, mouthparts or functional eyes) have molted. She inserts her chelicerae between the bowl and the lid and pulls the bowl away from the lid (Whitcomb, *et al.,* 1966). The females of groups II and III displayed the maternal care described above, and performed one previously unreported behavior — the adult females tilted the egg sacs at an angle from 40°–80° after opening the egg sac and prior to the 1st emergence of young. The egg sacs were tilted with the recently-made opening on the lowest side. The

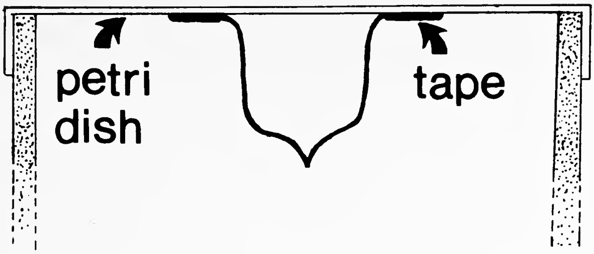


Figure 2. Technique used to prevent tilting of the egg sac.

Group II and Group III females tilted their egg sacs 6.4 and 6.1 days respectively, prior to the emergence of young; both groups with a range of 5–8 days. Due to the bowl shape, the egg sacs of Group I were tilted throughout development because of their position in plastic vials.

The young from all three groups emerged from the tilted egg sacs at the lowest bowl/lid juncture of the egg sac (Fig. 1B). Group I spiderlings opened the egg sac from within.

At this point in the investigation 15 more egg sacs were taken from the laboratory colony. Five egg sacs were taken from the females and taped to the underside of a petri dish lid, Fig. 2, thus making tilting of the egg sacs impossible. The remaining 10 egg sacs were allowed to remain with the females until after the females had opened and tilted the egg sacs. After opening and tilting had occurred five egg sacs were removed from the female and taped to a petri dish lid as described above. The remaining five egg sacs were taken from the females and artificially tilted with the opening made by the females at the highest point of the tilted egg sacs.

Young from all 10 untilted egg sacs emerged but not from the bowl/lid juncture as described for Groups I, II and III. Instead the young emerged in all directions from the bowl in an average 28.6 days compared to an average 24.6 days for the opened and tilted egg sacs of Groups II and III and the tilted egg sacs of Group I.

The young from the five egg sacs that had been artificially tilted with the opening at the highest point emerged from both the lowest bowl/lid juncture and from the opening made by the female.

CONCLUSION

Young *P. viridans* are able to emerge from their egg sacs without the aid of an adult female (Group I and untilted egg sacs). The adult female Green Lynx opens and tilts her egg sac approximately six days prior to the emergence of young. The opening and tilting of the egg sac is the primary maternal care comprising emergence aid. Other maternal care exhibited by *P. viridans* includes pre- and post-emergence protection.

Emergence of young from the lowest bowl/lid juncture in tilted egg sacs and all directions from the bottom of the bowl in non-tilted egg sacs would seem to indicate that gravity may play a role in the site of egg sac exit by young Green Lynx Spiders.

Emergence aid by an adult female made it possible for the young to emerge quicker than young where no emergence aid (tilting) was given. Tilting of the egg sac prior to emergence was in itself an aid but tilting of the egg sac was not a requirement for the young to emerge successfully. The adaptive significance of maternal care by the Green Lynx Spider is a higher percentage of young emerging from tilted egg sacs than from non-tilted. Although the number of young emerging was not documented, upon inspection of all the egg sacs cannibalism was in evidence in only the non-tilted egg sacs. Apparently the four extra days, on the average, spent in the non-tilted egg sacs resulted in cannibalism thereby reducing the percentage of young emerging from those egg sacs. No cannibalism was detected in the tilted egg sacs.

The females of Group III not only adopted another female's egg sac but opened and tilted their adopted egg sacs at the precise time they would have had they been their own eggs. These females would have opened and tilted their own egg sacs approximately 12 days earlier but waited for what is most logically a cue from within the egg sac. The cue was most likely the activity of the new 2nd instar spiderlings.

These findings are in contrast to those of Engelhardt (1964) who reported the maternal care exhibited by spiders of the genus *Trochosa* Koch (Lycosidae). He noted that like other lycosids *Trochosa* females must open the egg sac in order for the young to emerge successfully. The young are not able to hatch if the egg sac is opened too early. On the other hand, the egg sac must be opened no later than three days after the young have molted to the nymph

I stage. Unlike *P. viridans* the opening of the egg sac by adult female *Trochosa* is not triggered by a stimulus from the egg sac or the spiderlings in it. Engelhardt considers the opening of *Trochosa* egg sacs to be regulated by endogenous neurosecretory function, related to oviposition and influenced by temperature in the same manner as the development of the eggs and spiderlings in the egg sac.

ACKNOWLEDGEMENTS

I sincerely thank Dr. Willard Whitcomb for his generous guidance during this investigation. I also thank Dr. Jonathan Reiskind for his interest in my work and for reading and discussing the manuscript for this report.

REFERENCES

EASON, R.
1964. Maternal care as exhibited by wolf spiders (Lycosids). Ark. Acad. Sci. Proc. **18:** 13–19.
1969. Life history and behavior of *Pardosa lapidicina* Emerton (Araneae: Lycosidae). J. Kan. Entomol. Soc. **42**(3): 339–360.

ENGELHARDT, W.
1964. Die mitteleupropäischen Arten der Gattung *Trochosa* C. L. Koch, 1848 (Araneae, Lycopidae). Morphologie, Chemotaxonomie, Biologie, Autökologie. Z. Morph. Ökol. Tiere **54:** 219–392.

ROVNER, J. S.
1973. Maternal behavior in wolf spiders: The role of abdominal hairs. Sci. **182:** 1153–1155.

WHITCOMB, W. H.
1962. Egg sac construction and oviposition of the green lynx spider, *Peucetia viridans* (Oxyopidae). Southwestern Natur. **7**(3–4): 198–201.

WHITCOMB, W. H., AND R. EASON.
1964. A technique for determining the duration of egg incubation in wolf spiders. Turtox News **42**(12): 301–302.

WHITCOMB, W. H., M. HITE, AND R. EASON.
1966. Life history of the green lynx spider, *Peucetia viridans* (Araneida: Oxyopidae). J. Kan. Entomol. Soc. **39**(2): 259–267.

FIGHTING BEHAVIOR OF MALE *GOLOFA PORTERI* BEETLES (SCARABEIDAE: DYNASTINAE)*

By William G. Eberhard
Depto. de Biología
Universidad del Valle
Cali, Colombia, and
Smithsonian Tropical Research Institute
P. O. Box 2072
Balboa, Canal Zone

Large males of *Golofa porteri* possess several striking secondary sexual characteristics: the head has a long, curving horn with serrations along its edges; the prothorax has an even longer, thinner, nearly vertical horn which is smooth and covered on its anterior surface with a thick mat of golden hairs; and the front legs, especially the robust tibiae and tarsi, are monstrously elongate, with the last tarsomeres sporting thick growths of golden hair on their ventral surfaces.

Howden and Campbell (1974) observed two struggles between males in nature at apparent feeding sites on long thin stalks of a bamboo-like plant. Wille (1943) also noted *G. aegeon* (especially males) on sugar cane stalks. This study is a follow-up of these observations to determine the functions of the males' bizarre secondary sexual structures.

Methods

Males were captured near lights at night and kept individually in metal canisters where they were provided with pieces of ripe banana or plantain which they appeared to eat. Fights were staged in the evening on nearly vertical, 1.5–2.5 cm diameter stalks (mostly the central rachi of palm leaves from which I had stripped the leaflets). The first male was placed on the stalk facing down, and within 1–5 min. the second was added below him, facing up. Super-8 movies made of eight fighting sequences and associated behavior were analyzed frame by frame. Substantial enlightenment was also

---

**Manuscript received by the editor March 26, 1978.*

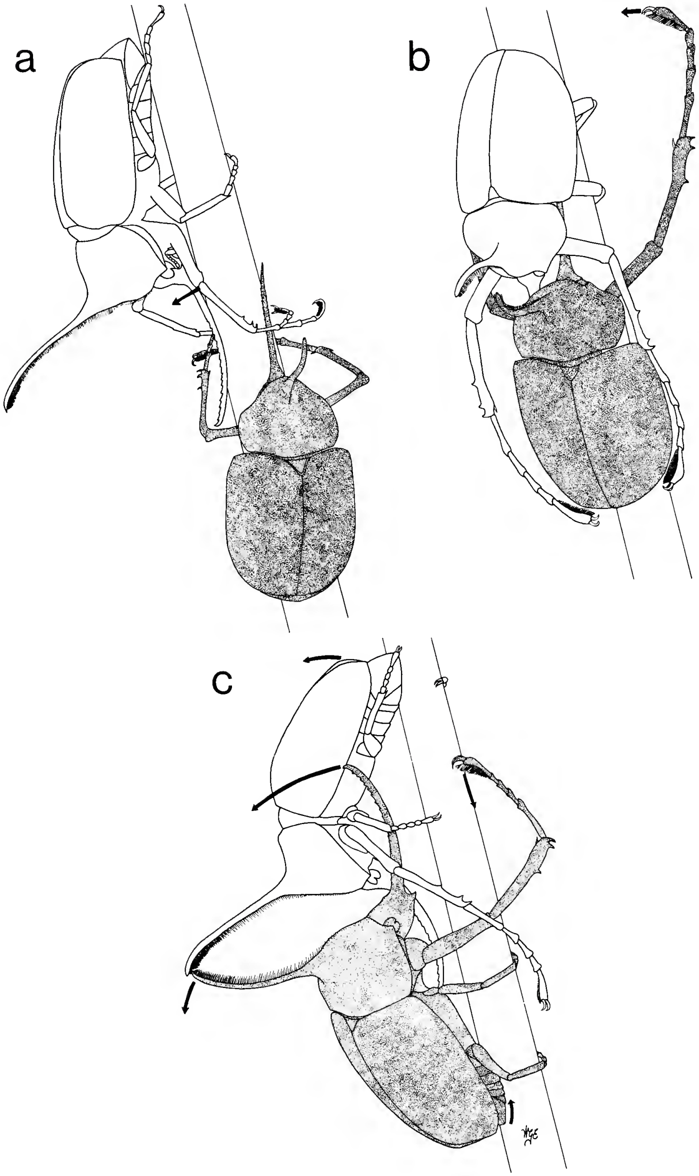
gained using the old technique, employed by Joseph (1928) in his study of *Chiasognathus grandti,* of watching partially senile males whose movements were slowed. Male *G. porteri* were extraordinarily pugnacious, and even attacked fingers poked at them (especially when the finger made contact with the base of the prothoracic horn). When in good condition, they fought readily.

RESULTS

A. Physical combat

Howden and Campbell (1974) described one fight they saw: "They grappled with their elongated forelegs, as each attempted to place the head horn under the opponent . . . suddenly the larger male successfully placed his head horn under his opponent and flipped him off the stalk." They were correct in attributing a lever-like use to the head horn, but the "grappling" with the forelegs turns out to be more complex and functionally interesting than suspected.

In outline, a beetle attacking a non-responsive opponent typically behaves in the following way. Before sensing the other, he uses his middle and hind legs to hold tightly to the stalk, leaving his front legs essentially inactive. Upon sensing the opponent's presence (in some cases apparently at long range, in others not until contact was made), he lowers his head horn so it is nearly but not quite parallel to the stalk. At the same time he spreads his front legs so as to nearly or completely encircle the stalk at about the level of his head (Fig. 1a). Particularly aggressive males assume this position with such a snap that the stalk quivers, and, as indicated in Fig. 1a, sometimes abruptly raise and lower the legs in an apparent threat. The male then attempts to insert his head horn under the opponent by raising his prothorax away from the stalk and lowering his head still more. Easing forward and/or pulling his opponent toward him with his front legs, he positions the end of the horn far back under the opponent's body. As he does so, he brings his long front legs along the opponent's sides (Fig. 1b). Finally he attempts to pry him loose with a double attack. The front legs are raked postero-ventrally, dislodging the opponent's middle and/or hind legs which grip the stalk, and an instant (about 1/30 sec.) later, the head is savagely flexed dorsally to lift him (Fig. 1c). The result of a successful attack is to break


a
b
c

the opponent's grip on the stalk and then pry him away from it, hold him briefly between the winner's head and prothoracic horn, and drop him. In some cases neither beetle was lifted completely free, but there was a clear winner, and the loser turned and walked away.

In most battles, of course, the chain of events was not this simple because each beetle resisted the other's attempts to dislodge him, and the result was often a confusing tangle of legs and horns. Periodic violent thrusting and lifting motions of the head horns occurred, sometimes accompanied by ripping motions of the front legs and sometimes not; of fifteen clear thrusts in filmed sequences, seven were immediately preceded by a ripping movement, five were probably preceded by ripping, two were not preceded by ripping, and one was unclear. Occasionally a beetle raised his front legs suddenly during the grappling between thrusts, and then held them in the circle position adopted at the start of encounters (Fig. 1a). This movement could conceiveably serve as a defense against encirclement by the opponent's front legs, and in this case the large lateral tibial spines might serve to catch his legs. The leg interchanges between beetles were so variable, however, that it was not possible to be certain of these functions.

Figure 1. Stages in a struggle between two male *G. porteri*, drawn from frames of movie film taken at 30 fps (arrows indicate movement by showing positions of legs, etc. in the next frame). a) The upper male has encircled the stalk with his front legs. In the next frame he made an apparent threat by abruptly raising his legs slightly, and then (in the following frame) lowering them again. b) Each beetle has inserted his lowered head horn under the opponent, and, while holding the stalk tightly with his middle and hind legs, is "embracing" the opponent with his front legs (note how the elongate legs just fit the length of the other beetle's body). c) The lower beetle has just executed the ripping motion with his front legs, dislodging his opponent's left middle and hind legs, and is about to (next frame) flex his head dorsally to pry the opponent away from the stalk. His head horn was not under the central part of the upper beetle's body but was somewhat to the right (as seen in the drawing), and the attack was not successful since the opponent managed to keep his right rear foot hooked to the stalk. (The upper beetle's left middle and left rear legs were out of the focal plane, and their positions are estimated in the drawing from shadows cast on the stalk and from other lifting sequences. The lower beetle's head horn was not distinguishable in the next frame, presumably because it was moving so fast, but was clear (the head flexion had finished) in the following frame; its movement (arrow) was estimated by halving the distance between its position prior to and after the flexion.)

B. Stridulation and substrate vibration

Physical combat was always associated with other behavior whose probable function was intimidation. As also noted by Howden and Campbell (1974), beetles produced soft "squeaking" or "chirping" sounds. These were made before, during, and after battles, and were the result of scraping a file running longitudinally on the dorsum of the tip of the abdomen back and forth against the tips of the elytra. The number of chirps varied from two (one downward and one upward stroke) to more than 20; chirps were made as fast as about 12 strokes/sec. Beetles being teased with a finger gave a single pair of chirps accompanying each thrust with the head horn.

Males also sometimes shook the entire stalk by vibrating the body rapidly from side to side (about 10 cycles/sec) while resting in one place. This behavior was usually performed by a winning beetle just after a battle, and was accompanied by simultaneous stridulation.

C. Climbing and flying behavior

The males' long front legs were not the encumbrance to walking along the stalk that might be expected. They were held bent ventrally so that the two tibiae touched each other, or nearly so, on the other side of the stalk, and were used in a manner similar to that of telephone linemen using belts as they climb poles. Beetles climbing upward moved each pair of legs simultaneously, the order being middle, hind, and, just slightly later, front. Descending beetles moved their legs in a similar manner, with the added variation that the strong spurs on the inner margins near the tips of the tibiae were apparently used as spikes to engage the stalk.

Beetles sometimes decamped after fights by climbing to the upper tip of the stalk and flying away. They flew strongly, and could hover more or less stationary for seconds at a time. They held their front legs folded with their tarsi projecting forward and upward, so that they reminded one, with these paired, hook-shaped structures, of a bat hanging by its hind legs.

DISCUSSION

There seems little doubt, from the combination of observations of fights in nature and in captivity, that the horns and elongate front legs of *G. porteri* males function in fights between conspecifics. This species is thus in accord with the tendency seen in other beetles for such male structures to function as weapons in intraspecific battles (Eberhard in press). It differs from the others investigated so far in that the legs and horns (at least the prothoracic horn) may have the additional function of intimidating opponents with prefight visual displays; the fights occur at least sometimes during the day in the open, and the jerking movements of the front legs may serve to focus attention on them.

The elongate front legs constitute the most unusual feature of this species, and it is possible to speculate on possible evolutionary sequences for their development. Head horns, functioning to pry up adversaries in what seems to be the usual beetle manner (see Eberhard in press) probably evolved first. The effective use of the head horn probably involved pushing ventrally with the front legs at the moment of dorsal flexion of the head to impart maximum dorsal thrust; it may have also involved clamping the opponent against a thoracic horn and lifting him away from the substrate. Two possible sequences leading to long legs occur to me. 1) Preliminary lengthening of the front legs might have been advantageous to permit the beetle to apply the downward thrust of the legs farther forward, thus giving greater mechanical advantage to the head's upward thrust since the lift would be exerted nearer the beetle's center of gravity. Both head horn and front legs might have then increased in parallel fashion since better purchase would increase the effectiveness of a longer horn as a pry. The next stage would begin when the front legs were long enough that they reached the opponent's middle legs and occasionally dislodged one accidentally as they pushed down during a thrust. Natural selection could then favor further elongation of the legs, perfection of the timing and form of the ripping movement, and concomitant loss of the bracing function during head thrusts until the present state was achieved. 2) Lengthening of the front legs might have begun as an adaptation to raise the opponent farther from the substrate after he had been clamped between the head and prothoracic horns. Raising him farther would be advantageous because he would be more likely to lose his contact with the substrate, and would thus be more likely to fall free when dropped. Selection of this sort may have occurred in other beetles like *Chiasognathus grandti,* which have moderately long front legs and which lift opponents in fights in the open (Joseph 1928). When these long legs also began to accidentally dislodge legs of opponents, they could have evolved as described above to the present state, again losing their original function in the process. A combination of sequences 1 and 2 could also have occurred.

SUMMARY

The horns and long front legs of male *Golofa porteri* function as effective weapons in intraspecific battles between males.

ACKNOWLEDGEMENTS

I am indebted to Sr. Jorge Garavito of Telecom, Colombia for providing me with a crucial batch of beetles, and I thank Drs. M. J. W. Eberhard and H. Howden for criticizing the manuscript. This work was supported financially by the Comité de Investigaciones, Universidad del Valle.

LITERATURE CITED

EBERHARD, W. G.
In press. The function of horns in the dynastine *Podischnus agenor* and other beetles. *In:* M. Blum and A. Blum (ed.) Sexual Selection and Reproductive Competition in Insects. Academic Press, New York.

HOWDEN, H., AND M. CAMPBELL
1974. Observations on some scarabaeoidea in the Colombian Sierra Nevada de Santa Marta. Coleop. Bull. **28**(3): 109–114.

JOSEPH, C.
1928. El *Chiasognathus Grandti* Steph. Rev. Universitaria (U. Católica) (Santiago, Chile). **13**(1): 529–535.

WILLE, J. E.
1943. Entomología Agrícola del Peru. Ministerio de Agricultura, Lima.

A REVIEW OF THE DISTRIBUTION AND BIOLOGY OF THE SMALL CARRION BEETLE *PRIONOCHAETA OPACA* OF NORTH AMERICA (COLEOPTERA; LEIODIDAE; CATOPINAE)*

By Stewart B. Peck
Department of Biology, Carleton University,
Ottawa Ontario K1S 5B6 Canada

With the continued interest shown by ecologists in studies of carrion insects it is now appropriate to present a summary of the known distribution and biology of *Prionochaeta opaca,* one of the most frequently encountered species of the Catopinae, the small carrion beetles. This paper is number 17 in a continuing series on the systematics, biology, and evolution of the catopine beetles of the Americas.

Prionochaeta opaca is the only North American member of the otherwise large Eurasian tribe Cholevini (*sensu* Jeannel, 1936; Szymczakowski, 1964). The genus *Prionochaeta* was erected by Horn (1880) to contain the North American species described as *Catops opacus* by Say (1825). Since then, three other species of *Prionochaeta* have been described from Asia: also in the *opaca* group is *P. sibirica* Reitter from southeastern Siberia; and in the *harmandi* group is *P. harmandi* Portevin from Japan, and *P. roubali* Hlisnikowski from Szechwan, China.

Diagnostic Description. From most other small beetles commonly occurring at carrion or other decomposing matter, the Catopinae can be distinguished by their antennae, having a five segmented club with segment 8 smaller than segments 7 and 9. *P. opaca* is easily separated from all other American catopines by the following combination of characters: It is the largest catopine in eastern North America (ranging from 4 to 5.5 mm in length in a normally reflexed condition). The pronotum and elytra have neither striae nor a coarsely granular surface, but are covered with abundant setae with prominent basal sockets. Males have expanded front tarsal segments but the first tarsal segment of the middle leg of males is not enlarged or swollen (a character of the tribe Catopini). The elytra appear to have a pale blue-grey pru-

---

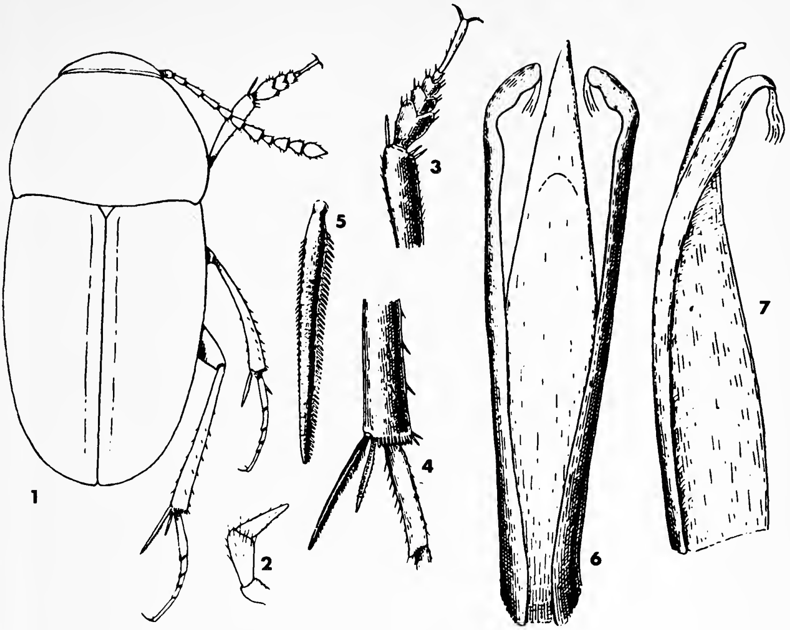
**Manuscript received by the editor December 22, 1977*

inose surface when viewed with a strong light at a low angle (caused by diffraction of light on the finely striate surface of small scales) but otherwise the species is of a reddish-to-dark brown color. The most distinctive character is the very long spur on the hind tibia. The spur is longer than the first metatarsal segment and has distinctly serrated fringes on two margins. Other descriptive and taxonomic details can be found in Horn (1880), Hatch (1930), Jeannel (1936), and Szymczakowski (1964), and in figures 1–7.

Variation. Except for differing body sizes, no morphological variation is evident in specimens from throughout the range of the species. On the male genitalia, differing degrees of sclerotization of the paramere tips causes them to twist to differing amounts when dried. The setae on the internal face and ventral margin of the paramere tips (not drawn in figs. 6, 7) do not vary.

Geographic distribution. The species has a wide distribution over most of the region covered by the deciduous broad-leaf forest of temperate eastern North America (fig. 8). Over this area the elevational range of the species is from coastal plain lowlands to upper elevations in both the North and South, from the White Mountains of New Hampshire to the Great Smokey and Black Mountains of North Carolina. The map is based upon specimens in the following collections (personal observation): Snow Museum (University of Kansas); Field Museum; California Academy of Sciences; Blatchley collection of Purdue University; Michigan State University; Cornell University; University of Alabama (Museum of Natural History); Museum of Comparative Zoology; U.S. National Museum of Natural History; Illinois Natural History Survey; Canadian National Collection (Ottawa); and Claude Chantal (Quebec City). These collections contain about 400 specimens. My own collection included 1200 specimens. Many of these are now deposited in the MCZ, Field Museum, and Canadian National Collection. Literature records of Blatchley (1910), Brimley (1938), Leonard (1926) and Kirk (1969) have also been used on the map because they are probably correct in reporting on this distinctive species. The imprecise record for "southwestern Arkansas" of Hatch (1933) and the doubtful record of Jeannel (1936) for Breckinridge, Colorado, have not been used.

The forest population near Marianna in Jackson county in northern Florida is probably disjunct and relictual. The Marianna lowlands is known as a floristic relict area (Mitchell, 1963) and a



Figures 1–7. Structures of *Prionochaeta opaca* Say. 1. Habitus of male. 2. Left maxillary palp. 3. Protibial tip and enlarged male protarsus. 4. Mesotibial tip and unexpanded male mesobasitarsomere. 5. Large internal spur of posterior tibia. 6. Dorsal view of aedeagus, setae on internal face of parameres omitted. 7. Lateral view of aedeagus. From Jeannel, 1936.

similar situation is suggested for many arthropods (personal data). The species probably does not occur in peninsular Florida because extensive trapping there by Dr. Alfred Newton and myself has failed to find it. Another disjunct population is in the forested Black Hills of western South Dakota. This population is separated from the rest of the species' range to the east by the grasslands of the Great Plains. The beetle undoubtedly reached the Black Hills when the intervening country was more forested (with at least more extensive streamside gallery forests) during a cooler and more moist glacial period. It has become isolated with the expansion of the prairies in the warmer and drier climate of the present interglacial.

Habitat preferences and feeding biology. Most specimen records show that the preferred habitat of the species is in moist and

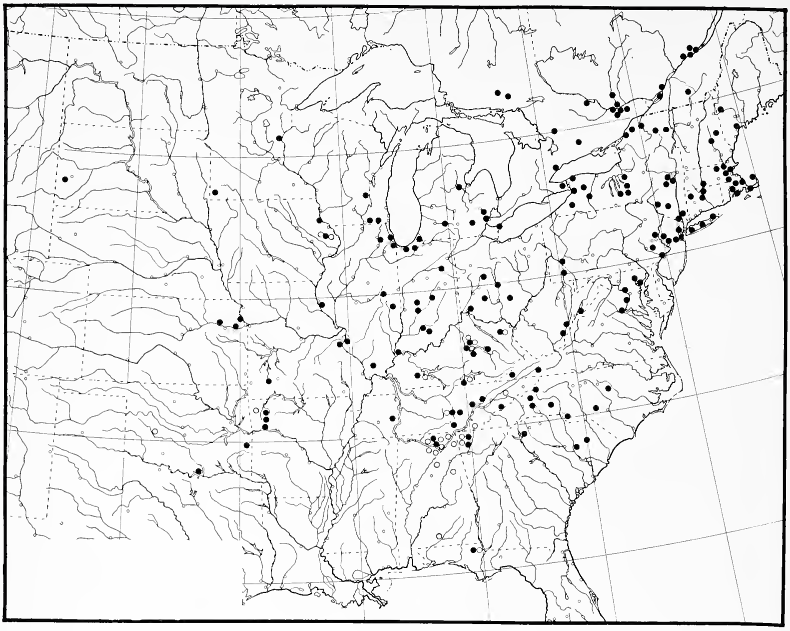


Figure 8. Map of distribution of *Prionochaeta opaca* Say. Closed dots, epigean records. Open dots, cave records. A dot may indicate more than one county locality record. Disjunct forest populations occur in the Black Hills of South Dakota, and in northern Florida. These and the prevalence of cave records in the south indicate adjustment of the species' range to post-glacial climatic conditions.

forested situations. Experimental field studies back this up. Walker (1957) took *P. opaca* during systematic trapping in Tennessee only in mesic and bottom forest, and not in drier ridge forest and old field habitats. Reed (1958) found the species in Tennessee on carrion in forests but never in pastures. Within a single mesic forest there is probably little microhabitat preference. Pirone (1974), in a trapping study in New York, collected about equal numbers of beetles in both forested slope and level sites. Shubeck (1969) found the species to be more common in a shrub community of arrowwood and greenbrier than in maple-leaved viburnum and black-haw shrub areas, in a New Jersey oak-hickory climax forest.

Wherever the beetle has been collected it seems to be a generalized scavenger on decaying organic matter, perhaps actually feeding on the fungi or bacteria associated with decomposition. It has been taken on carrion throughout its range and can be easily trapped with carrion baits (see above, and Newton and Peck, 1975). Shubeck (1969) noticed that *P. opaca* increased in numbers as other carrion beetles decreased, at a later stage of succession of the carrion fauna, when the carcass was drying out. In contrast, Johnson (1975) found the species in an Illinois forest to be most common in the decay stage of decomposition.

I have commonly taken *P. opaca* throughout its range in traps baited with human dung, and have found it on fox dung in Iowa. It occurs often in animal burrows and dens where it is probably a scavenger on nest or waste materials. So far, it have been recorded in literature and on specimen labels in woodchuck burrows in Indiana, New York, and Pennsylvania; in a fox hole in Massachusetts; in rabbit nests in Indiana; in a belted kingfisher nest in New York; and in a buzzard nest in Maryland. It has been taken by Berlese-Tulgren funnel processing of decaying plant debris from Florida to New York and Wisconsin, and in tree holes in Illinois and South Carolina. Decaying gill fungi and rotted puffballs have yielded it in Indiana, Kentucky, Maryland, Iowa, Illinois, and Massachusetts. The beetles prefer carrion over rotting fruits; Pirone (1974) took 462 specimens at fish carrion and only three at rotting melon in New York; Walker (1957) found this species only at fish carrion and not at rotting cantaloupe or cornmeal baits in Tennessee. Single occurrences in unusual places have been made under a kitchen sink in a Massachusetts house, in syrup traps in Virginia, by beating vegetation in Indiana, and from a tanglefoot screen and at blacklight in South Carolina.

P. opaca has been abundantly taken in the southern part of its range on carrion baits in cave habitats. I have observed the beetle in large and persistent populations feeding on moist bat guano and carcasses in Kentucky, and Florida, and Black (1971) reports the same in Oklahoma. The following specific cave sites are listed: *Alabama.* Blount Co., Catfish, Horseshoe-Crump, and Randolph caves. Calhoun Co., Robertson and Weaver caves. Conecuh Co., Turk Cave. DeKalb Co., Cherokee and Lois Killian caves. Jackson Co., House of Happiness and Rousseau caves. Madison Co., Burwell, Ellis, Hurricane, Matthews and Scott caves. Marshall Co., Eudy, Honeycomb, Merrill, Painted Bluff, and Terrill caves. Morgan Co., Lipscomb Cave. *Arkansas.* Washington Co., Corkscrew and Fincher caves. *Florida.* Jackson Co., Gerards and Miller (Florida Caverns State Park) caves. *Georgia.* Chatooga Co., Blowing Springs Cave. Walker Co., Bible Springs, Horseshoe, and Mountain Cove Farm caves (Holsinger and Peck, 1971). *Iowa.* Jackson Co., Barred (Maquoketa Caves State Park) and Hunters caves. *Kentucky.* Barren Co., Slick Rock Cave. Carter Co., Bat Cave (Carter Caves State Park). Clark Co., Jones Cave. Fayette Co., Phelps Cave. Russell Co., Rowe Cave. Scott Co., Slacks Cave. *Oklahoma.* Washita Co., Washita Bat Caves (Black, 1971). *Tennessee.* Bradley Co., Quarry Cave east of Cleveland. Cannon Co., Connell Creek, Davenport, and Highway Spring caves. Hamblen Co., Three Springs (Butry or Delap) Cave, 400 to 800 feet inside.

Seasonal activity. Data on specimen labels show the species to be active from March through November, in both northern and southern locations, with most specimens being taken from May to September. Generally, the more southerly populations are active earlier and later in the year. A few studies have experimentally followed the changes in abundances of the species throughout the year. Pirone (1974) found the species to be the most common catopid on carrion in southern New York; the beetles occurred from mid April through to November, and most were taken in August. Shubeck (1969), in a three year study in New Jersey, found the species to have differing abundances through the summer but to be most common in early-middle summer. In a repeat study in the same forest (Shubeck, Downie, Wenzel, and Peck, 1977) the species was again found from April to November, with a midsummer peak in abundance. In Tennessee, Reed (1958) collected the beetle on dog carcasses from mid June to late August. In another Tennessee study, Walker (1957) took *P. opaca* in midsummer, but did not trap at other times. In a carrion study in an Illinois forest, Johnson (1975) found the beetle to appear in April and to be present through November, being most abundant in September. Larvae appeared at the end of the decay stage and were mostly associated with the dry stage; they occurred in May, were most common in July, and last appeared in September.

During one of his trapping programs in a New Jersey forest, Shubeck (1971) found all catopids (which he called leptodirids) including *P. opaca,* to be diurnally active, in June and August, and to have no nocturnal activity.

A large number of cave populations are known. It could be expected that the beetles might be reproductively active in caves throughout much (if not all) of the year, because of the decreased seasonal variation of climatic factors in cave environments. However, collections or observations are not adequate enough to test this suggestion.

Reproduction. Larvae for the species have been long known, and are illustrated in Boving and Craighead (1931). Although it should not be difficult to keep and rear the beetles (methods in Peck, 1973, 1975) I know of no data on eggs, egglaying, or larval stages and their biology, other than Johnson's (1975) observation that larvae are most commonly associated with the dry stage of decomposition.

Evolution and Biogeography. The distribution of *Prionochaeta* and of other members of the Cholevini suggests that they originated in the Old World. Probably only one species of *Prionochaeta* migrated into the New World across a Bering land bridge in the Tertiary (see Hopkins, 1967, for a discussion of the Tertiary Bering Bridge). Although the genus must then have lived in western North America, it became extinct there (probably by the Pleistocene), and survived only in eastern North America. The resulting generic distribution in eastern North America and in eastern Asia is a not uncommon type of disjunct pattern (Darlington, 1957). It is believed here that the abundance of cave populations in the southern part of the species range is a reflection of distributional adjustments in the present post-glacial. Since the beetles apparently require a cool and moist temperate habitat, as climatic conditions have warmed, the beetles have become less able to survive in the now less-temperate southern forests where they lived during the Wisconsinan glacial. Caves, with their seasonally more uniform, cool and moist conditions, have thus become Recent southerly refugia for this beetle (although some southern forest populations yet remain) as they have for several other insects (Peck and Russell, 1976).

ACKNOWLEDGEMENTS

Henry Dybas, Hugh B. Leech, Vern Pechuman, John Lawrence, Herbert Boschung, John Kingsolver, Milton W. Sanderson, Roland L. Fischer, and J. M. Campbell allowed study of the collections under their care.

Alfred F. Newton, Walter Suter, and Quentin D. Wheeler generously contributed material to my collection. The many people, too numerous to mention individually, that have helped me with field work are thanked. Field work support has been provided by the U.S. National Science Foundation through the Evolutionary Biology Committee of Harvard University and by operating grants from the Canadian National Research Council. Dr. Newton has reviewed the manuscript.

LITERATURE CITED

BLACK, JEFFREY H.
1971. The cave life of Oklahoma, a preliminary study (excluding Chiroptera). Oklahoma Underground, J. Cent. Oklahoma Grotto, National Speleological Society, Oklahoma City. **4**(1 & 2): 2–53.

BLATCHLEY, W. S.
1910. An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana. Ind. Dept. Geol. and Nat. Res., Bull. 1, 1386 pp. Nature Publ. Co., Indianapolis.

BOVING, A. C. AND F. C. CRAIGHEAD.
1933. An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana, XI. 351 pp. 1973 reprint edition. Brooklyn Entomol. Soc.

BRIMLEY, C. S.
1938. Insects of North Carolina. Div. Entomol., North Carolina Dept. Agric., Raleigh. 560 pp.

DARLINGTON, P. J.
1957. Zoogeography: the geographical distribution of animals. John Wiley & Sons, New York. 675 pp.

HATCH, M. H.
1933. Studies on the Leptodiridae (Catopidae) with descriptions of new species. Jr. New York Ent. Soc. **41:** 187–239.

HOLSINGER, J. R. AND S. B. PECK
1971. The Invertebrate Cave Fauna of Georgia. Natl. Speleol. Soc. Bull. **33:** 23–44.

HOPKINS, D. M.
1967. The Cenozoic history of Beringia — A Synthesis. pp. 451–484, *in* Hopkins, D. M. (ed.), the Bering Land Bridge. Stanford Univ. Press, Stanford, California. 495 pp.

HORN, G. H.
1880. Synopsis of the Silphidae of the United States. Trans. Amer. Entomol. Soc., **8:** 219–322.

JEANNEL, R.
1936. Monographie des Catopidae. Mem. Mus. Nat. Hist. Natu., Paris, nouv. ser., **1,** 433 pp.

JOHNSON, MICHAEL D.
1975. Seasonal and microseral variation in the insect populations on carrion. Amer. Midl. Nat., **93:** 79–90.

KIRK, VERNON M.
1969. A list of beetles of South Carolina, part 1, northern coastal plain. South Carolina Agric. Exp. Stat., Clemson Univ., Tech. Bull. 1033.

LEONARD, M. D.
1926. A list of the insects of New York, with a list of spiders and certain other allied groups. Cornell Univ. Agric. Exp. Sta. Mem. 101.

MITCHELL, RICHARD S.
1963. Phytogeography and floristic survey of a relic area in the Marianna lowlands, Florida. Amer. Midl. Natur., **69:** 328–366.

NEWTON, A. AND S. B. PECK
1975. Baited pitfall traps for beetles. Coleop. Bull. **29:** 45–46.

PECK, S. B.
1970. The terrestrial arthropod fauna of Florida caves. Florida Entomol. **53:** 203–207.
1973. A systematic revision and the evolutionary biology of the *Ptomaphagus* (*Adelops*) beetles of North America (Coleoptera, Leiodidae; Catopinae), with emphasis on cave-inhabiting species. Bull. Mus. Comp. Zool., Harvard, **145**(2): 29–162.
1975. The life cycle of a Kentucky cave beetle, *Ptomaphagus hirtus* (Coleoptera, Leiodidae, Catopinae). Int. J. Speleology, **7:** 7–18.

PECK, S. B. AND D. R. RUSSELL
1976. Life history of the fungus gnat *Macrocera nobilis* in American caves (Diptera; Mycetophilidae). Can. Ent., **108:** 1235–1241.

PIRONE, D. J.
1974. Ecology of necrophilous and carpophilous Coleoptera in a southern New York woodland (phenology, aspection, trophic, and habitat preferences). 769 pp. Ph.D. dissertation, Fordham University. Xerox University Microfilms, 74-25078, Ann Arbor, Mich.

REED, H. B., JR.
1958. A study of dog carcass communities in Tennessee, with special reference to the insects. Amer. Midl. Natur., **59:** 213–245.

SAY, T.
1825. Descriptions of new species of coleopterous insects inhabiting the United States. J. Acad. Nat. Sci. Philadelphia, **5:** 160–202.

SHUBECK, PAUL P.
1969. Ecological studies of carrion beetles in Hutcheson Memorial Forest. J. New York Ent. Soc., **77:** 138–151.
1971. Diel periodicities of certain carrion beetles (Coleoptera:Silphidae). Coleopterists Bull., **25:** 41–46.

SHUBECK, PAUL P., N. M. DOWNIE, R. L. WENZEL, AND S. B. PECK.
1977. Species composition and phenology of carrion beetles in a New Jersey mixed-oak forest. Hutcheson Mem. For. Bull., in press.

SZYMCZAKOWSKI, W.
1964. Analyse systematique et zoogeographique des Catopidae (Coleoptera) de la region orientale. Acta Zool. Cracoviensia, **9**(2): 55–289.

WALKER, THOMAS J., JR.
1957. Ecological studies of the arthropods associated with certain decaying materials in four habitats. Ecology, **38:** 262–276.

THE GENERA OF EASTERN NORTH AMERICAN CHLOROPERLIDAE (PLECOPTERA): KEY TO LARVAL STAGES*

BY SANDY B. FIANCE
Department of Entomology
Cornell University
Ithaca, New York 14853

Considerable changes in the systematics of North American chloroperlid stoneflies have resulted from the elevation of subgenera created by Ricker (1943) to generic status by Illies (1966) and Zwick (1973). Most significant are the new combination *Rasvena terna,* and the division of *Alloperla* (s. l.) into five genera, only three of which occur in the region under study. Baumann (1974) separated the closely related species *Alloperla imbecilla* and *A. atlanticum.* Harper and Roy (1975) described the male of *Utaperla gaspesiana,* the first member of the Paraperlinae known from the Northeast, although Ricker (1952) found larvae from Tennessee that were referable to this subfamily. Hitchcock (1974) has summarized the status of members of the family found in Northeastern North America prior to 1971, and has provided species level keys for adults, but has retained the generic classification of Frison (1942).

At present, the family Chloroperlidae is represented in Eastern North America by 24 species in two subfamilies and six genera (Table 1). Larval stages are known only from four of these 24 species. This paper provides keys to genera of larvae needed because of nomenclatural changes and description of new species.

The larval stages of *Suwallia marginata* remain unknown. I have examined specimens of the Western North American species *Suwallia pallidula.* These may be separated from *Sweltsa* by the relatively fewer setae of the fore and hind femora, and on the eighth tergite, as well as the fewer long setae present on the apical corona of subterminal cercal segments.

---

*Manuscript received by the editor April 21, 1978.

Separation of larvae to the specific level appears to be quite difficult, but may become possible by employing relative differences in the distribution of setae on the lateral surfaces of the head, dorsum of the legs, pronotum, eighth tergite, and mouthparts.

Table 1. Chloroperlidae of Eastern North America

PARAPERLINAE
  Utaperla gaspesiana
CHLOROPERLINAE
  Alloperla
    atlanticum
    banksi
    caudata
    chloris
    concolor
    idei
    imbecilla
    quadrata
    leonarda
    neglecta
    usa
    voinae
    vostocki
  Hastaperla
    brevis
    orpha
  Suwallia
    marginata
  Sweltsa
    lateralis
    mediana
    nainina
    naica
    onkos
    urticae
  Rasvena
    terna

A KEY TO THE LARVAE OF EASTERN NORTH AMERICAN CHLOROPERLIDAE

1. Extensor surface of hind leg lacking a well developed fringe of fine, long setae (Fig. 1F); basal cercal segments having many long setae in apical corona, visible in lateral view (Fig. 1C) . . . . *Utaperla gaspesiana*

–. Hind tibia and often femur with a well developed fringe of long, fine setae on extensor surface (Fig. 2F); basal segments of cerci having few long setae in apical corona visible in lateral view (Fig. 2–5C) 2

2. Cerci with numerous long setae between apical coronas on distal segments forming a feather-like surface visible in lateral view (Fig. 2C); pronotum having few or no setae on front and hind margins, setae present only at corners (Fig. 2B); eighth tergite lacking setae at mesal posterior margin (Fig. 2D); integument yellow-gold . . . . *Alloperla* (s.s.)

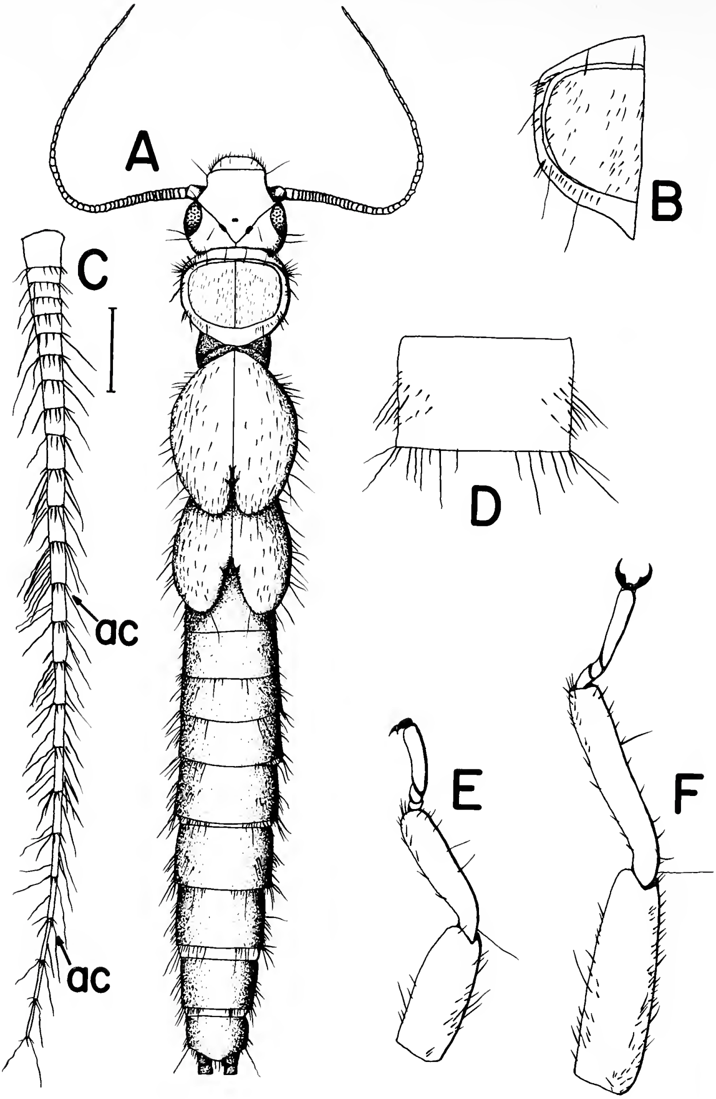


Figure 1. *Utaperla gaspesiana.* Mature larva, A. Habitus, B. Pronotum, C. Cercus, lateral view, D. Eighth tergite, E. Right foreleg, F. Right hindleg. New Hampshire, Grafton Co., W. Thornton, Pemigewasset River, 14 May, 1976, S. B. Fiance. (Scale: vertical bar = A – 1 mm, B-F – .5 mm; ac = apical corona.)

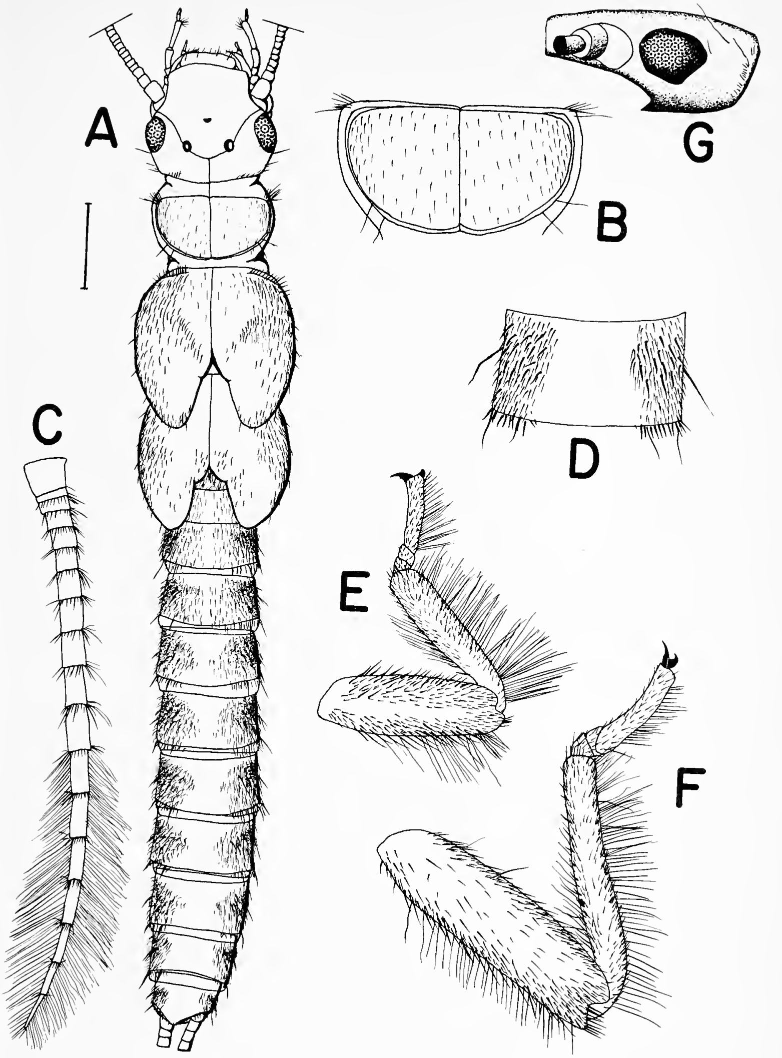


Figure 2. *Alloperla concolor.* Mature larva, A. Habitus, B. Pronotum, C. Cercus, lateral view, D. Eighth tergite, E. Right foreleg, F. Right hindleg, G. Left lateral view of head. New Hampshire, Grafton Co., W. Thornton, Hubbard Brook, 26 May, 1975, S. B. Fiance. (Scale: vertical bar = A – 1 mm, B-G – .5 mm.)

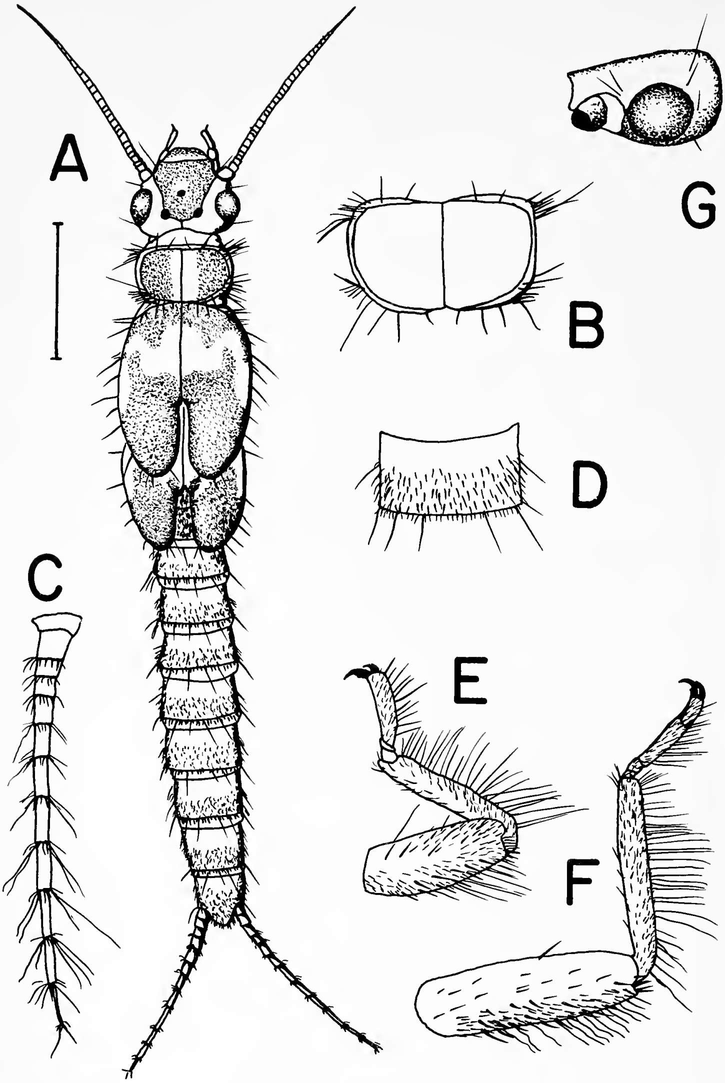


Figure 3. *Hastaperla brevis.* Mature larva, A. Habitus, B. Pronotum, C. Cercus, lateral view, D. Eighth tergite, E. Right foreleg, F. Right hindleg, G. Left lateral view of head. New Hampshire, Grafton Co., W. Thornton, Hubbard Brook, 5 June, 1975, S. B. Fiance.

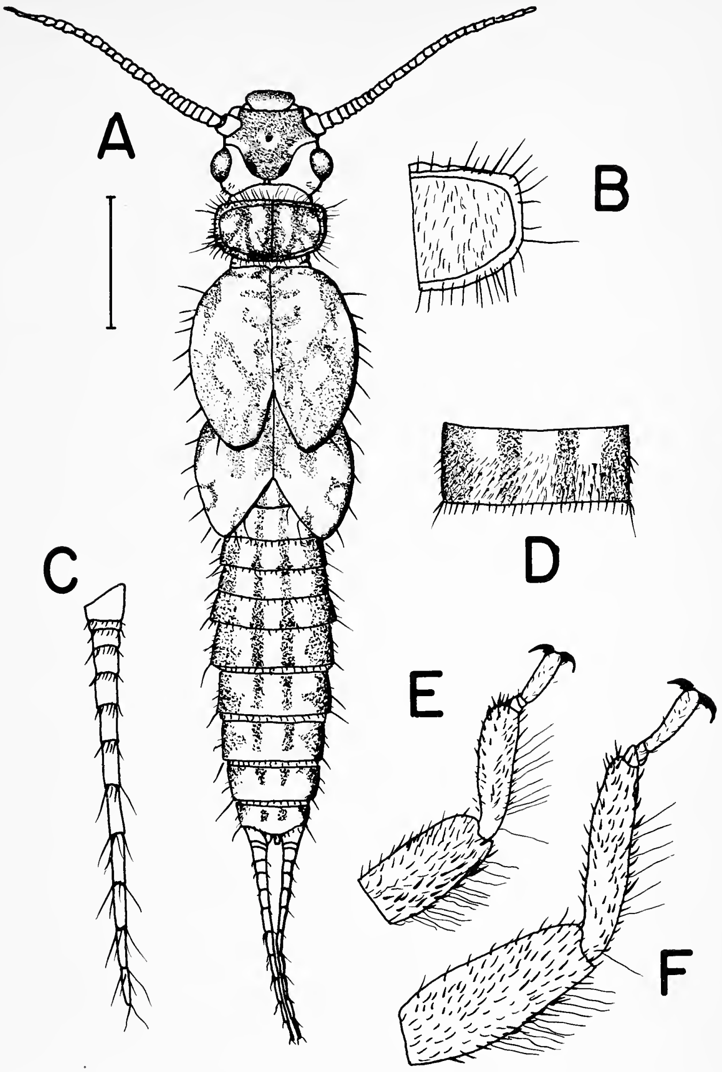


Figure 4. *Rasvena terna.* Mature larva, A. Habitus, B. Pronotum, C. Cercus, lateral view, D. Eighth tergite, E. Right foreleg, F. Right hindleg. New Hampshire, Grafton Co., W. Thornton, Pemigewasset River, 28 May, 1975, S. B. Fiance.

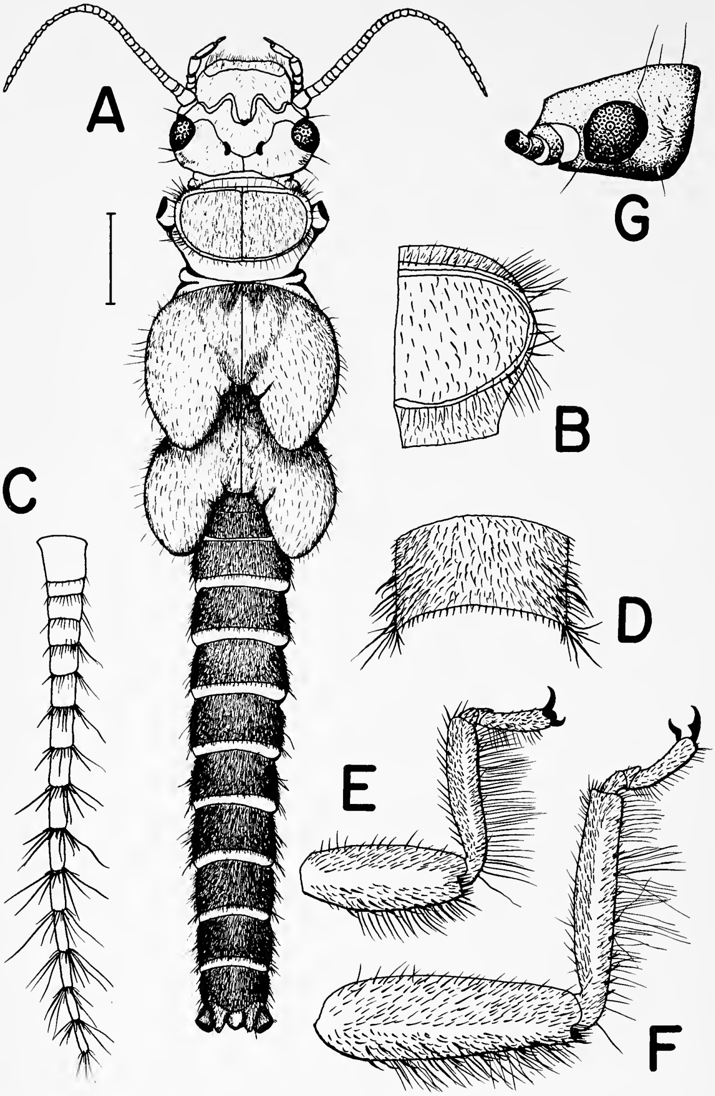


Figure 5. *Sweltsa onkos.* Mature larva, A. Habitus, B. Pronotum, C. Cercus, lateral view, D. Eighth tergite, E. Right foreleg, F. Right hindleg, G. Left lateral view of head. New Hampshire, Grafton Co., W. Thornton, Bear Brook, 1 June, 1974, S. B. Fiance.

–. Cerci entirely lacking or with scattered long setae between apical coronas (Fig. 3–5C); pronotum with setae on posterior margin and usually on anterior margin as well (Fig. 3–5B); setae present on entire posterior margin of eighth tergite (Fig. 3–5D); integument gold-brown 3

3. Inner margin of hind wing pads parallel to body axis (Fig. 3A); less than 6 short, coarse setae between compound eye and hind margin of head (Fig. 3G); abdominal tergites lightly setose; pronotum having only sparse, fine setae on dorsal surface .... *Hastaperla*

–. Inner margin of hind wing pads angled away from body axis (Fig. 4A); greater than 6 short, coarse setae between eye and hind margin of head (Fig. 5G); abdominal tergites heavily setose; pronotum with coarse, closely appressed setae on dorsal surface (Fig. 4–5B) 4

4. Dorsum of abdomen unicolorous except when adult coloration shows through; eighth abdominal tergite with setae absent from a proximal band at most 1/5 the length of the tergite (Fig. 5D) .... *Sweltsa, Suwallia*

–. Dorsum of abdomen with longitudinal dark stripes in mature larvae; setae absent from a band comprising the proximal 1/4 to 1/3 of the eighth tergite (Fig. 4D) .... *Rasvena terna*

ACKNOWLEDGEMENTS

The author would like to thank Dr. W. L. Brown, Jr., Cornell Univ., for his critical reading of the manuscript. The Grace Griswold Fund has generously provided funding for publication costs.

LITERATURE CITED

BAUMANN, R. W.

1974. What is *Alloperla imbecilla* (Say)? Designation of a neotype, and a new *Alloperla* from Eastern North America (Plecoptera: Chloroperlidae). Proc. Biol. Soc. Washington **87:** 257–264.

FRISON, T. H.

1942. Studies of North American Plecoptera, with special reference to the fauna of Illinois. Bull. Illinois Nat. Hist. Surv., Urbana **22:** 235–355.

HARPER, P. P. AND D. ROY

1975. *Utaperla gaspesiana* sp. nov., le premier Plécoptère Paraperlinaé de l'est Canadien. Can. J. Zool. **53:** 1185–1187.

HITCHCOCK, S. W.
1974. Guide to the insects of Connecticut. Part VII. The Plecoptera or stoneflies of Connecticut. St. Geol. Nat. Hist. Surv. Conn., Bull. **107:** 1-262.

ILLIES, J.
1966. Katalog der rezenten Plecoptera. Das Tierreich, Berlin **82:** I-XXX; 1-632.

RICKER, W. E.
1943. Stoneflies of Southwestern British Columbia. Indiana Univ. Publ., Sci. Ser., Bloomington **18:** 1-200.

ZWICK, P.
1973. Insecta: Plecoptera. Phylogenetisches System und Katalog. Das Tierreich, Berlin **94:** I-XXXII; 1-465.

PSYCHE

INDEX TO VOLUME 84, 1977

INDEX TO AUTHORS

INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

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 Ave., 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.