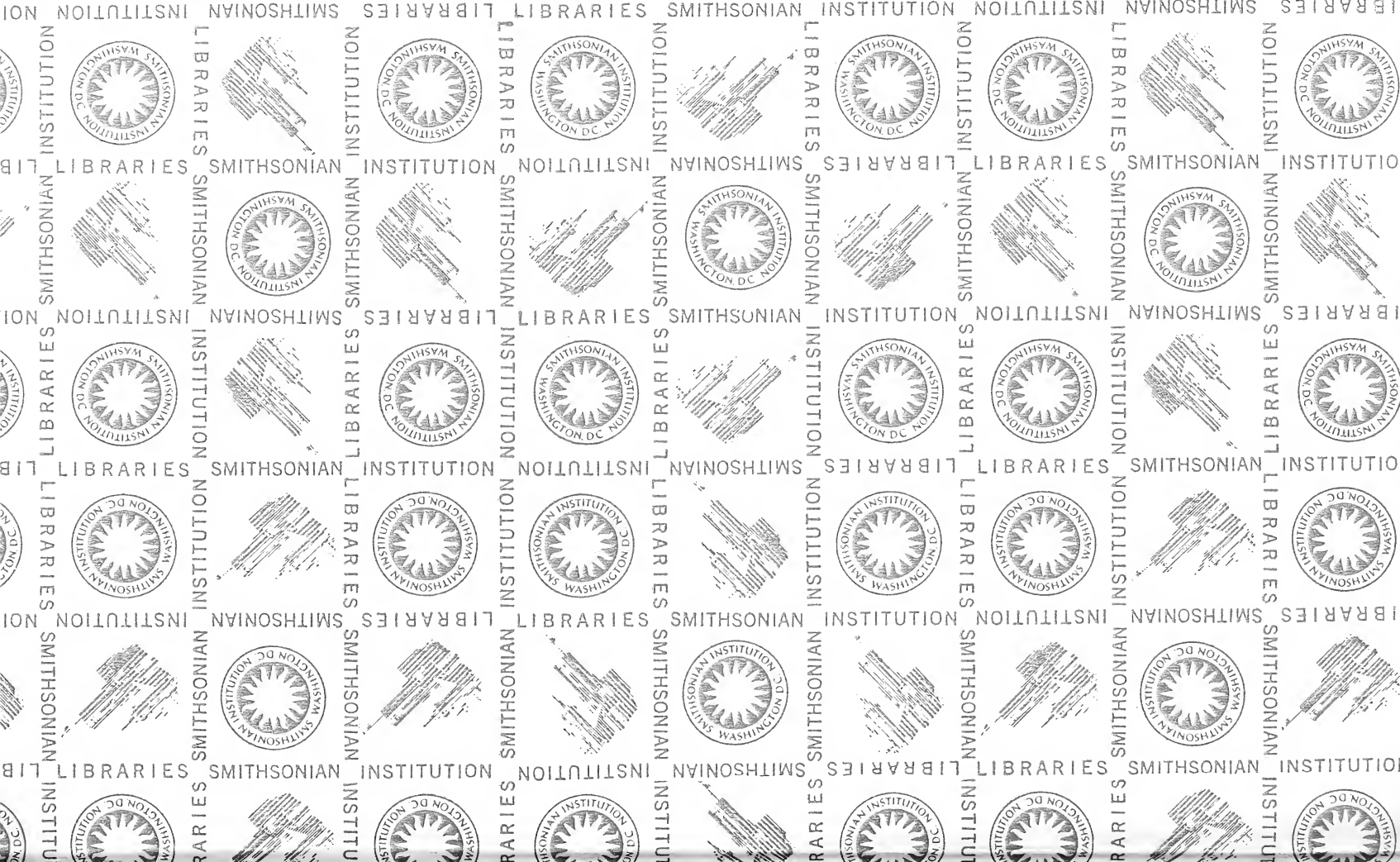
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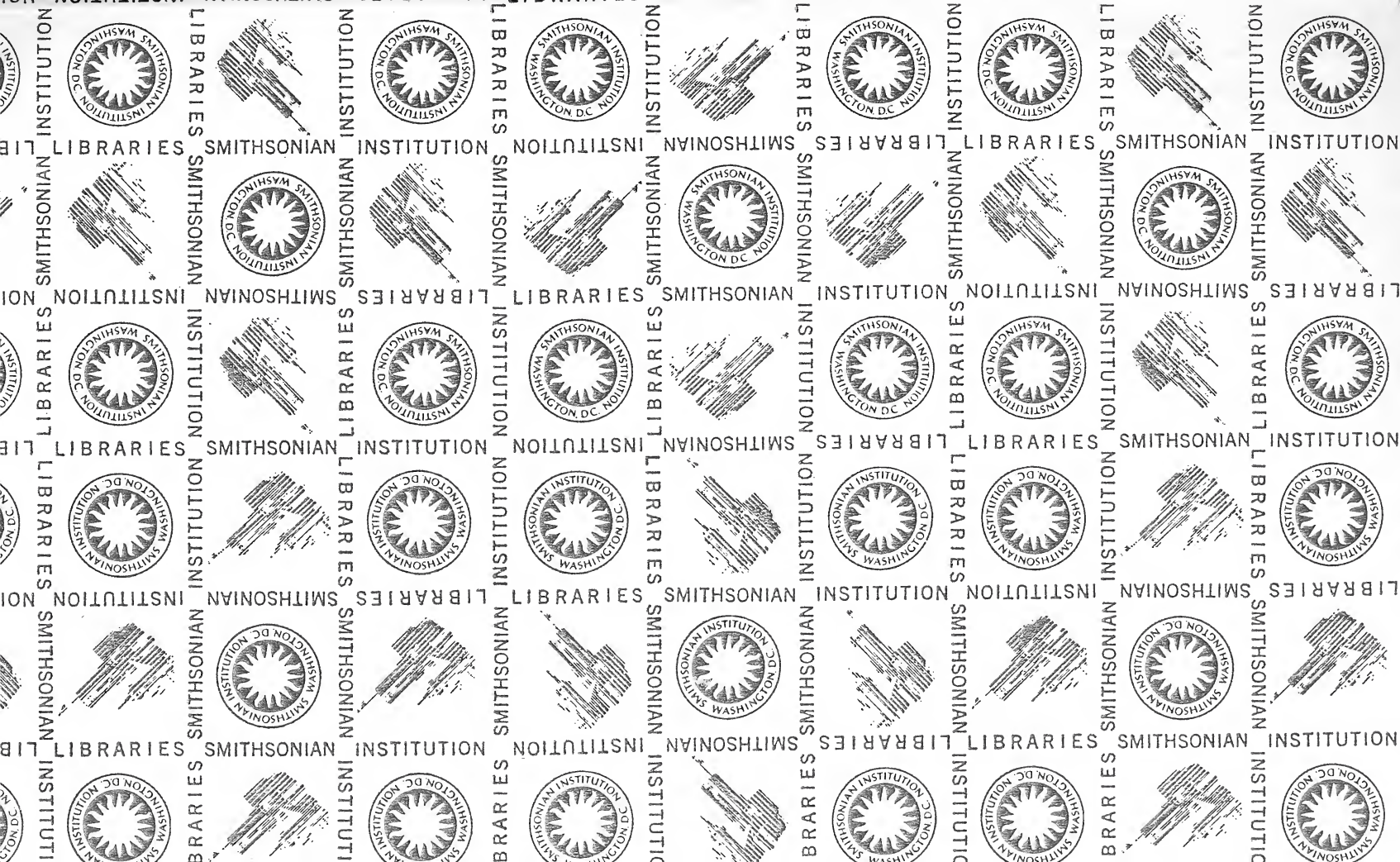
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Devoted to Entomology in General

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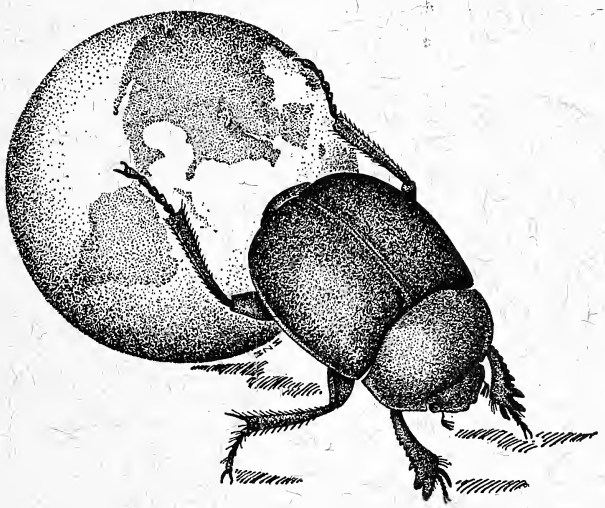

Devoted to Entomology in General

The New York Entomological Society
Incorporating The Brooklyn Entomological Society
Incorporated May 21, 1968

The New York Entomological Society
Organized June 29, 1892—Incorporated February 25, 1893
Reincorporated February 17, 1943

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Founded in 1872—Incorporated in 1885
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Journal of the New York Entomological Society

VOLUME LXXX JULY 13, 1972 No. 1

CONTENTS

Parthenogenic Reproduction in the Silverfish *Nicoletia meinerti* (Thysanura)

Veronica Dougherty Picchi
Department of Entomology, the American Museum of Natural History
New York, New York 10024

Received for Publication October 6, 1971

Abstract: Two successive generations of *Nicoletia meinerti* Silvestri raised in individual isolation demonstrated that this species could reproduce parthenogenetically. The eggs are described and illustrated and several biological observations are recorded.

Nicoletia meinerti Silvestri is widely distributed in greenhouses of Europe, northern South America, western Africa and Hawaii. Because of the scarcity of males (Wygodzinsky, verbal communication) it is believed that it reproduces parthenogenetically.

To demonstrate parthenogenesis in *N. meinerti* I isolated 26 female adults from a terrarium population which had originated with six female specimens from Pará, Brazil. The adults were placed in glass-covered rearing dishes lined on the bottoms with a mixture of crushed bone carbon and Plaster of Paris. This facilitated locating the pale gray *Nicoletia* eggs and the newly hatched, translucent white offspring. Humidity was the most important factor in rearing these animals. They were watered and fed lettuce two or three times a week and kept at a room temperature of 65°–75° F. in an area of light shade. Every other week methyl p-hydroxy benzoate ("Nipagin") was added to the water as a fungicide.

Each of the 26 females laid one or two eggs per month. Fifty-five eggs were obtained of which 74 per cent hatched in 46 to 59 days. When they were about three days old the young were placed in individual containers. These young, all females, were the first laboratory isolated generation. They matured to egg-laying age in an average of 137 days and all laid eggs. The eggs of two individuals did not hatch. Sixty per cent of the first laboratory generation eggs hatched, in an average of 44 days and were the first parthenogenetic generation. Isolated members of the second laboratory generation, again all females, also laid viable parthenogenetic eggs which hatched. Throughout the entire observa-

Acknowledgments: The Stereoscan Electron Microscope photographs in this paper were provided by Drs. Vincent Pallidino and John Duffy, and taken by Mr. Fred Miller of the Meadowbrook Hospital. I would like to thank Dr. Lee H. Herman, Jr. for his help and advice in obtaining these photographs.

I would like to thank Dr. Pedro Wygodzinsky for his help, encouragement, and patience through the production of this little paper.

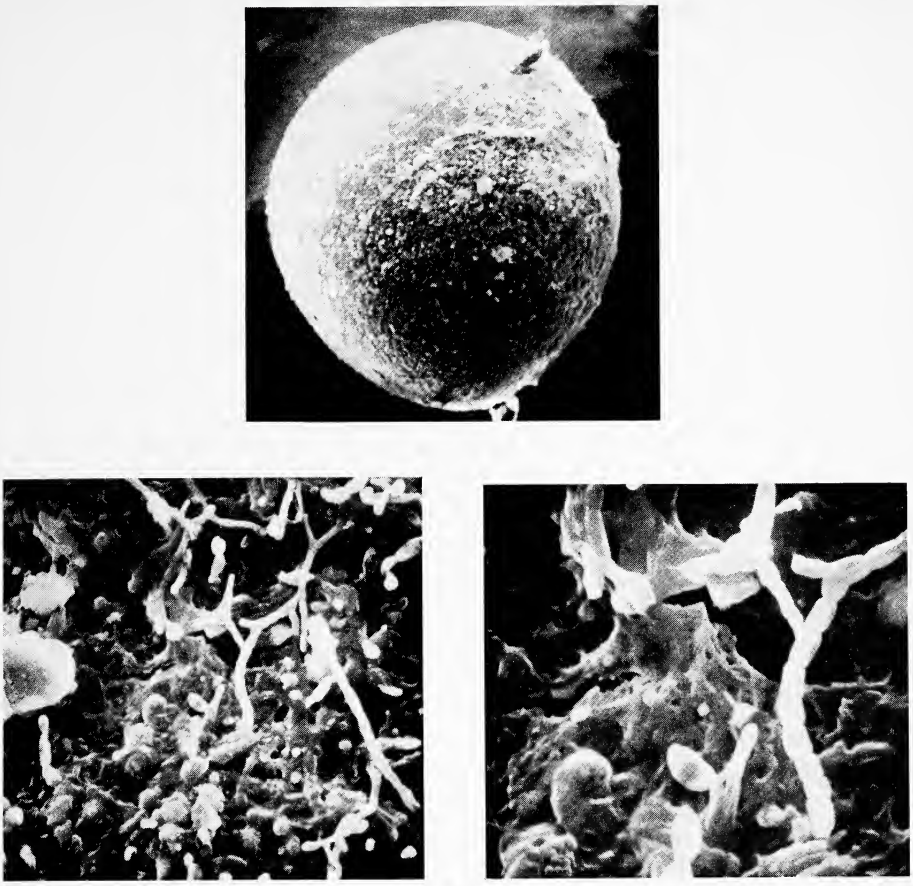

FIG. 1. Egg of *Nicoletia meinerti* Silvestri, above: general appearance at magnification of 120 times; lower left: egg at 2,400 magnification; lower right: 6,000 magnification.

tion period no male *N. meinerti* were seen, hence two generations were reared on the parthenogenetic ability of the female *N. meinerti.*

Nicoletia meinerti eggs varied in color from pale to dark gray and were more or less polar, having definite ends on the longer axis giving them a lemon-like shape. The eggs were laid free and unattached to the substrate. This is significant as the closest known relatives of the Nicoletidae, the Lepismatidae, are known to lay eggs which are attached to the surrounding substrate. *N. meinerti* eggs averaged 0.75 mm. × 0.68 mm. Electron scanning scope pictures of *Nicoletia* eggs show the nature of the egg surface (Fig. 1). The eggs photographed were viable and relatively unclean and show debris and fungal hyphae on the chorion. The eggs are irregularly pitted and have rounded cresting surfaces when seen at 6,000 × magnification.

Several interesting behavior patterns were noted. These insects always avoided contact with drops of water but often congregated around substrate that had just absorbed water. They were cannibalistic, especially when an injured individual was left in a community container. If the injured insect responded to another with normal antennal and cerci movements it was left alone. The adults seemed to eat some of the eggs. Several times adults were observed carrying eggs and later I counted fewer eggs.

Individual adult animals spent much of their time running along the bottom inner walls of their circular containers. When the covers were removed only a few would climb to the top of the quarter inch high container walls and still fewer completely left the containers. The very young were most often found under lettuce covering and rarely in the mainstream of adult traffic along the container walls. These behavior patterns may indicate a tendency of these silverfish to keep as much contact with the substrate as possible.

Nicoletia meinerti moults periodically throughout its entire life, but rarely could I find signs of a shed skin; therefore, I assume the skins are eaten.

I kept several of the original terrarium generation adults under observation for over a year, after which they appeared darker, larger and seemingly thicker than the average terrarium adult. These larger animals measured an average length of 7.2 mm from antennal base to the base of the cerci.

Nicoletia meinerti is an interesting experimental animal. It is easily reared in the laboratory but little is known about its behavior and biology. Because of its parthenogenetic nature its chromosome behavior should be studied as various types of polyploidy have been found in other insect groups where parthenogenesis occurs. In view of its scattered geographic distribution it would be interesting to know if this parthenogenesis occurs only in individual populations or throughout the species.

Phonotaxis of Male Meadow Grasshoppers (Orthoptera: Tettigoniidae)

Glenn K. Morris

Department of Zoology, Erindale College,
University of Toronto, Toronto, Canada.

Received for Publication November 9, 1971

Abstract: Phonotaxis occurs in males of two *Orchelimum* species. Conspecific male song transmitted by a speaker elicited rapid direct approach over distances up to 2 meters. Certain individuals responded repeatedly as the speaker was relocated, the latency of their response decreasing in successive trials. This taxis is interpreted as the approach phase of male aggression.

The present paper documents a taxic response by males of *Orchelimum gladiator* Bruner and *O. vulgare* Harris to a purely acoustical stimulus.

A speaker (ionophone) was used to expose males to the relayed or tape-recorded song of male conspecifics. The relay technique required a caged male located at least 15 meters from the study area. A microphone and amplifier system conveyed this male's song to the speaker. The sound level was crudely matched to the level typically produced by the species by adjusting the speaker output to give identical deflections of a recording level meter for identical microphone to insect and microphone to speaker distances.

Several sound systems were employed at various times, all of which distorted the normal carrier frequency of the song by attenuating or removing frequencies above 18 kHz. Since the principal peaks in the spectra of both species lie below this frequency, the speaker output was considered a reasonable model of the real signal.

Trials were conducted in typical meadow habitat of waist-high sedge and grass where staked grids aided in mapping displacements. The timing of events was derived from a tape-recorded description. Males were usually released in study areas several hours in advance. The speaker horn was placed at a distance of 0.5 to 2 m. from a male and directed toward him. Males tested were at least 3 m. from any other conspecific.

Disturbance, in the form of a stereotyped hiding behavior, usually coincided with the placing of the speaker. Singing stopped and the animal pivoted quickly, putting the perch between itself and the source of the disturbance. Jumping legs were fully extended posteriorly and the ventral body surface pressed against the sedge or grass perch. The insect remained rigidly motionless for as much as 1

Acknowledgments: These studies formed part of a Ph.D. dissertation submitted to Cornell University. Further work at the University of Toronto was supported by the National Research Council of Canada. Thanks are due Mr. Robert E. Pipher, Dr. G. Gyrisco and Dr. P. J. Pointing.

minute and then renewed its song. After several song sequences the speaker was turned on and a trial begun.

Orchelimum singers do not move more than a few centimeters an hour. Locomotory response toward the speaker signal was thus a striking behavioral change. It consisted of 15 to 60 cm leaps alternating with periods of walking and occasional pauses accompanied by singing. The advance was only slightly affected by the abundance and position of the intervening vegetation. The insect usually arrived within 10 to 20 cm of the speaker after 1 to 2 minutes. Frequent height changes might occur during the approach but horizontal displacement was always markedly direct. Individuals sometimes began their movement with a single long jump directly at the speaker.

Approximately 15 to 20% of the individuals tested made at least one approach. Ten *O. gladiator* males responded a total of 25 times; 10 *O. vulgare* males responded 16 times. Two meters was the maximum speaker to male distance over which a phonotaxis was observed.

The latency of the approach response is the time from the onset of speaker stimulus till the insect begins its horizontal movement. The mean latency for the initial approaches of 8 *O. vulgare* males was 1 minute 26 sec. Responding males were often tested again by repositioning the speaker. The horn was placed to offer a new approach direction differing from the old by as much as 180°. Males usually remained responsive through several such trials in succession with a decreasing threshold of response. In a typical result one male showed successive latencies of 4, 2 and 1 minutes.

Males of these species interact aggressively with conspecifics (Morris, 1967 and 1971). This behavior involves the approach of one male to another and often results in grappling physical contact. The speaker song is presumably eliciting this same aggressive approach.

The aggressive nature of the phonotaxis is suggested by the actions of a male *O. vulgare* which encountered a newly-killed male conspecific on arrival at the speaker horn. The dead insect had been glued to a dowel in a natural pose and placed beside the speaker. As the speaker signal continued, the advancing male walked along the dowel and touched the corps with his antennae. He directed bites to its head region and climbed on top of the dead male. A similar response was obtained when an *O. gladiator* male made a phonotaxic approach under the same conditions.

It is commonly assumed that the function of male song in katydids is to attract and guide the female. For these two species the male song also stimulates aggressive behavior and guides its initial approach phase.

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Morris, G. K. 1967. Song and aggression in Tettigoniidae. Ph.D. Thesis, Cornell University. 229 pp.

Morris, G. K. 1971. Aggression in male conocephaline grasshoppers (Tettigoniidae). Anim. Behav., **19:** 132–137.

Undescribed Species of Crane Flies from the Himalaya Mountains (Diptera: Tipulidae), XX[1]

Charles P. Alexander
Amherst, Massachusetts 01002

Received for Publication December 2, 1971

Abstract: Six new species of crane flies from Uttar Pradesh, Sikkim, and Assam are described, these being *Limnophila* (*Eloeophila*) **diacis**, *L.* (*E.*) **subdilata**, *Atarba* (*Atarbodes*) **crassispina**, *Rhabdomastix* (*Sacandaga*) **normalis**, *Ormosia* (*Parormosia*) **saturnina**, and *Erioptera* (*Erioptera*) **connata**.

Limnophila (*Eloeophila*) **diacis**, n. sp.

Size medium (wing of male to about 7 mm.); antennal flagellum bicolored; knobs of halteres brownish black; legs yellow, femoral tips broadly brownish black; wings whitened, conspicuously patterned with brown, including about seven larger costal areas, markings of the interspaces small and numerous, several not reaching the veins; male hypopygium with lateral spine of outer dististyle at near two-thirds the length; phallosome with gonapophyses appearing as slender acute darkened spines that are directed caudad, lying parallel to the relatively short slender aedeagus.

MALE: Length about 5.5–5.8 mm.; wing 6.2–7.3 mm.; antenna about 1.3–1.5 mm.

Rostrum brownish gray, palpi black. Antennae with scape and pedicel brownish black, flagellum bicolored, yellow, bases of segments narrowly dark brown; segments oval with long verticils. Head light gray.

Pronotum obscure yellow medially, sides darker. Mesonotal praescutum with disk virtually covered by three brownish black stripes that are gray pruinose, humeral region yellowed; posterior sclerites brown, gray pruinose, mediotergite with a narrow black central stripe. Pleura gray, lined longitudinally with dark brown, dorsal stripe including the propleura, anepisternum and dorsal pteropleurite and pleurotergite. Halteres brownish yellow, more yellowed basally, knobs brownish black. Legs with coxae and trochanters brownish yellow, gray pruinose; femora yellow, tips broadly brownish black, outer end slightly paler; remainder of legs yellow. Wings with ground whitened, heavily patterned with brown, including seven larger costal areas, the proximal two confluent behind, third area forming a complete band at level of origin of *Rs* and the supernumerary crossvein in cell *M*; fourth and fifth costal areas extensive, including the stigmal region, united behind over the *r-m* crossvein; supernumerary crossvein in cell *M* lying in the darkened cross band; darkenings of the interspaces small and numerous, several not connected with the veins; veins light brown, slightly darker in the patterned areas. Venation: *m-cu* at near one-third M_{3+4}.

Abdomen laterally dark brown, central parts of both sternites and tergites yellowed, outer

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[1] Contribution from the Entomological Laboratory, University of Massachusetts.

[2] Part XIX of this series of papers was published in the Journal of the New York Entomological Society, **78**: 201–205, 1970. Six further species are described, all from India, in Uttar Pradesh, Sikkim and Assam, collected by the veteran entomologist, Dr. Fernand Schmid, to whom I again express my thanks for this series of Himalayan Tipulidae.

segments more uniformly dark brown. Male hypopygium with outer dististyle terminating in a short curved outer spine and a stouter inner point, outer margin at near two-thirds the length with a conspicuous appressed spine; inner style narrowed on outer half. Phallosome small, gonapophyses appearing as slender acute darkened spines that are directed caudad, lying parallel to the relatively short slender aedeagus.

HOLOTYPE: ♂, Lata, Pauri Garhwal, Kumaon, Uttar Pradesh, India, 7,500 feet, July 6, 1958 (Schmid).

PARATOPOTYPES: two ♂♂, pinned with type.

PARATYPES: 2 ♂♂ on a single pin, Rupa, Northeast Frontier Agency, Kameng, Assam, India, May 2–3, 1961 (Schmid).

Other small regional species having the wing pattern generally as in the present fly include *Limnophila* (*Eloeophila*) *bicolorata* Alexander, of Nepal-Assam, and *L.* (*E.*) *fascipennis* Brunetti, of Assam, all differing among themselves in hypopygial structure, especially the outer dististyle and the phallosome.

Limnophila (*Eloeophila*) **subdilata**, n. sp.

Characters generally as in *perdilata*; wings not conspicuously dilated opposite outer end of vein *2nd A* as in males of *perdilata*; wing pattern including a conspicuous band at level of origin of *Rs*, paler behind, ending before apex of cell *2nd A*, remainder of this cell commonly with darkenings that attain the posterior border, in cases with this part of cell unpatterned; male hypopygium with lobe of margin of outer dististyle narrow.

MALE: Length about 6–6.5 mm.; wing 7–8 mm.

FEMALE: Length about 7–7.5 mm.; wing 8.5 mm.

Head gray, palpi brownish black. Antennae with basal segments light yellow, flagellum light brown.

Thorax light gray, with an interrupted brown pattern that includes a central line on pronotum, three narrow stripes on anterior half of praescutum, with broader lateral margins on posterior part, the remaining darkened pattern of praescutum, scutum and pleura paler brown. Halteres with stem yellow, knob dark brown. Legs with coxae brownish gray, trochanters obscure brownish yellow; femora yellow with a broad dark brown subterminal ring, the apex narrowly paler brown; tibiae yellow, tips narrowly darkened; proximal tarsal segments yellow, extreme tips and outer segments brown. Wings not conspicuously dilated opposite outer end of vein *2nd A* in male, as in *perdilata*. Darkened pattern including a major brown band at level of origin of *Rs*, paler behind, terminating before apex of cell *2nd A*, remainder of cell with darkened areas that reach the posterior border, in certain specimens (as in the paratypes from Gawana, Khumyara and Tarsali) posterior margin of cell *2nd A* unpatterned; a nearly solidly darkened triangular area in stigmal region; veins of the interspaces with small brown spots, those in cubital and anal fields more elongate.

Male hypopygium with the outer dististyle of the *perdilata* type, the apex a slender curved spine; lobe of outer margin of style narrow, in *perdilata* much broader, its apex truncate.

HOLOTYPE: ♂, Hanuman Chatti, Pauri Garhwal, Kumaon, Uttar Pradesh, 9,000 feet June 17, 1958 (Schmid).

ALLOTOPOTYPE: ♀, pinned below type.

PARATOPOTYPE: ♀, lowermost of three specimens on pin with types. Paratypes, two ♂♂, Binaik Chatti, Pauri Garhwal, 7,000–7,500 feet, June 16, 1958; one ♂, Gawana, Teri Garhwal, 6,000 feet, May 23, 1958; one ♂, Khumyara, Pauri Garhwal, 4,300–5,000 feet, May 4, 1958; one ♂, Tarsali, Pauri Garhwal, 6,000–7,000 feet, May 6, 1958 (all Schmid).

The most similar described species is *Limnophila* (*Eloeophila*) *perdilata* Alexander, as discussed above.

Atarba (*Atarbodes*) **crassispina**, n. sp.

Allied to *flava* and *decincta*; general coloration of body light yellow, two subterminal abdominal segments very slightly darkened; male hypopygium with spines of outer dististyle few in number, very stout, their diameter across base nearly one-half the length of spine.

MALE: Length about 4.8 mm.; wing 5.3 mm.; antenna about 1 mm.

Rostrum, palpi and antennae yellow. Head uniformly yellow.

Thorax light fulvous yellow, unpatterned. Halteres yellow. Legs with coxae and trochanters yellow; remainder of legs broken. Wings yellow, veins only slightly darker than the ground. Veins beyond general level of origin of *Rs* with trichia, with a few on outer ends of basal section of Cu_1 and both Anals. Venation: Sc_1 ending about opposite two-thirds *Rs*, branches of the latter slightly divergent, at margin cell R_3 about twice as extensive as cell R_2; *m-cu* shortly beyond fork of *M*.

Abdomen yellow, segments seven and eight weakly darkened. Male hypopygium with outer dististyle blackened, short-clavate, macelike in appearance; outwardly with a double row of very stout spines, including about six or seven on either side, the stoutest spines across their bases about one-half the length of spine; inner style slightly longer, parallel-sided, apex obtuse. Phallosome with each gonapophysis appearing as a nearly straight blade, aedeagus slightly longer; paired elements very pale, straight, virtually contiguous at midline.

HOLOTYPE: ♂, Rahung, Northeast Frontier Agency, Kameng, Assam, 7,000 feet, April 25, 1961 (Schmid).

The present species is generally similar to *Atarba* (*Atarbodes*) *decincta* Alexander and *A.* (*A.*) *flava* Brunetti, differing especially in hypopygial characters, including the unusually stout spines of the outer dististyle. In the species listed these spines are more numerous and more slender, in the extreme cases being approximately five times as long as their basal diameter.

Rhabdomastix (*Sacandaga*) **normalis**, n. sp.

General coloration of head and thorax light gray, abdomen dark brown, hypopygium yellowish brown; antennae 16-segmented, with no fusion of proximal flagellar segments; halteres light yellow; legs light brown; wings subhyaline, veins pale brown; veins R_4 and R_{2+3+4} subequal, R_5 and M_{1+2} with sparse trichia; ovipositor with cerci very long and slender.

MALE: Length about 2.9–3 mm.; wing 3.4–3.6 mm.; antenna about 0.7–0.75 mm.

FEMALE: Length about 4 mm.; wing 4 mm.

Rostrum obscure yellow, heavily gray pruinose, palpi brown. Antennae black; flagellum

with fourteen distinct segments, with no fusion of basal elements. Head light gray; anterior vertex very broad.

Thorax almost uniformly light gray; praescutum with four vaguely indicated darker stripes, intermediate pair widely separated, tuberculate pits and pseudosutural foveae blackened, conspicuous. Halteres light yellow. Legs with coxae light brown, sparsely pruinose, trochanters obscure yellow; remainder of legs light brown. Wings subhyaline, slightly more yellowed basally, veins pale brown. Very sparse trichia on outer ends of veins R_5 and M_{1+2}. Venation: Sc_1 ending about opposite midlength of Rs, Sc_2 not apparent; vein R_3 short, erect in type, suberect in other specimens, distance on costa between R_{1+2} and R_3 about one and one-half times the length of the latter vein; vein R_4 unusually long, subequal to R_{2+3+4}; basal section of vein M_3 variable in length, in cases, including holotype, very short; *m-cu* at from one-third to one-half M_{3+4}; cell *2nd A* broad.

Abdomen dark brown, hypopygium yellowish brown. Ovipositor with cerci very long and slender, nearly straight. Male hypopygium with outer dististyle only slightly expanded at outer end. Gonapophysis with apical blade elongate, narrow, about twice as broad as the stem.

HOLOTYPE: ♂, Ranibagh, Naini Tal, Pauri Garhwal, Kumaon, Uttar Pradesh, India, 1,778 feet, October 13, 1958 (Schmid).

ALLOTYPE: ♀, Salkhola, Pauri Garhwal, 4,240 feet, August 22, 1958.

PARATOPOTYPES: 2 ♂♂, pinned with type. Paratype, 1 male, with allotype.

The most similar regional species include *Rhabdomastix* (*Sacandaga*) *almorae* Alexander and *R.* (*S.*) *emodicola* Alexander, which differ in the short vein R_4 and in further minor characters. The first named species has the proximal flagellar segments united into a fusion-segment whereas in the present fly all flagellar segments are distinct, suggesting the specific name.

Ormosia (*Parormosia*) **saturnina**, n. sp.

Thoracic dorsum light brown, unpatterned, postnotum and pleura darker brown; halteres light yellow; legs black; wings strongly infuscated, restrictedly variegated by whitened areas, including especially the cord and outer end of cell *1st* M_2, the color including the veins; abdomen dark brown.

FEMALE: Length about 6 mm.; wing 6.5 mm.

Rostrum and palpi black. Antennae basally light yellow, outer segments brownish black. Head dark brown.

Thoracic dorsum light brown, unpatterned, pseudosutural foveae almost concolorous, postnotum darker brown. Pleura dark brown to brownish black, dorsopleural membrane brownish yellow. Halteres light yellow. Legs with coxae brownish black, trochanters obscure yellow; femora black, remainder of legs slightly paler, brownish black. Wings strongly infuscated, especially the costal third, sparsely variegated by paler areas that include broad diffuse more whitened markings at cord and outer end of cell *1st* M_2, with a smaller spot at origin of Rs, the pale color including the veins; stigma with a small more yellowed mark at either end, the outer one smaller; veins pale brown, distal section of R_5 darker brown. Venation: R_2 about three times R_{2+3}; *m-cu* at fork of M.

Abdomen uniformly dark brown. Ovipositor with valves very slender, cerci gently upcurved, more yellowed.

HOLOTYPE: ♀, Jhum La, Northeast Frontier Agency, Kameng, Assam, India, 7,800 feet, May 13–14, 1961 (Schmid).

The most similar species is *Ormosia* (*Parormosia*) *discalba* Alexander, from Northeastern Burma that differs evidently in the wing markings, the whitened pattern being reduced to a single small area at the fork of vein *M*.

Erioptera (*Erioptera*) **connata**, n. sp.

Allied to *litostyla*; general coloration yellowed, head slightly darker; antennae, halteres and legs yellow; wings pale whitish yellow; male hypopygium with outer dististyle a slender smooth rod that narrows to a subacute point, inner style about two-thirds as long, an entirely pale blade that bears a small fingerlike lobule at near midlength of outer margin; gonapophysis a slender blackened spine; aedeagus a flattened subhyaline shield without a lateral blackened spine, the two enclosed filaments terminating before the apex.

MALE: Length about 4.5 mm.; wing 4.7 mm.; antenna about 1 mm.

Rostrum light brown, palpi dark brown, terminal segment about one-fourth longer than the penultimate and more slender. Antennae yellow. Head brown, eyes very large.

Pronotum light yellow. Mesonotum fulvous, sides of praescutum more yellowed. Pleura fulvous with a narrow pale brown longitudinal stripe from and including the fore coxae, continued backward to base of abdomen, passing beneath the halteres. Halteres uniformly yellow. Legs with fore coxae darkened, as described, remaining coxae and all trochanters light yellow; remainder of legs uniformly yellow. Wings pale whitish yellow, veins slightly darker yellow, trichia brown. Venation: R_{2+3+4} and R_{2+3} subequal; *m-cu* at fork of *M*; vein *2nd A* very strongly sinuous at near midlength.

Abdomen yellowed, tergites vaguely infuscated medially, subterminal segments more extensively darkened. Male hypopygium with dististyles nearly terminal, outer apical angle of basistyle with very long setae, the longest about four-fifths the length of longer style. Outer dististyle a slender smooth rod, very gently curved, outer half more darkened; inner style about two-thirds as long, appearing as an entirely pale blade that narrows to an obtuse point, on outer margin at near midlength with an appressed fingerlike lobule. Gonapophysis a very slender blackened spine. Aedeagus a flattened subhyaline shield, the enclosed filaments ending before apex, margins of style not provided with a blackened spine as in *litostyla*.

HOLOTYPE: ♂, Doling, Sikkim, 5,900 feet, April 29, 1959 (Schmid).

In general appearance the present fly is similar to *Erioptera* (*Erioptera*) *litostyla* Alexander, likewise from Sikkim. Both species have the structure of the aedeagus generally the same, the genital filaments ending before the arched and flattened apex, in *litostyla* bearing a strong blackened spine that resembles the gonapophysis, presenting the appearance of four apophyses instead of the normal single pair.

Tracheal System in the Larvae of the Bruchidae (Coleoptera: Bruchidae)

L. K. VATS
DEPARTMENT OF ZOOLOGY, KURUKSHETRA UNIVERSITY, KURUKSHETRA (INDIA)

RECEIVED FOR PUBLICATION FEBRUARY 4, 1972

Abstract: The tracheal system of the larvae of eight species of the family Bruchidae were studied with reference to its taxonomic importance. Differences in the arrangement of the tracheal branches in the anterior region of the body and in the number of the air sacs at the subfamily level were observed. The species studied were *Callosobruchus maculatus* (F.), *Callosobruchus analis* (F.), *Bruchidius saundersi* (Jek.), *Bruchidius albizziae* Arora, *Bruchus pisorum* L., *Zabrotes subfasciatus* (Boh.), *Caryedon gonagra* (F.) and *Caryedon languidus* Gyll.

INTRODUCTION

The tracheal system in the larvae of the Bruchidae is an important character for separation of the larvae at the subfamily level.

Zacher (1930), Mukerji (1939), de Luca (1959) and Pajni (1968) described the tracheal system in *Zabrotes subfasciatus* (Boh.), *Bruchus quadrimaculatus* F., *Bruchidius trifollii* Motsch and *Callosobruchus maculatus* (F.) respectively without realizing its taxonomic significance. The present study is concerned with a comparative account of the tracheal system and an evaluation of its taxonomic significance in the last instar larvae. Of eight species examined five are referrable to the subfamily Bruchinae (two each from the genera *Callosobruchus* and *Bruchidius* and one from the genus *Bruchus*), one to the subfamily Amblycerinae (represented by the genus *Zabrotes*), and two to the subfamily Pachymerinae (represented by the genus *Caryedon*).

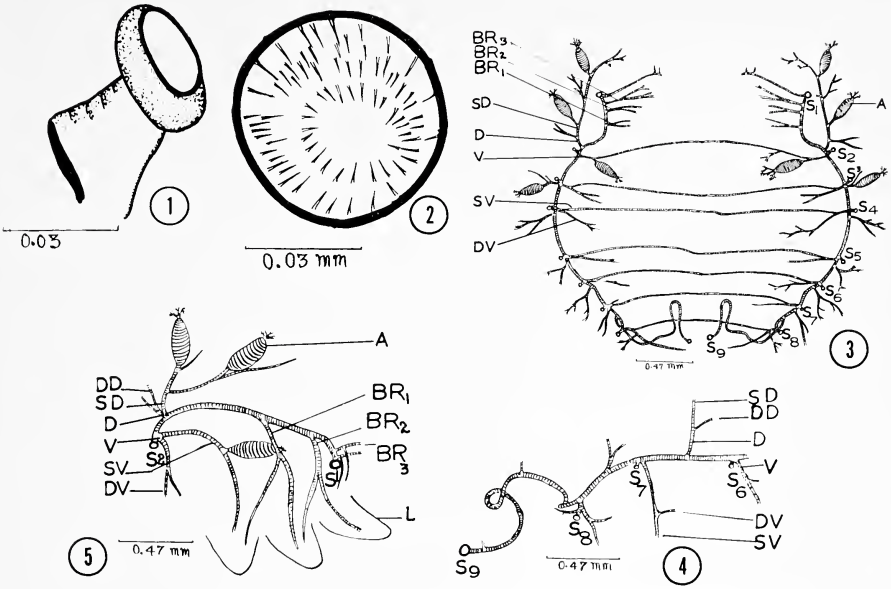
The larvae were collected during U.S. PL.480 Scheme on Bruchidae under Principal Investigatorship of Prof. G. L. Arora, Panjab University, Chandigarh (India).

OBSERVATION AND DISCUSSION

A peripneustic type of hemipneustic respiratory system is present in all the species studied.

Nine pairs of spiracles are located symmetrically on either side of the body. The first pair of spiracles is in the mesothorax posterior to the intersegmental

Acknowledgments: I am grateful to Prof. G. L. Arora, Principal Investigator, U.S. PL.480 Scheme on Bruchidae and Dr. H. R. Pajni for their guidance and help. The generosity of the authoritites of U.S. PL.480 Scheme for providing necessary facilities is gratefully acknowledged.



ABBREVIATIONS

A = Air-sac; BR_1 = First thoracic tracheal branch; BR_2 = Second thoracic tracheal branch; BR_3 = Third thoracic tracheal branch; D = Dorsolateral branch of longitudinal trunk; DB = Additional dorsal branch; DD = Deep seated branch of dorsolateral branch (D); DV = Deep seated branch of ventrolateral branch (V); S_1 = Meso-thoracic spiracle; S_2–S_9 = Eight abdominal spiracles; SD = Superficial branch of dorsolateral branch (D); SV = Superficial branch of ventrolateral branch (V); V = Ventrolateral branch of longitudinal trunk.

Fig. 1. Spiracle of *Callosobruchus maculatus*.

Fig. 2. Surface view of *Callosobruchus maculatus* spiracle.

Fig. 3. Tracheal system of *Callosobruchus maculatus*.

Fig. 4. Lateral view of the posterior part of the tracheal system of *Callosobruchus maculatus*.

Fig. 5. Lateral view of the tracheal system in the anterior part of the body of *Callosobruchus maculatus*.

line dividing the prothorax and the mesothorax. The remaining eight pairs are on the first eight abdominal segments, a pair on each segment. Each spiracle (Fig. 1) is annular, uniforous and atriate with an internal closing apparatus. The inner wall of the atrium bears numerous small cuticular hairs (Fig. 2).

Zacher (1930), Mukerji (1939), de Luca (1959) and Pajni (1968) reported nine pairs of spiracles, one thoracic and eight abdominal, in *Zabrotes subfasciatus*, *Bruchus quadrimaculatus*, *Bruchidius trifollii* and *Callosobruchus maculatus* respectively. According to Zacher (1930), Mukerji (1939) and Pajni (1968) the thoracic spiracle is present on the intersegmental line between the pro- and the meso-thorax however, de Luca (1959) mentioned that this

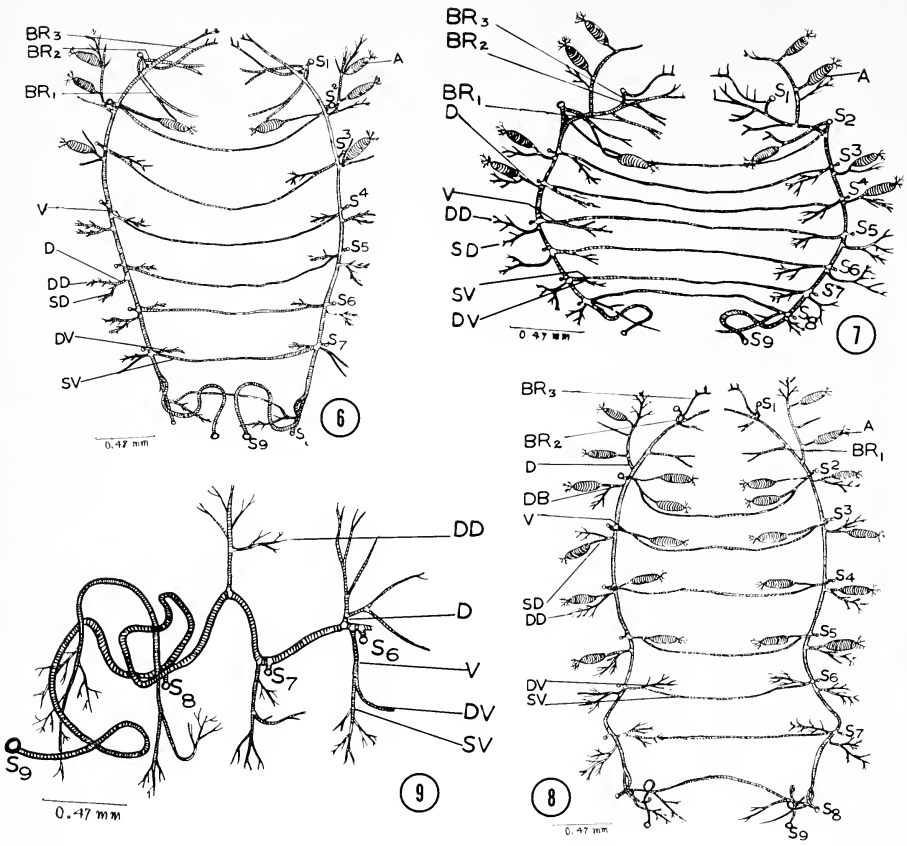


FIG. 6. Tracheal system of *Bruchus pisorum*.
FIG. 7. Tracheal system of *Zabrotes subfasciatus*.
FIG. 8. Tracheal system of *Caryedon languidus*.
FIG. 9. Lateral view of the tracheal system in the posterior region of the body of *Caryedon gonagra*.

spiracle is on the mesothorax which is in accordance with the present investigation. Pajni (1968) stated that in addition to this thoracic spiracle, a closed spiracle is also found on the mesothorax. I have not observed such a spiracle in any of the species studied.

A pair of lateral longitudinal tracheal trunks runs on either side of the body from the eighth abdominal segment to the mesothoracic segment. Each of the first seven abdominal segments is supplied with a pair of dorsolateral and a pair of ventrolateral tracheal branches, but in *Caryedon* (Fig. 8) there is an additional dorsal branch arising behind the first abdominal spiracular trunk. It supplies the anterior part of the alimentary canal.

In *Callosobruchus* (Fig. 3), *Bruchidius*, *Zabrotes* (Fig. 7) and *Caryedon* (Fig. 8) the dorsolateral branch of the first abdominal segment originates from the lateral longitudinal trunk in front of the first abdominal spiracular trunk, whereas in *Bruchus* (Fig. 6) it originates behind the first abdominal spiracular trunk. The dorsolateral branch in each of the segments from second to sixth arises behind the spiracular trunk of the same segment in all the species. It branches into a deep-seated and a superficial branch in each segment, both supplying the dorsal parts of the body.

The ventrolateral branch of the first abdominal segment always originates from the spiracular trunk whereas in the segments from second to sixth it arises from the longitudinal tracheal trunk. The ventrolateral branch supplies the ventral and the lateral parts of the body and, like the dorsolateral branch, divides into a deep-seated and a superficial branch. The latter forms the ventral transverse commissure in each of the first seven segments.

The spiracular trunk of the eighth abdominal segment is extremely long and coiled in all the species (Figs. 4, 9). The last two segments receive the tracheal supply from the dorsolateral and the ventrolateral branches of the 7th segment.

The thorax is supplied with three tracheal branches on either side. These branches arise either from the lateral longitudinal tracheal trunk or from the mesothoracic spiracular trunk or from both. This character can be utilized in separating the genera. In *Callosobruchus* (Fig. 3), *Zabrotes* (Fig. 7), and *Bruchidius* all the three branches arise from the lateral longitudinal trunk between the mesothoracic and the first abdominal spiracles, whereas in *Caryedon* (Fig. 8) the first branch arises from the lateral longitudinal trunk and the remaining two branches arise from the mesothoracic spiracular trunk. In *Bruchus* (Fig. 6), all three branches originate from the meso-thoracic spiracular trunk. Regardless of their origin, these branches supply the same respective parts in all the species. For example, the first thoracic branch bifurcates into an anterior branch entering the mesothoracic leg and a posterior branch goes to the metathoracic leg. The second branch, like the first branch, divides into an anterior branch going to the prothoracic leg and a posterior branch entering the mesothoracic leg. The third branch also bifurcates into an anterior and a posterior branch. The anterior branch after sending the tracheae to the prothorax enters the head, whereas the posterior branch supplies the mesothorax.

The thorax also receives the tracheae from the dorsolateral and the ventrolateral branches of the first abdominal segment. The superficial branch of the dorsolateral branch supplies the tracheae to the dorsal region in the mesothorax, whereas its deep-seated branch after entering the thorax bears a pair of air sacs. Similarly, the superficial and the deep-seated branches of the ventrolateral branch supply the tracheae to the metathoracic legs and the metathorax.

A pair of tracheal branches on either side enters the head from the thorax.

Of these the dorsal branch sends the tracheols to the antennae, the mandibles and the brain whereas the ventral branch supplies the labium and the maxillae. The dorsal branches of the two sides units to form a dorsal head commissure.

Air sacs are present in every species. They are distensible and when inflated are seen as glistening white oval vesicles. From the apex of each air sac a tracheal branch arises which immediately divides into finer branches that enter the fat bodies. Air sacs reduce the compressibility of the body and increase the capacity for storing air. The number of sacs differ in the different subfamilies and is significant in classification at the subfamily level. There are four pairs of air sacs in Bruchinae (Figs. 3, 6), five pairs in Amblycerinae (Fig. 7) and eleven pairs in Pachymerinae (Fig. 8). They are borne on the dorsolateral and the ventrolateral branches of the first four abdominal segments.

Zacher (1930) mentioned five pairs of air sacs in *Zabrotes subfasciatus*. Mukerji (1939) and de Luca (1959) reported four pairs in *Bruchus quadrimaculatus* and *Bruchidius trifollii* respectively. These investigations confirm that the number of air sacs in a subfamily is fixed.

The arrangement of the air sacs on either side of the body is as follows:

1. The dorsolateral branch of the first abdominal segment bears a pair of air sacs located in the pro- and the meso-thorax, whereas the ventrolateral branch of the same segment carries an air sac lying in the mesothorax in all the species. In *Caryedon* (Fig. 8) the additional dorsal branch also bears an air sac.

2. The dorsolateral branch of the second abdominal segment bears an air sac located in the same segment in all the species. The ventrolateral branch of the same segment bears no air sac in *Callosobruchus* (Fig. 3), *Bruchus* (Fig. 6), *Zabrotes* (Fig. 7) and *Bruchidius* whereas an air sac is present in *Caryedon* (Fig. 8).

3. The dorsolateral branch of the third abdominal segment bears no air sac in *Callosobruchus*, *Bruchus* (Fig. 6), and *Bruchidius* whereas it carries an air sac in *Zabrotes* (Fig. 7) and *Caryedon* (Fig. 8). The ventrolateral branch of the same segment is without any air sac except in *Caryedon* in which there is an air sac on this branch.

4. The dorsolateral and the ventrolateral branches of the fourth abdominal segment are without air sacs in *Callosobruchus*, *Bruchus* (Fig. 6), *Zabrotes* (Fig. 7) and *Bruchidius* whereas an air sac is present on each of the above mentioned branches in *Caryedon* (Fig. 8).

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Comparative Virology Conference

The 2nd International Conference on Comparative Virology, sponsored by the University of Montreal and McGill University is planned for Sept. 3–5, 1973 at Mt. Gabriel, Que., Canada.

Prof. Edouard Kurstak (U. Montreal) and Dr. Karl Maramorosch (Boyce Thompson Institute) will serve as joint chairmen, assisted by Dr. André Lwoff (Cancer Institute, Villejuif, France) and Dr. Joseph L. Melnick (Baylor Univ., Houston, Texas).

Additional information may be obtained from Prof. E. Kurstak, Dept. Microbiology and Immunology, Faculty of Medicine, Univ. of Montreal, P.O. Box 6128, Montreal, Que., Canada.

Biology of *Morpho polyphemus* (Lepidoptera: Morphidae) in El Salvador

ALLEN M. YOUNG[1] AND ALBERTO MUYSHONDT[2]

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Abstract: This paper summarizes various studies on the biology of *Morpho polyphemus* (Lepidoptera: Morphinae) in El Salvador. Emphasis is placed upon the interpretation of observed life cycle, larval host plant specificity, parasitism of eggs and larvae, larval behavior, and adult behavior in terms of a generalized adaptive evolutionary strategy that accounts for the ability of this butterfly to successfully colonize isolated patches of second-growth forest. In Central American countries the butterfly is generally confined to the canopy of undisturbed primary-growth rain forest (Costa Rica). In El Salvador, where virtually all primary-growth forest has been destroyed through land-clearing agricultural practices (slash-burn systems), the species has survived in small second-growth habitats where a major larval host plant, *Paullinia pinnata* (Sapindaceae), is abundant. Comparisons of development time with two subspecies of *Morpho peleides*, indicate that the ability of *Morpho polyphemus* to survive in second-growth forest communities is a relatively recent event. Various hypotheses are advanced to account for observed seasonal differences in adult abundance since the dry season is pronounced at the study site.

Herein we describe the biology of *Morpho polyphemus polyphemus* (Morphinae) in El Salvador for this Central American species, which, according to various authors (e.g., Seitz, 1924; Le Moult and Real, 1962) has previously been undescribed. We also summarize the first records of larval host plants, and notes on the ecology and behavior of adults and immatures. This paper is one of a series on the biology of Central American *Morpho*.

Our ultimate goal in studying the biology of Central American *Morpho* is to account for the evolutionary biology of the genus as a whole. In this paper we hypothesize about the evolutionary history of *Morpho polyphemus*, relative to its presumed South American heritage with the *catenarius* series (Seitz, 1924) and in contrast with a sympatric species, *Morpho peleides hyacinthus*.

Acknowledgments: The senior author is grateful for funds given to him from a College Science Improvement Program (COSIP) Grant, GY-4711 awarded to Lawrence University which enabled him to visit the study site during the summer of 1971. The junior author was frequently assisted in field work by his sons Alberto Jr. and Pierre. The senior author is grateful to Dr. Alexander B. Klots (American Museum of Natural History) for initially calling to his atttention Muyshondt's studies on *Morpho* in El Salvador. Dr. D. C. Wasshausen (Smithsonian Institution) confirmed the identification of *Paullinia pinnata*; Dr. C. W. Sabrosky (Smithsonian Institution and U. S. Dept. of Agriculture) identified the egg and larval parasites discussed in this paper.

[1] Dept. of Biology, Lawrence University, Appleton, Wisconsin 54911.
[2] Alberto Muyshondt, Lomas Verdes, San Salvador, El Salvador, C.A.

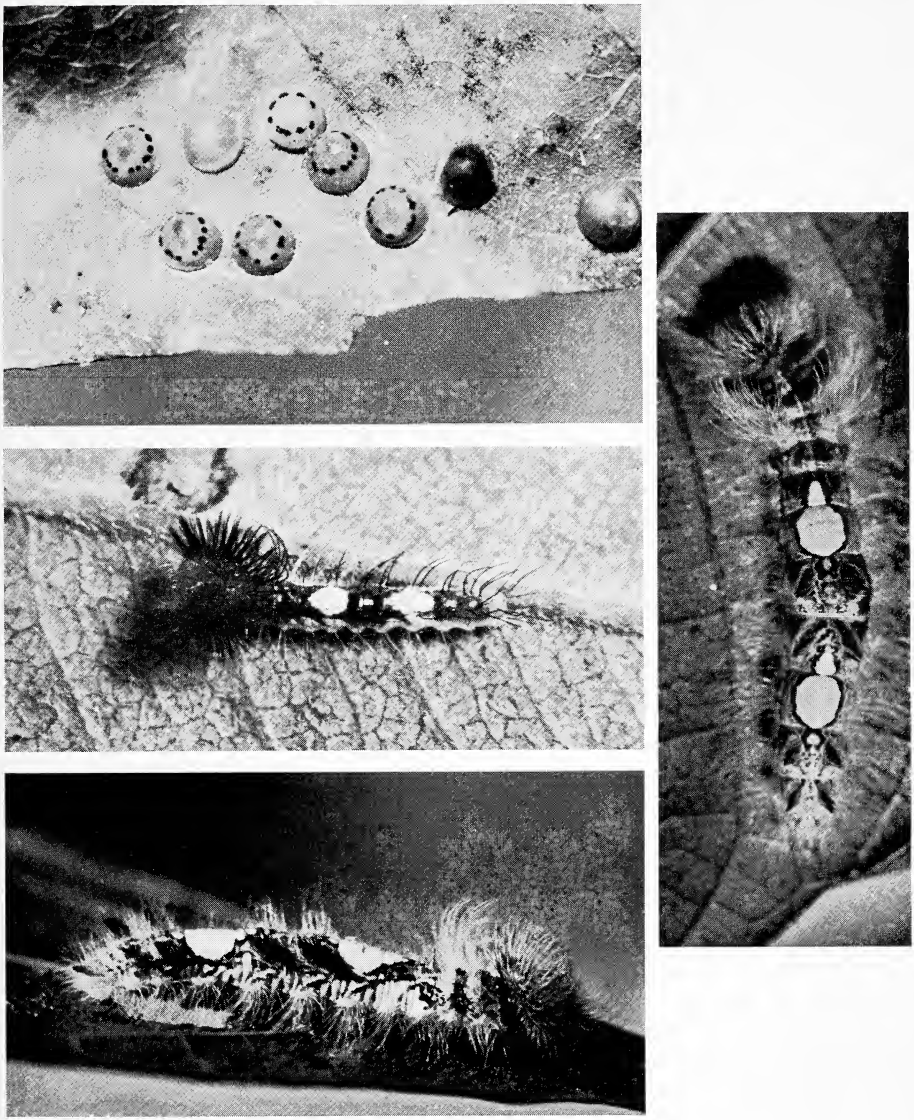

Fig. 1. Life cycle of *Morpho polyphemus*. Vertical column (from top to bottom): eggs (as laid in the laboratory); first instar larva, dorsal aspect; third instar larva, lateral aspect. Single right photograph: third instar larva, dorsal aspect.

HABITAT AND STUDY PROCEDURES

All field studies were made in heavily-disturbed early second-growth seasonal tropical wet forest forming a narrow strip of dense vegetation along the banks of a small stream running through the village of Barranca Colonia Campestre

(800 m. elev.) in the northeastern sector of San Salvador. Although we have observed *Morpho polyphemus* occurs in heavily-disturbed forest from sea level to 1800 meters (Cerro Verde and Sierra Apaneca), we noted (from 1968 to 1971) that the butterfly is locally common at Barranca Colonia Campestre, and therefore, we have concentrated our studies at this locality. We realize that the various aspects of its biology (most notably host plant specificity of larvae) may vary greatly with geographical and topographic factors.

Our study site consisted of a section of shallow ravine (about 30 m. deep) with the stream (quebrada) running through in an east-west direction. One of the most striking features of this particular study site, and one which we believe may act as a major selective force of the local adaptations of *Morpho polyphemus,* is the high density of human habitation situated along the ridges of the ravine at Barranca Colonia Campestre. Houses and cleared patches of land were only a few meters from the beginning of the second-growth strip which covered the sides of this ravine. The vegetation associated with the sides of the ravine, and in which oviposition by *Morpho polyphemus* was commonly seen, formed a thick layer of undergrowth.

Morpho polyphemus in this area of El Salvador is a typical component of the butterfly fauna associated with cleared areas with breeding activity restricted to the dense, shaded second-growth vegetation that tracks streams in ravines. The undergrowth apparently results from the high sunlight intensity throughout most of the year because a tall, overshadowing canopy (Odani, 1963) is lacking. The original habitat of *Morpho* butterflies in El Salvador has been severely reduced and modified as a result of massive land clearing efforts by man.

Studies conducted include: (1) collection of eggs and larvae for laboratory rearing, (2) records of larval host plant specificity in the field, (3) feeding experiments in the laboratory, (4) observations on predators and parasites on eggs and larvae in the field, and (5) notes on behavior of larvae and adults in the field. Observations were also made on seasonal abundance of adults at the study site. For laboratory rearing studies, cultures of *Morpho polyphemus* were usually maintained in tightly-sealed clear plastic 8″ by 12″ bags.

RESULTS

The results of field and laboratory observations on the biology of *Morpho polyphemus* are summarized below, in the following order: (1) life cycle, (2) host plant specificity, (3) mortality factors, (4) larval behavior, and (5) adult behavior.

Life Cycle: Life cycle studies were concerned with development time from egg to adult and description of life stages. The development time, and size of various stages are summarized in Table 1. The mean development time is about 127 days.

Table 1. Some life cycle statistics of *Morpho polyphemus* in El Salvador.[a]

Statistics	Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar[c] 5	Pupa	Total Time Egg-adult
Mean duration ($\bar{x} \pm$ S.E.) in days	11 ± 0.5	8 ± 1.0	9 ± 0.5	14 ± 1.0	23 ± 1.0	35 ± 1.5	20 ± 1.0	126.5
Mean size[b] ($\bar{x} \pm$ S.E.) in mm.	1.9 ± 0.5	9 ± 0.4	15 ± 0.2	35 ± 0.5	40 ± 1.0	71 ± 5.5	30 ± 0.5	—
Mean head capsule width ($\bar{x} \pm$ S.E.) in mm.	—	1.8 ± 0.2	2.5 ± 0.1	3.2 ± 0.1	5.2 ± 0.1	7.2 ± 0.2	—	—
N[d]	140	19	19	13	13	11	11	—

[a] All measurements were made in the same laboratory.
[b] Refers to diameter for egg, and body length (head-tail) in larvae and pupae.
[c] Instar 5 includes an active non-feeding prepupa which lasts 2–3 days.
[d] N is the number of individuals measured.

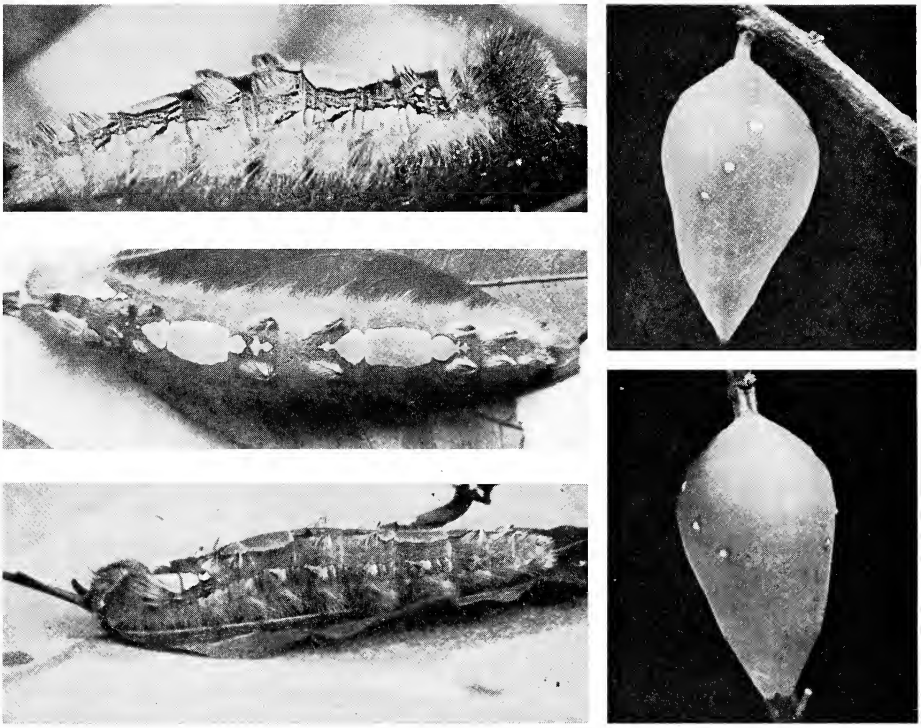

FIG. 2. Life cycle of *Morpho polyphemus*. Left vertical column (top to bottom): fourth instar larva, lateral aspect; fifth instar larva, dorsal aspect; fifth instar larva, lateral aspect. Right column: pupa, lateral aspect; pupa, dorsal aspect.

The egg, when first laid, is light green but soon (2–4 days) develops a noticeable broken dark brown band outlining the lid through which the first instar larva will emerge (Fig. 1). Near hatching time, the egg turns dark reddish-brown and the larva (especially the head) is clearly visible inside. In the field, eggs are usually laid singly, although occasionally an ovipositing female will deposit from 1–4 eggs on a single leaf of the host plant; however, in such unusual instances, the eggs are never clustered (i.e., touching one another), but rather scattered on the dorsal surface of the leaf. Occasionally a female will oviposit several eggs within a cluster of leaves on a single host plant. Eggs are affixed to the dorsal surface of a leaf but the actual site on the leaf is seldom consistent (i.e., eggs are not always laid near the edge of the leaf, etc.). Eggs are usually laid on the older leaves of the host plant.

First instar larvae (Fig. 1) devour their empty egg shells immediately upon hatching and then move to the ventral surface of the leaf. The body of the first instar is white interspersed with large patches of red dorsally, which are connected laterally by a thin line on each side. Hairs projecting dorsally are black, while lateral hairs are white (Fig. 1). The head is broader than the width of

the body and is reddish-brown with multiple rows of black hairs along the lateral and dorsal edges. The entire surface appears finely pitted and possesses reflective properties. The ventral portion of the body is translucent greenish-white.

The second instar closely resembles the first instar, although pairs of thin tufts of white hair now appear dorso-laterally on segments 1, 4, and 7; the tufts associated with segment 4 are longer than those of segments 1 and 7. The appearance of these tufts represents the appearance of a *Morpho* character that persists and is further developed in later instars. The second instar is generally the same color as the first instar, with the single noticeable exception being the possession of reddish hairs on the head where the black hairs had been in the first instar. These hairs are also shorter than in the first instar.

It is during the third instar (Fig. 1) that the larva takes on a markedly different external appearance. First, the general body color becomes gray-grown and infiltrated by a network of light yellow lines bordered with black. The dorsal white patches of the first and second instars now take on a yellowish-green color with their outlines more well-defined by a pronounced border of black (Fig. 1). The larva no longer appears red and white but grayish-brown with two prominent yellow-green spots. The head becomes hairy, with hairs now arising from frontal regions in addition to the lateral edges. The head is now light brown in color and the hairs are silvery-brown in color. There is a noticeable increase in numbers and lengths of hairs associated with the false and true feet, at the latero-ventral edge along each side of the body; these hairs appear as loose brushes arising directly opposite the feet and directed downward, giving the appearance of a series of small brushes obscuring the ventral edges of the body. These hairs are light silvery-brown in color. There is the appearance of new pairs of tufts, on segments immediately behind those in which tufts were already present in the second instar. Therefore, the tufts appear as double sets, arising from segments 1 and 2 (first doublet), segments 4 and 5 (second doublet), and segments 7 and 8 (third doublet). While each tuft is thicker than those of the second instar, they are also shorter in length and take on a "chopped-off" appearance. However, the tufts of the first doublet remain long and directed forward towards the head (Fig. 1), while the remaining two doublets are directed upwards. The latter two sets of tuft doublets are purplish-brown in color while the longer first doublet is light brown.

The tufts comprising the first doublet arise from the anterior edges of segments 1 and 2, while tufts of the more posterior sets arise from the center of their segments. During the fourth instar (Fig. 2), a new doublet of small tufts appears from the middle of segments 2 and 3, and a single new pair of very small tufts appears on segment 9. All tufts are generally light brown and the lateral regions of the body become light yellow-green, like the two major dorsal patches (Fig. 3). The formerly grayish-brown regions of the body now become a more uniform brown color, with less interspersion of lighter lines as seen in the third

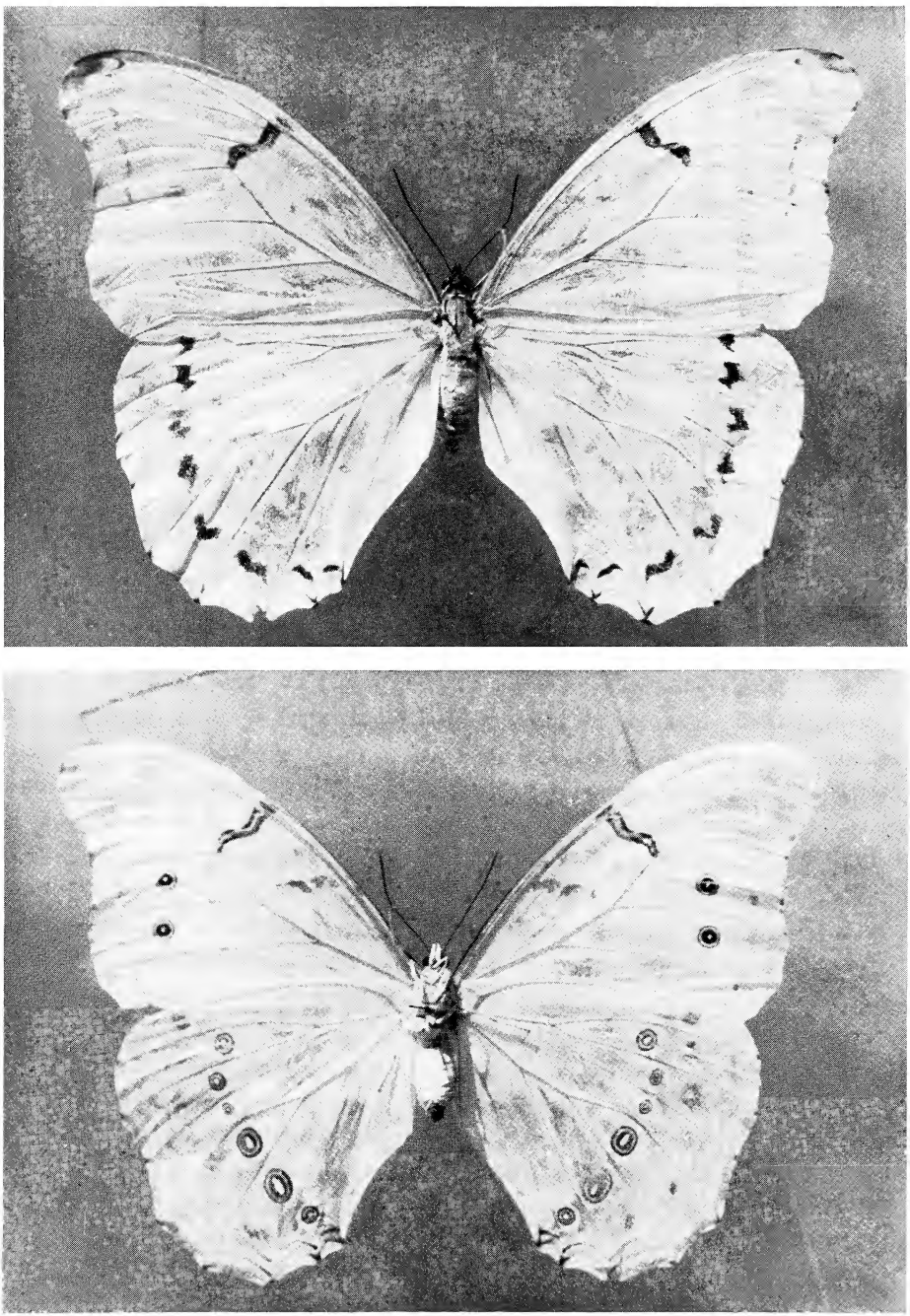

FIG. 3. Life cycle of *Morpho polyphemus*. Above: female, dorsal aspect. Below: female, ventral aspect.

instar. The head retains its light brown color, but the frontal region takes on a cream color in the form of an isosceles triangle with the apex continuing back along the head suture as a faint cream-colored line. The head retains the hairy condition of the third instar.

The fifth instar larva is generally a pale brown color, with the formerly yellow-green patches of the dorsal region now uniformly light green (Fig. 2). The dorsal patches have also become further subdivided into small isolated dorso-lateral (segment 2) or dorsal (segments 5, 9) irregularly-shaped spots of bright green. The tufts, with the exception of the first doublet, are now greatly reduced in length and thickness, and in conjunction with a reduction in the thickness of tufts associated with the legs, give the larva a generally smooth appearance unlike the previous instars. The hairs on the head are reduced in number and are generally of a finer texture than in previous instars. The lateral rather continuous yellow-green stripes of the fourth instar are now reduced to small patches (one per segment) of bright green (Fig. 2). Tufts of the first doublet remain long and filamentous, and directed horizontally towards the head. At this instar, the larva appears to be a light brown object and takes on a more cryptic appearance than the previous instars.

About 2–3 days prior to pupation, the larva changes to a light green color all over, with only the head and tufts of hairs remaining brown in color; this is an active prepupa stage characterized by increased locomotor activity resulting in dispersion of larvae from the host plant, and by the complete cessation of feeding. The wandering prepupa eventually pupates in nearby heavily-shaded undergrowth, with the resulting pupa being uniformly light-green (same color as the prepupa) with the major markings being the yellow spiracle opening (Fig. 2). The pigmented spiracle openings are largest on the most anterior segments and gradually being reduced in size to the cremaster, which is bluish-green. The anterior end of the pupa is strongly forked with the paired projections being tipped in wine red. There is no noticeable change in the coloration of the pupa as the adult develops, although usually within 24 hours of eclosion, it darkens slightly. The pupa is very cryptic in appearance since larvae usually pupate on stems and leaves of vines and shrubs in heavily-shaded undergrowth. Empty pupa shells remain intact for several months in the field, making it easy to estimate local abundance of the species. Empty pupa shells were found close to host plants containing eggs and first instar larvae, suggesting that the ravine at Barranca Colonia Campestre is a major breeding site for *Morpho polyphemus* throughout the year.

Adult *Morpho polyphemus* exhibit little sexual dimorphisms in body and wing coloration (Figs. 3–4), although males are generally smaller than females in terms of average wingspan. Neither Seitz (1924) nor Le Moult and Real (1962) allude to sexual differences in this Central American *Morpho*. We observed that one sexual difference is the pronounced submarginal row of crescent-shaped black spots on the dorsal surface of the hindwings in females (Fig. 3),

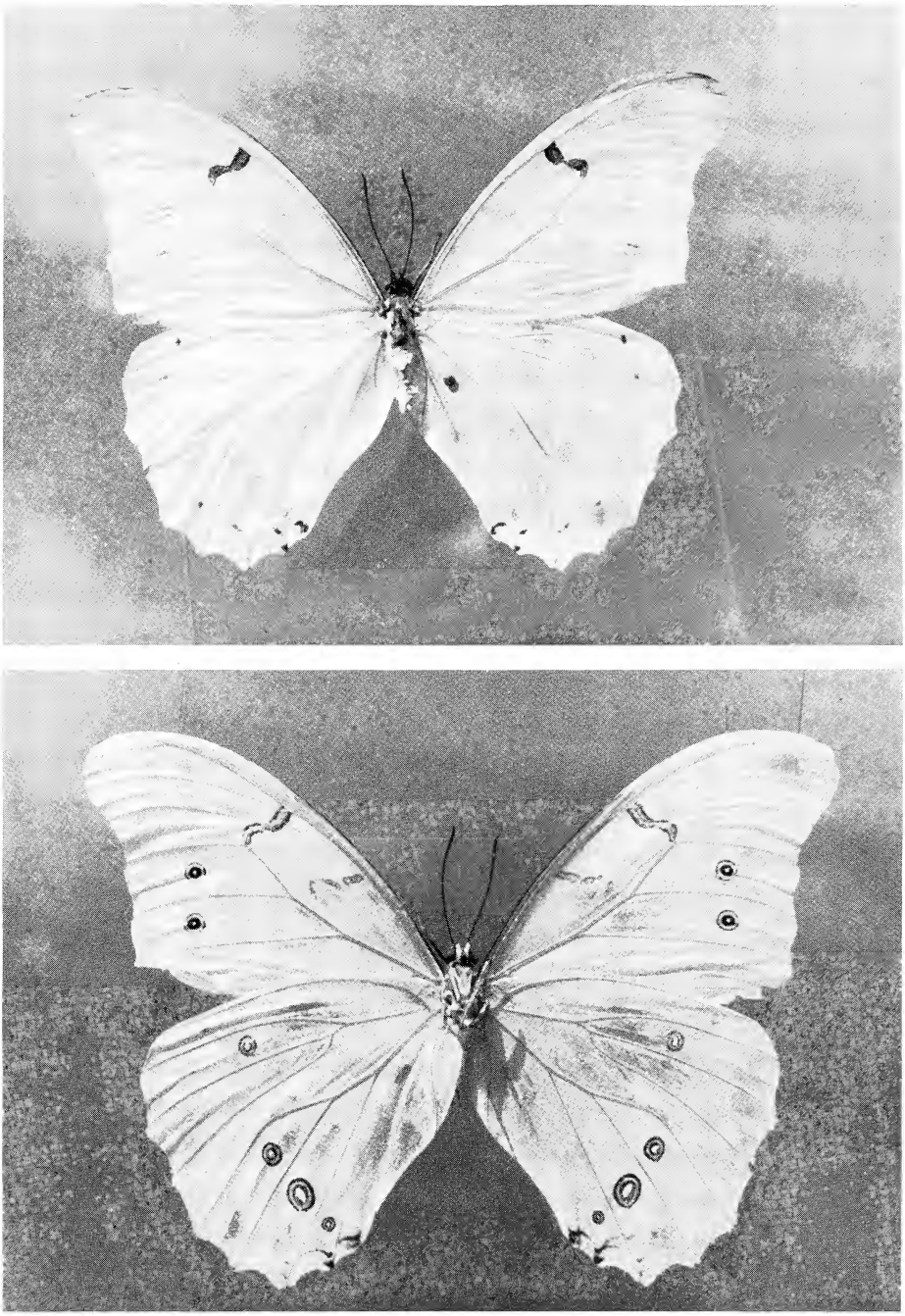

FIG. 4. Life cycle of *Morpho polyphemus*. Above: male, dorsal aspect. Below: male, ventral aspect.

which is almost totally absent in males (Fig. 4). With respect to ventral markings of the wings, the submarginal series of small ocelli of the hindwing (yellow, ringed with black) is more complete in the female (Fig. 4). General wing coloration both ventrally and dorsally ranges from white to pale greenish white in most specimens at the study site; wings are highly translucent so that ventral ocelli are usually visible dorsally (Figs. 3–4). *Morpho polyphemus* is morphologically unique from any other species of Central of South American species of the genus because of paucity of scales on the wings, permitting well-developed translucence. Males develop faster than females, by about 1–2 days, as commonly occurs in many species of butterflies.

Host Plant Specificity: At Barranca Colonia Campestre, the major larval host plant is *Paullinia pinnata* L. (Sapindaceae). This plant grows as a tall wiry shrub along the stream edges at the bottom of the ravine. Here, it is exceedingly abundant along sections of the stream, and grows both in sunny as well as heavily-shaded areas. Larger plants tend to lean over the water, sometimes actually having the tips of branches submerged, especially during the wet season (May–October). It is evident that this species forms a major component of the secondary-growth plant community associated with the edge of the stream. Occasionally larvae of *Morpho polyphemus* were found on seedlings of an unidentified species of *Inga* (Leguminoseae) which form a minor part of this plant community. Another legume, *Machaerium salvadorensis* is also abundant at this site, where it grows as a large sprawling armed liana, sometimes growing over *Paullinia*. This legume is the major larval host plant of *Morpho peleides hyacinthus* at this site. Neither eggs nor larvae of *Morpho polyphemus* have ever been found on *Machaerium salvadornesis* at this site, despite intensive searching. Larvae of *Morpho peleides* have never been found on *Paullinia pinnata* at this site, although in the laboratory, both species of *Morpho* readily feed and develop on each others host plant. We also observed that *Morpho polyphemus* from the study site completes its development when fed a species of *Inga* from Costa Rica. A few larvae of *Morpho peleides* were found on the same species of *Inga* at the study site. Other host plants have not been found to date, although from study of *Morpho peleides* in Costa Rica (Young and Muyshondt, 1972), we suspect broad larval host plant specificity. In light of our prediction of broad larval host plant specificity in this butterfly, surprisingly we have not found eggs and larvae of it in *Paullinia fuscescens*, which is almost as abundant as *P. pinnata* at the study site. Furthermore, we have consistently failed to find *Morpho polyphemus* on other genera of Sapindaceae also abundant at the study site, most notably *Serjania* and *Urvillea*.

Mortality Factors: Preliminary findings on rates of mortality in natural populations of *Morpho polyphemus*, suggest that mortality due to parasitism may be high. Out of 47 eggs collected in a few days at the study site, 27 produced wasps of the genus *Ooencyrtus* (Encyrtidae), a genus noted to parasitize aphids

and to reproduce by polyembryony. Since it has been noted that a single egg of members of the Encyrtidae gives rise to individuals of only one sex (Leiby, 1929), the observed emergence of both males and females of *Ooencyrtus* from a single egg of *Morpho polyphemus* indicates that at least two eggs of the parasite were initially oviposited. No other egg parasite has been found to date.

We estimate levels of larval mortality as high as 50% to be due to parasitism by a species of tachinid fly in the genus *Zenillia*; this figure is based on field samples collected over a two-year period, in which data was pooled to obtain a gross estimate of mortality from this parasite. To date, we have only one species of *Zenillia* recorded for this *Morpho* at the study site. Like many species of tachinids, the species of *Zenillia* which attacks the larvae of *Morpho polyphemus* does so by ovipositing eggs on leaves of the host plant, which are then ingested by the feeding host larvae.

We have failed to observe predation on eggs and larvae in the field and we suspect that predation by ants and other leaf-wandering forms is low.

In the laboratory, large numbers of larvae die in later instars from what appears to be a form of virus intestinal infection, resulting in discharge of large amounts of partially-digested leaf material. We do not know if such mortality occurs in the field, although we suspect that it does since such a disease is probably transmitted on leaves of the host plant.

Estimation of survivorship of adult *Morpho polyphemus* has not been studied, although we are planning an extensive mark-recapture program to study mortality on adults.

Larval Behavior: Larvae always occur singly in the field, with no indications of gregarious behavior, so well observed in other species of South American *Morpho*. During the first four instars, larvae remain on the ventral surfaces of older leaves of *Paullinia*. Here, each larva builds a thin silken mat which functions as both an anchoring device during resting periods as well as during periods of molting. Larvae only leave their silken resting mats for feeding episodes. Although we have not yet studied the diurnal feeding pattern in the larvae of *Morpho polyphemus*, we know that the larvae of *Morpho peleides* are strictly "dawn-dusk" feeders. We suspect that feeding in larval *Morpho polyphemus* may be either nocturnal or of the "dawn-dusk" variety, since both forms of behavior have been noted for the genus (Seitz, 1924; M. Barcant, pers. comm.; L. S. Otero, pers. comm.). Our field observations rule out diurnal feeding in this species.

Fifth-instar larvae rest on heavily-shaded branches of the host plant, lower than the leaves where they concentrate the bulk of their feeding. In such a resting position, the crypsis of the coloration of the fifth instar becomes evident. Fifth instars also construct resting mats along the branches. Sometimes, fifth-instar larvae appear to be aggregated on branches. We interpret this as a result of a shortage of space when several such larvae occupy an individual host plant,

rather than as a coordinated behavioral pattern in which larvae collectively congregate and exhibit collective responses for feeding, defense, etc.

We have conducted some preliminary tests on the defense systems of larvae—especially fourth and fifth instars. When initially prodded with small bristle brushes, a larva responds by violent pushing and waving movements of the anterior region of the body. When this is repeated several times within a few seconds, the larva raises the anterior end of the body and everts a small orange gland from a slit located between the first pair of true legs; a strong odor similar to that of rancid butter is emitted apparently from this everted gland. We interpret this as a chemical defense system perhaps similar to those known for certain papilionid butterflies and noctuid moths (Eisner, 1970). We have not studied this defense system outside of the laboratory, nor have we yet studied it with simulated attacks by ants, in the laboratory. Such studies, however, are planned.

The larvae of *Morpho polyphemus* exploit three systems of defense that follow in sequence: (1) strategy of hiding underneath leaves and on shady branches, (2) violent physical movements upon initial contact with a potential predator, and (3) the bringing into operation of a chemical system of defense when the first two strategies fail to deter the attacker.

Adult Behavior: Our major observations on behavior patterns of the adults concern movements of ovipositing females at the study site. Females generally oviposit in the early afternoon (12:30–2:00 P.M.) and reproductive effort (Labine, 1968) tends to be concentrated over small sections of the habitat. A single female will soar down the side of the ravine where *Paullinia* is abundant, and lay several eggs encompassing a few oviposition sequences within a small area. Such oviposition episodes are repeated several times by the same female, interrupted by short periods of resting in tall trees. While we have no data on the vagility of fecundated females, we believe that individuals will often deposit a large number of eggs in a given area where the host plant is abundant; whether or not the same female returns on several days to the same spot for oviposition cannot be ascertained. We do know that such behavior commonly occurs in *Morpho peleides* in Costa Rica. Elucidation of such behavior and how it contributes to the distribution of reproductive effort in space is an important aspect of understanding the evolutionary biology of the species. With respect to fecundity, females dissected immediately after eclosion usually contain about 15 eggs, while females captured in the field may contain as many as 80 eggs. Egg maturation probably peaks in *Morpho polyphemus* following insemination.

During oviposition, the female grabs the petiole of the leaf, holds her wings partly closed, and deposits the egg. Eggs are firmly attached to the dorsal surfaces of leaves, and are not easily dislodged. We suspect that oviposition is accurate in this species, with minimal erring known to occur in other species of butterflies (Dethier, 1959). There is no consistent pattern with respect

to site-selection on an individual *Paullinia* bush since an individual female may oviposit on leaves near the top as well as on leaves near the bottom of the bush. However, eggs are always laid on older leaves. We noted similar oviposition site-selectivity in *Morpho peleides* (Young and Muyshondt, 1972).

While adults of both sexes are presumably vagile in their daily movements, they are most abundant at three different times of the year: December–January, April–May and August–September. The adult population present during April–May, the beginning of the wet season, is the largest of the three peak abundances, being about four times as large as the smallest peak which occurs during the dry season (December–January); the remaining peak, which we term "moderate," occurs during the wet season (August–September) and is about one-half the size of the peak occurring during April–May. Our estimates of adult numbers are taken from daily records taken several times each month at the study site, and entail intensive search periods for about one hour each day. Marking studies, however, have not yet been conducted.

DISCUSSION

We feel that our observations on *Morpho polyphemus* are best discussed in terms of the following considerations intimately associated with the biology of the species: (1) sympatry with *Morpho peleides*, (2) effects of habitat destruction, (3) models of seasonal abundance, and (4) an evolutionary adaptive strategy.

Sympatry with Morpho peleides: In another report (Young and Muyshondt, 1972) we summarized the life cycle and biology of *Morpho peleides* in Costa Rica and El Salvador. The El Salvadorian population of this species is sympatric with *Morpho polyphemus* in the ravine at Barranca Colonia Campestre. Both species are common with having two of the four peak periods of adult abundance of *Morpho peleides* coinciding with the two peak periods of adult abundance in *Morpho polyphemus*. Both species oviposit in the ravine but the major larval host plant of *Morpho peleides* is *Machaerium salvadorensis*. There appears to be competitive exclusion so that each species exploits a different host plant for oviposition and larval development. The operation of this ecological process is further suggested by the free cross-feeding of larvae in the laboratory. Both species have the necessary physiological machinery to feed on each other's major local host plant, although ecologically, this does not occur in the field. This difference in larval host plant specificity in the field may be the major mechanism accounting for co-occurrence of the two species at Barranca Colonia Campestre. We emphasize the apparent larval host plant exclusion exhibited by sympatric populations of these two species of *Morpho* since previous host plant records for other species (Seitz, 1924; Costa Lima, 1936; Otero, 1971) do not consider the question of local host plant specificity as related to sympatry among species of the genus. Ehrlich and Raven (1964)

summarize various plant families known to contain host plants for *Morpho*, although again, data are apparently lacking on local host plant lists of sympatric species.

Such niche separation may also operate with respect to adult food sources, although previous study (Young, 1972a) has suggested that sympatric species of *Morpho* are characterized by adult populations exploiting the same food sources, on a regular basis. We have no records on food selectivity in adults of the species in El Salvador.

Morphologically, it is apparent that both species belong to different taxonomic groups within the genus. Seitz (1924) assigns *Morpho polyphemus* to the *catenarius* series, while *Morpho peleides* belongs to the *achilles* group. Both species groups show their greatest speciation in South America while *Morpho polyphemus* represents the single extension of the *catenarius* series into Central America, and *Morpho peleides*, together with a closely related species, *Morpho granadensis*, represents the geographical expansion of the *achilles* group in a similar northward manner. Other expansions of the South American fauna into Central America are represented by *Morpho theseus* (*hercules* group), *Morpho cypris* (*rhetenor* group), and *Morpho amathonte* (*rhetenor* group). Of all six species occurring in Central America, only *Morpho peleides* and *Morpho polyphemus* regularly occur in El Salvador. The remaining species, all of which occur in Costa Rica, are generally confined to undisturbed primary-growth lowland and montane tropical wet forest, a major vegetational habitat virtually extinct in El Salvador. On the other hand, species such as *polyphemus* and *peleides* are considered to be more often associated with second-growth plant communities and represent a major ecological expansion of the genus into such less stable environments. For these reasons, it is of tremendous ecological interest to determine the point of sympatry among the two species, and to contrast their biologies in such habitats.

Morpho peleides is a "brownish morpho" (Young, 1971a) while *Morpho polyphemus* is a "glossy white morpho." Their life stages differ to some degree, especially instars 3–5, and the pupa (see Young and Muyshondt, 1972a). Such differences reflect differences in the evolutionary history and divergence between species. *Morpho peleides hyacinthus* has an average developmental time of 76 days, while a Costa Rican subspecies, *peleides limpida* takes an average of 108 days for development from egg to adult (Young and Muyshondt, 1972a). Both subspecies of *peleides* therefore possess shorter developmental times than *Morpho polyphemus* (120) days, and we speculate that the prolonged ontogeny of this species is a result of a long evolutionary processes involving adaptation to survivorship in more stable plant communities, most notably primary-growth montane tropical wet forest. Adults of *Morpho polyphemus* are significantly larger than adults of *Morpho peleides*, lending further support to the idea that the former species has experienced a long evolutionary history in stable forest

communities; long developmental time and large size are among some of the traits predicted to be characteristic of insect species that are members of stable terrestrial tropical communities (e.g., Margalef, 1968). Seitz (1924) points out that the South American species of the *catenarius* series are typically associated with high altitude "primeval" forests. Furthermore, he mentions that in Central America, *Morpho polyphemus* is often found in areas of high human habitation as well as being a "canopy-dweller" in undisturbed forests. *Morpho peleides* has apparently experienced a long evolutionary history involving geographical expansion into montane forests from lowland forests, and from stable plant communities into highly disturbed plant communities. Such high plasticity with respect to adaptive radiation is implied for other members of the *achilles* group (Blandin and Descimon, 1970). Furthermore, *Morpho peleides* has undergone more extensive adaptive radiation in Central America than has *Morpho polyphemus* as indicated by the occurrence of no less than 17 subspecies of the former species in contrast with only two subspecies of the latter species (Seitz, 1924). A shorter average developmental time is predicted as one of several adaptations to colonization of less stable environments (MacArthur, 1962). Therefore, the invasion by *Morpho polyphemus* into highly disturbed second-growth plant communities represents a recent ecological expansion in evolutionary time, while that of *peleides* is more ancient.

We believe that the successful and persistent concurrence of both species of *Morpho* in a relatively restricted habitat at Barranca Colonia Campestre has been facilitated by differences in the past evolutionary history of each species, in addition to the capacity of each species to exploit different larval host plants. Carrying our argument further, we predict average smaller size in *peleides* than in *polyphemus*, which does occur (average wingspan of male *peleides* is 8.5 ± 1.4 cm, $N = 10$; average wingspan of male *polyphemus* is 11.5 ± 2.0 cm, $N = 10$), and also higher fecundity in *peleides*, which we have not yet measured in either species. From theory of intrapopulational adaptation to stable environments (e.g., Levins, 1968), we also predict lower genetic variability in *Morpho polyphemus*, which may in fact be undergoing transient polymorphism in response to entering a new adaptive zone.

Effect of Habitat Destruction: Seitz (1924) mentions that *Morpho polyphemus* occurs locally as both a species associated with the canopy of tropical forests, and also near the ground in areas of massive land clearing and human habitation. In light of the fact that the majority of other species of *Morpho* are associated with either understory or canopy of primary-growth forests (with the exception of the *achilles* group), we find this dichotomy in habitat selection of *Morpho polyphemus* of particular interest. Although Seitz mentions that the species occurs at high altitudes (i.e., 1300 m. elev. in Guatemala), we find that it occurs over a wide altitudinal range in El Salvador. Seitz (1924) also points out that the majority of other species of *Morpho* belonging to the same series as

polyphemus (i.e., *perseus*, *theseus*, *laertes*, *catenarius*, etc.) are primarily distributed at high altitudes, where they occur primarily as canopy-dwellers. For example, in Costa Rica, *Morpho peleides* and *Morpho theseus* are sympatric locally at high altitudes (900–1000 m.), although the latter species is strictly a canopy-dweller while the former is common in low second-growth vegetation. All of these species possess white color patterns on their wings, and we argue that such coloration is an adaptation for unpalatable species inhabiting montane or cloud forests, where diffuse light (rather than direct sunlight) permits the exploitation of a color-contrast strategy for advertisement (i.e., white butterfly against dull backgrounds). Such considerations assume that such species of *Morpho* have evolved primarily in primary-growth montane forests, rather than in lowland wet forests, where various forms of bright blue reflective coloration of wings in association with direct sunlight would be a morphological adaptation associated with unpalatability or other predator-escape defense mechanisms (Young, 1971a).

In Costa Rica, the geographical distribution of *Morpho polyphemus* is generally restricted to the hills (200–300 m. elev.) near Rincon on the Osa Peninsula (Puntarenas Province). Here, the species occurs above primary-growth tropical wet forest and is seldom seen at lower elevations near the coast. The canopy of the evergreen forest at Osa typically occurs at 30–45 meters height and this is where adults of *Morpho polyphemus* are usually seen. Baiting experiments on the ground consistently fail to attract adults of this species at Osa, while readily attracting *Morpho peleides*. *Morpho polyphemus* at Osa in every sense of the word appears to be a canopy-dweller. We have consistently failed to find this species in areas of human habitation in Costa Rica, whereas the reverse is true in El Salvador. The geographical distribution of *Morpho polyphemus* in Costa Rica is restricted despite the availability of similar habitats in other parts of the country. We interpret this difference in habitat selection between Costa Rica and El Salvador as the result of recent (about 2,000 years) land clearing movements in El Salvador. The original habitat of *Morpho polyphemus* however is preserved to some degree in Costa Rica.

Depending on the amount and kind of selection pressures operating between Costa Rica and El Salvador, predictions can be made regarding the evolutionary adaptive strategy of the species in both places.

Models of Seasonal Abundance: Adults are most common at the study site three times each year, corresponding roughly to January–February, April–May, and August–September. Many dicots and monocots lose their leaves during the dry season. Others, such as *Paullinia* and *Inga* retain most of their leaves, but become less succulent, and covered with thick layers of dust. Leaves in this condition appear less edible to herbivorous insects. Vegetative growth on *Paullina* and *Inga* is absent during the dry season. The dry season usually falls been late November and early April so that adult *Morpho polyphemus* is most

abundant during the early dry season (December–January), beginning of the wet season (April–May), about mid-way through the wet season (August–September). Each of these three peaks of adult abundance in the ravine varies considerably in magnitude from the others: adults are most abundant at the beginning of the wet season, moderately abundant at the middle of the wet season, and least abundant during the early dry season. Moreover, adults are virtually absent from the study site during intervening months. This apparent seasonal abundance is correlated with its development time: of about four months (Table 1). The peaks of adult abundance fall about four months apart and suggests the occurrence of essentially non-overlapping generations of the butterfly at the study site. Preliminary data on monthly distribution of eggs and various larval instars supports this view.

Seasonal abundance of adults has also been noted for other species of *Morpho*. Seitz (1924) comments that an allied species, *Morpho laertes* which is common in the Brazilian provinces of Rio de Janeiro and Espiruto Santo during January, and steadily declines in numbers towards March. He also mentions that a similar trend takes place for a second allied species of the *catenarius* series, namely *Morpho catenarius*, at Santa Catharina in Brazil. The situation in El Salvador for *Morpho polyphemus* is in part analogous to the situation in Brazil, although data are lacking for peak abundance at other times of the year in the latter situation. Virtually nothing is known about the adaptations of the life cycles in species of tropical butterflies with respect to season variation in rainfall. Therefore, it may very well be that certain species of Brazilian *Morpho*s need at least 10 months to mature so that adults are found at only one time each year. Such an adaptation could evolve as a selective response to regional climatic variation in which a series of short dry seasons ("veranillos") are interspersed with wetter periods, and perhaps one long dry season ("verano"). Selection would tend to favor long development time for species in stable environments (Margalef, 1968; Connell and Orias, 1964; Slobodkin and Sanders, 1969). However, we wish to view the problem in terms of life cycle adaptation to patterns of rainfall.

Many tree species in wet tropical forests become deciduous during periods of high water stress (e.g., Richards, 1952) even though the forest as a whole appears to remain evergreen. Herbivorous insect species feeding on plant species that go deciduous may therefore be temporarily deprived of their food sources. An adaptive strategy for such herbivores would be "switch off" to new host plants that remain evergreen during dry periods, or become metabolically less active until the preferred host plants leaf out again. The latter appears to be the major adaptive strategy for lepidopterous species caught up in such an ecological crisis, since most species are relatively sedentary (on the host plant) during the larval stage. In the specific case of *Morpho*, we have noted that larvae of both *polyphemus* and *peleides* will only eat fresh leaves and reject less succulent and dusty leaves. In host plants such as *Paullinia*, *Machaerium*, and

Inga, leaves appear susceptible to water stress both in the laboratory and in the field. In the field, during the dry season, the majority of leaves on an individual bush or vine of these larval host plants become markedly less succulent and acquire heavy coatings of dust. They therefore appear less palatable to larvae than they do during the wet season. Leaf-fall, however, is spotty in these plants.

We wish to advance several hypotheses that could account for the seasonal abundance of *Morpho polyphemus* in El Salvador. From rainfall data gathered by the Servicio Meteorologico de El Salvador, the pattern of seasonality is generally the same in most parts of the country.

Our first hypothesis has to do with the possible existence of a diapause synchronization in larval populations, as a dry season adaptation. The majority of young larvae present at the beginning of the dry season do not complete development by the December–January adult emergence period, but enter into a diapause condition as their host plants become less succulent. With the beginning of the wet season, these larvae complete development and produce adults. At the same time, adults appearing during December–January lay eggs which hatch, and these larvae also enter into a diapause at the height of the dry season, which normally occurs between February and April. This generation also completes development with the beginning of the wet season, so that the adult emergence at this time is composed of individuals from two generations. The next generation, eclosing in August–September, is smaller since adults are produced from a single generation. Some testable predictions generated by this hypothesis include the following: (1) the adult population present during April–May should be made up of mostly young adults, and (2) there should be a preponderance of fourth and fifth instar larvae during late March and early April as a response to diapause synchronization in the population. An indirect result of diapause synchronization in the larval population may be a reduction in parasitism from tachinids. Decreased larval feeding during diapause would decrease the probability of ingesting tachinid eggs (oviposited on leaves, stems, etc.) assuming that the adult flies actually oviposit during the dry season. As to the possible mechanism initiating a dry season diapause in lepidopterous larvae such as those of *Morpho*, clearly we must rule out any photoperiodic effect comparable to that known for initiation of diapause in temperate zone insects. Since the dry season results in a major physiological change in plants in response to water stress, a possible mechanism for herbivorous insects may involve their response to changes in leaf succulence. This is of particular interest in light of studies on humidity receptors in lepidopterous larvae (Dethier and Schoonhoven, 1968). Increased isolation during the dry season may be another important environmental cue initiating diapause, as this may elevate air temperatures close to the ground. Lepidopterous larvae have been known to initiate feeding in response to changes in air temperature (Dethier and Schoonhoven, 1968).

Another hypothesis concerns massive mortality of larvae from heavy rainfall and stream-flooding at the study site. Many larvae die because of heavy rainfall during September and October, the wettest months of the year, resulting in a smaller number of adults maturing by December–January. Larvae also die from indirect effect of heavy precipitation in the form of mold on eggs and perhaps larvae also. We observed substantial egg mortality due to mold in *Morpho peleides* during the wet season in Costa Rica (Young and Muyshondt, 1972). The major larval host plant, *Paullinia pinnata*, is frequently flooded along the stream edges during the wettest months, and any small larvae present may drown. Such mortality factors would be minimal during the dry season, resulting in a large emergence of adult *Morpho polyphemus* during April–May. Since larvae are in the fifth instar or have actually pupated by the beginning of the wet season they would be relatively unaffected by heavy rainfall. A substantially greater number of larvae should survive at this time. Theoretically the large crop of adults in April–May is the result of a single generation characterized by high survivorship from abiotic mortality factors. Thereafter, rainfall would be more or less moderate throughout the remaining wet season, resulting in some mortality of eggs and larvae, and producing a moderate-sized adult population in August–September. Another possible source of mortality under this hypothesis would be massive mortality of adults during October and November (produced by the August–September emergence peak) due to heavy rainfall, and the inability for adults to mate and oviposit successfully on rainy days of the wettest months of the year. Optimal breeding conditions may be associated with the dry season where flying activity may be maximized. Thus, more females may mate successfully in the adult population appearing at December–January than in adult populations appearing at other times (wet months) of the year.

In a third hypothesis we consider the adverse effect of dryness on oviposition of tachinid flies parasitizing larval *Morpho polyphemus*. The decreased succulence of host plant leaves and the acquisition of dusty coatings on leaves decreases the incidence of successful oviposition by tachinids on these plants; eggs may be less firmly affixed and thus become more easily dislodged during windy periods. *Morpho* larvae feed less on less succulent leaves making feeding more erratic during the dry season. Tachinid eggs are therefore less likely to be eaten before they either desiccate or are blown away. Under this hypothesis, larval survivorship from parasitism is maximal during the dry season resulting in a large cohort of adult butterflies during April–May. A moderate adult population is produced later in the wet season (August–September) presumably since the parasite population is still slowly recovering from its previous massive mortality during the height of the dry season. However, the next generation of adult butterflies (December–January) will be markedly affected by tachinid parasitism, resulting in the smallest peak of adult numbers, since the parasites

are exploiting larvae produced by the August–September adult cohort. The generation(s) of parasites associated with these larvae are presumably able to successfully complete development before the height of the dry season, which begins in early February. The resiliency of the parasite populations to recover after the beginning of the wet season is in part due to new suitable oviposition sites resulting from increased vegetative growth during the wet months.

To account for seasonal differences in peak adult numbers in terms of a massive movement of adult butterflies into the relatively wetter ravines (such as Barranca Colonia Campestre) during the dry season we wish to present a final hypothesis. Adult fecundated females in search of succulent plants for oviposition move into the more humid ravines during the dry season. Since the height of the dry season occurs between February and April, this results in a large adult population resident there by the end of the dry season. We predict that the large adult population present during April–May will consist of old individuals rather than a new cohort of young butterflies as predicted under the other hypotheses. The small adult population occurring during December–January is explained away under this hypothesis by it being a residual population left behind during exodus of many adults out of the ravine before the driest period sets in, presumably a mechanism of population dispersion allowing young adult females to oviposit elsewhere. As the dry season advances, however, the bulk of the adult population contracts in distribution to the humid ravine.

We are at present in no position to support any of the above hypotheses; clearly, more concise assessments of adult numbers, population age-structure, and adult vagility are needed to account for seasonal adult abundance patterns. Any combination of factors relating to the different hypotheses may determine seasonal differences in population productivity.

Regardless of the precise mechanisms accounting for seasonal differences in productivity there is apparent synchronization of highest adult numbers with the beginning of the wet season. For many plant species, the beginning of the wet season is a period of rapid vegetative growth. Therefore, more plant biomass is available to herbivores such as larval *Morpho polyphemus*. Tempered by egg and larval parasitism, the next generation of adults would be of moderate size (August–September), and with decreased vegetative growth at the beginning of of the dry season, population numbers might dwindle due to decreased suitable food supply and parasitism.

Due to observed seasonal patterns of fruit production (Janzen, 1967), we predict that adult food sources would not be a major factor contributing to seasonal differences in productivity. Adults of *Morpho polyphemus* apparently exploit a wide range of fermenting fruits in El Salvador, in addition to decaying fungi. During the short dry season in the Caribbean lowlands of Costa Rica, various species of *Morpho* exploit fallen decaying fruits of *Coumarouna* as a major food source (Young, 1972a, b).

An Adaptive Evolutionary Strategy

We believe that *Morpho polyphemus* represents a species that originally experienced a geographical adaptive radiation into montane tropical wet forests, and subsequently underwent ecological adaptive radiation into less stable second-growth habitats in regions where extensive land clearings by man had occurred over a long period of time.

Central America has experienced extensive and intensive land cultivation practices involving the establishment of monoculture crops, much of which is concentrated in El Salvador (Palerm and Wolf, 1960). The effects of extensive establishment of crop monocultures in the New World Tropics has been recently discussed in terms of the apparent close coevolution between plant species and herbivorous insects characteristic of tropical terrestrial communities (Janzen, 1970). When tropical communities are destroyed (e.g., through primitive slash-burn agriculture systems), many herbivorous insect species confronted with a major ecological crisis, must exploit a more restricted distribution of suitable habitats, or else face extinction. In the case of *Morpho polyphemus*, it is apparent that this species is in the process of adjusting to a very patchy distribution of suitable habitats, most notably those restricted to ravines—the remaining refuge of relatively undisturbed second-growth forest.

We maintain that this ecological adjustment is a relatively recent event which is still evolving. The species in El Salvador no doubt still possesses many of its original ecological and behavioral traits that are in the process of being altered in response to new selective pressures associated with new adaptive zones.

Aside from adaptations associated with life cycle, and seasonality of larval and adult food sources, we believe that another major aspect of the adaptive strategy in this species concerns the evolution and expression of unpalatability.

The evolution of the unique glossy white translucent wings of this species may be an adaptive response for rendering the insect noticeable in the diffuse light so characteristic of montane and cloud forests. Selection favors the advertisement of the butterfly since most individuals in a local population are presumably highly unpalatable as prey for most potential predators. We find some indirect evidence for this in terms of the major larval host plant, *Paullinia pinnata*. Many Sapindaceae have been long suspected of containing noxious compounds in both leaves and bark. Some species of *Sapindus* possess a saponifying glucoside ("saponin") irritating to human skin, while in other species pollen causes severe inflammation of the eyes, throat, and bronchial surfaces. More specifically, for *Paullinia pinnata*, we note, from the *Botanique Pharmaceutique*, a brief comment by Dr. L. Beille, in 1909 (Paris): "L'ecorce contiente un alkaloide: Timboine (Martin, 1877). Elle est acre, irritante. Les graines servent a étourdir le poisson." Translation: The bark contains an alkaloid: Timboine. It is bitter and irritant. The seeds serve to stun fish." An earlier publication in the *Histoire des Plantes* **5**, carried an article by H. Baillon, Paris, 1874, in reference to

Paullinia pinnata: "*Paullinia pinnata* L., espece qui se trouve a la fois en Amerique et dans L'Afrique tropicale, passe, dans ce dernier pays surtout, pour un poison terrible. Les negre emploient sa racine et ses semences. Les indiens qui habitent les forets bresiliennes exprimment, dit-on le suc ses feuilles. . . " . Translation: *Paullinia pinnata* L., a species found both in tropical America and Africa, it is reputed, most of all in Africa, to have a terrible poison. The natives use the roots and seeds. The Indians living in Brazilian forests extract the juice from the leaves. . . " . Such statements suggest medicinal and hunting uses of *Paullinia pinnata* because of its toxic properties. Recently (Levin, 1971), summarizing the adaptive significance of secondary compounds associated with plant species, pointed out that many insect species which feed on plants receive protection against predators in the form of unconverted or converted secondary compounds derived from host plants.

We predict that local larval host plant specificity in *Morpho polyphemus* is narrow; we have only found one species of *Inga* to be a second host plant at the study site. Recently (Brower, 1970), discussed automimicry for other butterflies, and a similar defense strategy may occur in *Morpho polyphemus*. Here, the major host plant, *Paullinia*, is unpalatable while a minor host plant, *Inga*, may be palatable. (Levin, 1971; Whittaker and Feeny, 1971), pointed out that different plant groups vary both qualitatively and quantitatively in the types of secondary compounds they contain. If we assume such differences between *Paullinia* and *Inga*, larvae feeding on these plants may differ in their palatability as prey. This could result in a local population of adult *Morpho polyphemus* being automimetic, primarily of unacceptable individuals (those reared on *Paullinia*) but also including a small fraction being more acceptable (those reared on *Inga*) as prey.

Any unpalatability of *Morpho polyphemus* acquired through feeding on *Paullinia* is most likely a result of modification of some compounds ingested from the host plant. We conclude this from the fact that *Thecla marsyas* which also feed on this plant show a high incidence of hymenopterous parasitism in the larval stage. Such parasites lay their eggs directly on the integument of the host and unless the host possesses an effective defense system, substantial rates of mortality may result. The larvae of *Morpho polyphemus* exhibit defensive movements in addition to cryptic resting behavior, as well as having a chemical defense system. These three devices may lower parasitism rates in natural populations. More data on the mortality rate of insect herbivores associated with *Paullinia* resulting from predation and parasitism, may make it possible to correlate mortality rates with the presence or absence of the butterfly's defense system. It might also be possible to show indirectly that the secondary compounds of *Paullinia per se* do not insure protection against biotic mortality agents. The incorporation and modification of them by the herbivore species as a chemical defense system may account for unpalatability and defense.

South American species of the *catenarius* series exhibit cluster oviposition and larval gregariousness on the host plants (Seitz, 1924; L. S. Otero, pers. comms.). The single Central American representative of this species cluster, *Morpho polyphemus*, consistently exhibits single oviposition and non-gregarious larvae. For example, Luis S. Otero (pers. comms.) has studied *Morpho laertes* in Brazil, and has observed that one female may lay as many as 150 eggs on a few adjacent leaves of the host plant (various species of Leguminoseae). Upon hatching, the larvae collectively remain close together on leaves until the fourth instar, at which time they construct a single continuous silken tent over the extremities of several branches. At the end of the fifth instar, larvae disperse from the host plant for individual pupation. Similar behavior has been noted for *Morpho catenarius* at Rio de Janeiro (Seitz, 1924). Our studies of the allied species, *polyphemus*, show that no such group behavior patterns occur.

Cluster oviposition and larval gregariousness are specialized forms of behavior that must be accompanied by the evolution of effective defense systems. To some extent, the construction of a silken tent in which larvae may rest when not feeding represent a form of behavior related to protection against predators even though younger instars remain exposed to predators and parasites. It is unlikely that only species which exploit unpalatable host plants will be able to evolve larval gregariousness resulting in part, from cluster oviposition. In this way, predators or parasites will be discouraged from attack, as a result of both aposematic coloration of larvae (i.e., red and yellow) and collective movements associated with defense. Such behavior patterns tend to localize breeding populations in stable forest communities since reproductive effort (Labine, 1968) becomes restricted and the distribution of breeding populations is patchy. Such specialization possesses high adaptive value for species inhabiting primary-growth tropical wet forests (Margalef, 1968).

From such considerations, we interpret single oviposition and non-gregarious larval behavior in *Morpho polyphemus*, to be recently evolved forms of adaptive behavior associated with the colonization of less stable environments such as restricted patches of second-growth vegetation. From the theory of *r*-selection (MacArthur, 1962), it is predicted that high adult vagility linked with reproductive patterns that increase population dispersion (i.e., single oviposition as opposed to cluster oviposition) are valuable requisites for successful colonization of less stable (predictable) environments. The geographical distribution of South American species in the *catenarius* series is generally restricted to primary-growth montane wet forest, realized to some extent for *Morpho polyphemus* in Costa Rica, but lacking in El Salvador. Such environments are generally considered to be more stable since they represent later stages in the ecological succession of plant communities. The formation of less stable environments through the impact of man on tropical terrestrial ecosystems has meant that species such as *Morpho polyphemus*, formerly so well integrated into stable

forest communities, had to undergo a major directional shift (i.e., from K-selection to *r*-selection—MacArthur, 1962) in adaptive evolutionary strategy in order to cope with problems of survivorship in less stable environments. Through an evolutionary history entailing exploitation of unpalatable larval host plants and the development of defense systems (larval gregariousness, larval defense movements, and chemical systems of defense) and automimicry, species such as *Morpho polyphemus* could make the appropriate adaptive shifts in ecological and behavioral traits associated with entering less stable adaptive zones. Presumably these traits involved the evolution of single oviposition, nongregarious larval behavior, well developed chemical systems of defense, shorter development time, higher fecundity, and perhaps broader host plant specificity.

An alternate explanation for the colonization of second-growth plant communities by *Morpho polyphemus* would concern severe competitive interaction with other species of *Morpho* associated primarily with the canopy of primary-growth forests, i.e., Central American species of the *rhetenor* group (*Morpho amathonte*, *Morpho cypris*). We rule this out primarily on the basis of the persistent co-occurrence of all three canopy species on the Oso Peninsula in Costa Rica. Presumably a major mechanism for this concurrence is divergence in larval host plant specificity. Further study of the biology of all three species at Osa in Costa Rica should elucidate such a mechanism if in fact it exists.

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Ecology and Yearly Cycle of the Firefly *Photuris pennsylvanica* (Coleoptera: Lampyridae)

Ronald R. Keiper and Lynn M. Solomon
Pennsylvania State University, Mont Alto, Pa. 17237

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Abstract: Several preliminary experiments were conducted to examine factors influencing the daily feeding rhythm and the yearly developmental sequence of the larval stage of the firefly *Photuris pennsylvanica.* Loose, loamy, well-drained soil allowed normal circadian behavior while sand, sawdust, and clay-like mud prevented larval migration. The yearly developmental sequence could be duplicated in the laboratory by simulating environmental conditions, and acceleration of this sequence was achieved by manipulating the length of exposure to simulated winter temperature.

Photuris pennsylvanica is the common late summer species of Lampyridae found in the northeastern United States, where both the larval and adult forms are quite common from June until early September. Lampyridae larvae resemble the female glowworm (Darwin, 1859) with each segment possessing a horny brown plate dorsally, soft, rose-colored sides with white spiracles on brown patches, and a cream colored ventral surface with one pair of short legs (Boving and Craighead, 1931). The larvae of *Photuris pennsylvanica* are nocturnal (Arnett, 1960), remaining in subterranean burrows during the day and feeding on soft-bodied insects, earthworms, and snails on the surface at night. Lampyridae larvae have long, hollow, and slender mandibles with which they inject a digestive enzyme into their prey (Winkler, 1964). This enzyme causes the body of the prey to liquify, and this aqueous flesh is then consumed. Perhaps the most interesting aspect of the anatomy of these larvae is the two singular light organs located on the ventral surface of the next-to-the-last segment of the abdomen. The larvae possess similar luminous characteristics to that of the female *Photuris*, and in fact are often mistaken for a female at night when observed among the foliage. On the last segment of the abdomen there is a ventral prop-leg that aids in surface locomotion and also serves as a brush for grooming.

Although the literature concerning the anatomy, physiology, and behavior of the adult firefly is fairly extensive, few observations have been made on the larval stage, and those that do exist have been gathered primarily through limited field observations. For example, Darwin (1859) made some observations on lighting, feeding, and grooming behavior, while Riley determined that a two-year period was required for larval maturity (Arnett, 1960). Due to the general scarcity of information regarding the ecology of this larval stage, the following preliminary studies were undertaken to determine:

1. whether the normal developmental sequence of larval feeding, inactivity, pupation, and eventual adult emergence could be maintained in the laboratory under simulated environmental conditions.
2. whether this sequence could be altered by experimentally manipulating the length of exposure to different temperatures.
3. whether the texture of the soil is an important factor in determining the circadian feeding behavior of the larvae.

METHODS

While an overall attempt was made to maintain the larvae within terraria in the laboratory under conditions similar to those existing in the normal environment, three major variables were examined: Effect of Soil Texture on Larval Migration; Simulation of Winter Temperature, and Length of Exposure to the Simulated Winter Temperature.

The experimental terraria were large wide-mouthed, one gallon pickle jars approximately 6 inches in diameter and 14 inches in height. Approximately ⅙ of the bottom of the terrarium was filled with stones, to ensure drainage, then soil was placed on top of the stones until approximately ⅔ of the terrarium was filled. Next, the surface of the soil was partially covered with grass and foliage. The mouth of the terrarium was covered with fine mesh cheesecloth to prevent the escape of the garden slugs (used as food for the larvae) and the adult fireflies after they emerge. Finally, 50 *Photuris pennsylvanica* larvae, each at least ½ inch in length, were caught and placed in each terrarium.

The initial experiment consisted of storing terrarium 1 in a cold storage area with an approximate temperature of 9° C. to simulate fall external temperature for a period of 30 days. This terrarium was then stored in a refrigerator with an average temperature of 6° C. for 120 days and 3° C. for 73 days. The terrarium was then placed on a windowsill having an average ground temperature of 24° C. for a period of 40 days when emergence of adult flies occurred. This experiment was designed to demonstrate that normal daily migratory patterns and proper life cycle sequences can be maintained in the laboratory.

The second experiment dealt with the effects of different types of soil upon the migratory habits and life cycle of *Photuris* larvae. One terrarium was filled with loose loamy soil (the control terrarium), a second was filled with sand, while a third was filled with decomposing sawdust, and the fourth was filled with a heavy clay-like moisture-retaining soil. Each of these terraria was filled with 50 larvae, and exposed to the sequence of simulated temperature described above.

The third experiment was designed to determine if the basic yearly sequence could be accelerated by exposing the larvae to the same temperature pattern as in the control situation, but for a shorter interval. Thus, terrarium 2 was maintained at 9° C. for 30 days, 6° C. for 100 days, and 3° C. for 20 days.

After exposure to temperatures of 24° C. emergence of adults took place in 35 days. The cycle had thus been reduced from 263 total days, and emergence in June, to only 185 days and emergence during April.

Finally, an attempt was made to see if the yearly sequence could be accelerated by eliminating the 3° C. temperature from the simulated temperature pattern. Larvae in this terrarium were exposed to 9° C. for 30 days, 6° C. for 120 days, then 24° C. for 45 days until emergence of adults took place.

OBSERVATIONS AND RESULTS

In an attempt to determine if the normal behavior and development of *Photuris pennsylvanica* larvae could be maintained in the laboratory through simulation of natural temperature variations, an original population of 50 larvae was exposed to a series of temperatures beginning on September 22, 1970 and continuing to June 12, 1971, a total of 263 days. By this date, only 6 adult fireflies had emerged, or 12% of the original population. While this percentage is low, it nevertheless suggests that the proper life pattern is maintained when exposed to laboratory conditions and suggests that larvae of this species might be a useful laboratory animal for future studies.

In the second experiment, designed to determine the effects of different soil types upon larval migration and life span, the control terrarium (the one used in the previous experiment), filled with loose, loamy soil, was compared to three other types of substrate. In the terraria filled with sawdust and sand respectively, no adult flies emerged. On the surface, the sawdust did not retain any water, while the sawdust beneath the surface was saturated. The larvae did not practice daily migration, perhaps due to the hard surface crust and/or the saturated lower soil, and remained on the surface. When this terrarium was refrigerated, the unprotected larvae perished, as evidenced by the 14 dead larvae found on the surface. The sand maintained acceptable moisture, compared to the control terrarium, except for the immediate surface which became a hard-packed crust due to drying. This crust was broken twice during the course of the experiment, but quickly reformed. Once again this crust prevented daily larval migration to and from the surface, and caused the larvae to remain on the surface. At the conclusion of the experiment, 17 dead larvae were found on the surface, where they apparently perished from the cold. In the last terrarium, a heavy, clay-like, moisture-retaining soil was used. Once again, evaporation produced a crust on the surface, but the soil from about 1 inch below the surface to the bottom of the jar remained quite soft. This soil allowed larval movement up to about 1 inch of the surface. Eventually, 2 adults emerged, but the remaining larvae apparently perished, either from the cold temperatures or from suffocation due to a water-saturated lower soil. From these rather poor results, it appears that larvae of *Photuris pennsylvanica* thrive best in loose,

well-drained, loamy soil. This view is substantiated from field observations, for the greatest number of larvae are found in this type of soil.

In the third experiment, the yearly sequence was accelerated by exposing larvae to temperatures of 6° C. for only 100 days (rather than 120) and 3° C. for only 20 days (rather than 73 days). By late March, adults began to emerge, and eventually 18%, or 9 of 50 possible adults emerged. Thus it appears that the yearly cycle can indeed be accelerated, although further study is needed to determine the exact time requirements for each temperature.

Finally, an attempt was made to determine if the 3° C. temperature could be eliminated without altering the sequence. Instead of exposure to this low temperature, larvae were submitted to 120 days at 6° C. Of the original 50 larvae present, only 10%, or 5 of the 50 possible adults emerged. Once again, the percentage of emergence is low, but the results suggest that the low temperature is not needed for completion of the developmental cycle.

Several interesting observations were also made in the course of this study relating to the behavior of the larvae. The larvae migrate to the surface each night, using the same tunnels, and are most plentiful on the surface between 9:00 P.M. and 3:00 A.M.

Larvae of *Photuris pennsylvanica* seems to prefer the gray garden slug (*Deroceras reticulatum*) as a food source because the larvae could be collected in good numbers among garden litter where the slugs were prevalent. Also, garden slugs were preferred to many other types of food presented during the course of their captivity. When feeding on the slugs, the larvae apparently injected a flesh destroying enzyme that liquified the slugs flesh, allowing the liquid to then be consumed. It appeared that the slugs seemed unaware that they were literally being eaten alive. In addition to these slugs, captive larvae also consumed blue grapes, generally by drinking the juice of a broken grape. In the wild, larvae have also been observed feeding in this manner.

Photuris pennsylvanica larvae, like the adults, possess primitive light organs on the eighth segment of their body. By subjecting them to repeated flashings from an amber pen-light, imitating the normal one second lighting interval of *P. pennsylvanica* males, they have been stimulated to repeat erratic flashing responses. It is interesting to note that these responses can also be elicited by stimulating the larvae with repeated flashings of the amber light at six second intervals, the normal lighting response of males of the species *Photuris pyralis*. Such results suggest that these larvae may possess a crude understanding of the sexual communication practiced by adult Lampyridae and demand further study.

The pupae of *P. pennsylvanica* are of the exarate form where the appendages develop free of the body of the organism. The pupae resemble an enlarged, stiff image of a mature larva and remains luminous while it develops an earthen cell around itself below the surface of the soil. After between 20 and 24 days of

pupation, emergence occurs as adult fireflies escape the earthen cell and move to the surface of the soil.

Thus, while the experimental results obtained were not dramatic as far as numbers were concerned, they suggest that the yearly cycle can be manipulated experimentally and that the type of soil is important to the behavior and the survival of the larvae. Observations of larval behavior also suggest some areas for additional study.

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Thoracites B.B. in the Ethiopian Region, with Descriptions of Two New Species (Diptera: Sarcophagidae)

F. ZUMPT
SOUTH AFRICAN INSTITUTE FOR MEDICAL RESEARCH, JOHANNESBURG

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Abstract: Of the genus *Thoracites* B.B., *T. abdominalis* (Fabricius) from the Oriental Region and *T. cingulatus* Bezzi from the Ethiopian Region have been described. The dissection of the male genitalia has now revealed some of the specimens attributed by Zumpt (1958) to *T. cingulatus*, represent two new species, which are described as *T.* **neglectus** n. sp. and *T.* **nigeriensis** n. sp. The status of *T. cingulatus* is discussed and a key to all species of *Thoracites* is given.

In the revision of the Rhiniini of the Ethiopian geographical region (Zumpt, 1958), I re-described *Thoracites cingulatus* Bezzi, based on a pair of flies from Mozambique, identified by Peris (1952). Under this name I listed a male from Zululand, S. Africa, and 3 ♂ ♂ from Nigeria. The cerci and paralobi of the male from Mozambique were figured for the first time, whereas those males from the two other localities were referred to *T. cingulatus* according to the non-hypopygial features, taking into consideration that in nearly all Rhiniini, a fairly broad variation exists.

The dissection of the terminalia of the males from Zululand and Nigeria have revealed that we are dealing with two more distinct species.

The genus *Thoracites* was founded by Brauer and Bergenstamm (1891) in order to lodge *Rhyncomya pulmata* Schiner = *Musca abdominalis* Fabricius. This species, recorded from India and Ceylon, is easily separable from the African species by the male genitalia as well as by non-hypopygial features:

Key to the Species
(males only)

1. (2) Abdominal tergites III and IV with a long and thick lateral discal bristle. Abdomen wholly dark yellow, without pattern. Hypopygium with slender cerci and paralobi (Fig. 1). 7–9 mm.—Oriental species ..... *T. abdominalis* (Fabricius)
2. (1) Abdominal tergites III and IV without an outstanding long lateral discal bristle. Abdomen with a blackish pattern, consisting of broad transverse and a medium longitudinal stripe on tergites III to V, tergite I + II almost completely darkened.—Ethiopian species 3

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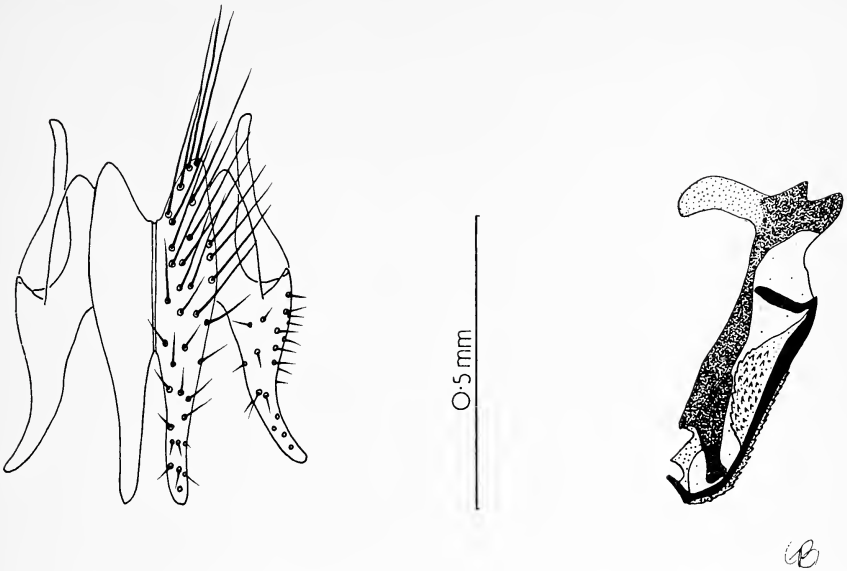

Fig. 1. *Thoracites abdominalis* (Fabricius). Cerci with paralobi and phallosome (specimen from Mahagony, Ceylon).

3. (4) Paralobi terminally hook-shaped (Fig. 2). 6 mm.—Natal ..... *T.* **neglectus** n. sp.
4. (3) Paralobi terminally not hook-shaped 5
5. (6) Cerci and paralobi densely haired, terminal part of cerci more slender (Fig. 3). 5–6 mm.—Nigeria ..... *T.* **nigeriensis** n. sp.
6. (5) Cerci and paralobi relatively sparsely haired, terminal part of cerci broader (Fig. 4). 6 mm.—Mozambique ..... *T. cingulatus* Bezzi.

DESCRIPTIONS OF THE *Thoracites* SPECIES FROM THE ETHIOPIAN GEOGRAPHICAL REGION.

Thoracites **neglectus** n. sp.

This new species is separable from *T. cingulatus* only by the structure of the hypopygium.

MALE: Eyes bare, with small facets. Frons at its narrowest point measuring 1/7 of eye-length (frontal index = 0.14). Frontal stripe complete, black, parallel, parafrontalia and -facialia with dense silvery-white pollinosity and with black setae of moderate density; *iv* long and thick, *ev* not distinguished from the postocular bristles, *oc* proclinate, long and thick and accompanied by several black bristly hairs; lower half of parafrontalia with 6 pairs of *paf*. Antennal segments blackish, except the terminal margin of the second segment, which is yellow; third segment a little more than twice as long as the second and densely covered with a short yellow setulosity, arista with long dorsal and ventral hairs; 2nd segment with a long black bristle. Antennal groove yellowish pollinose, a median convexity is not developed. Bucca measures 2/5 of eye-length, densely pollinose like the parafacialium, with a small brown spot at the anterior eye-margin. Facial ridge with 2 bristly hairs above the vibrissa, peristomal bristles black and forming a complete row, hairs yellow, but in the

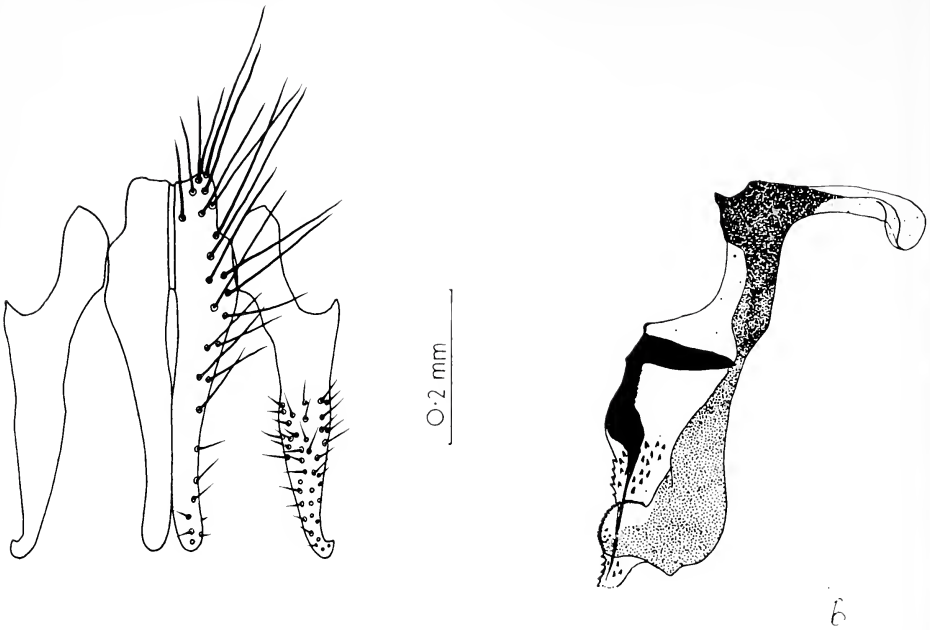

FIG. 2. *Thoracites neglectus* n. sp. Cerci with paralobi and phallosome (holotype from Mtubatuba, Natal).

anterior part of the bucca they are replaced by black setae as found on the parafacialium. Palpus slender, slightly enlarged terminally, yellow with the tip moderately darkened, proboscis black.

Thorax metallic dark green, with an irregular yellow or whitish pollinosity, the pattern of which changes with the incidence of light. Pro- and poststigma black. Bristles long and black, *ac* = 3 + 3, *dc* = 2 + 4, *ia* = 1 + 3, outer *ph* wanting, *prs* present, *h* = 3, *n* = 2, *sa* = 3, the scutellum is partly broken, but apparently 3 marginal bristles are present, *st* = 1:1, *pp* and *pst* present. Mesopleuron with black hairs and at the posterior margin with a row of long bristles, sternopleuron with thin pale hairs. Suprasquamal ridge, post-alar declivity and propleuron bare. Wing hyaline, veins including basicosta yellow, stem-vein with black bristles, base of r_{4+5} with 2 black setae, R_5 open, thoracic squama longer than broad, halter yellow. Legs black, fore-femora metallic green; fore-tibia with 2 *ad* and a long submedian *pv*; mid-tibia with 2 *pd* and one *ad* and *pv*; hind-tibia with 2 *pd* and 2 *ad*, but *av* is wanting.

Abdominal tergite I + II black, following tergites with the posterior parts broadly blackened and with a continuous median longitudinal vitta, lateral anterior parts yellow and densely pollinose, sternites and hypopygium (Fig. 2) black. Hairs and bristles black, the latter fairly long.

LENGTH: 6 mm.

LOCALITY: Mtubatuba, Zululand, V. 1941, 1 ♂ leg. H. K. Munro (in the collection of the S.A.I.M.R., Johannesburg).

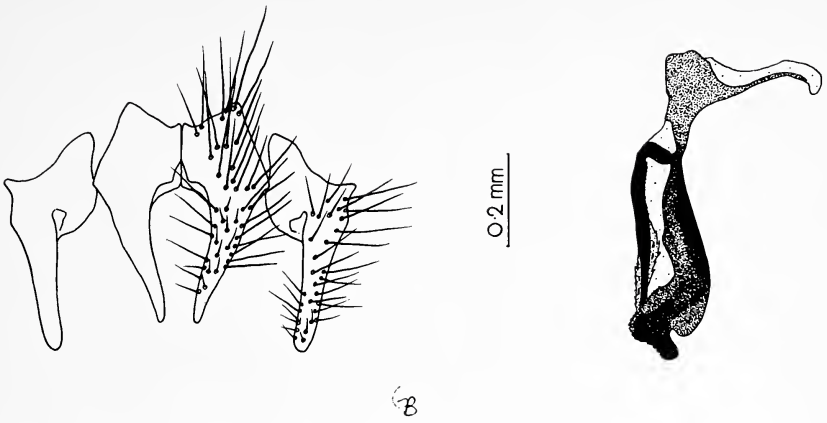

Fig. 3. *Thoracites nigeriensis* n. sp. Cerci with paralobi and phallosome (paratype from Maiduguri, Nigeria).

Thoracites **nigeriensis** n. sp.

Apart from the hypygial structure, this species is separable from *T. cingulatus* as well as *T. neglectus* by pale setae on the parafacialia.

male: Eyes bare, with small facets. Frons at its narrowest point measuring 1/7–1/6 of eye-length (frontal index = 0.14–0.17). Frontal stripe complete, yellow-brown, slightly widened towards the antennal groove, parafrontalia and -facialia with a dense white pollinosity and setae of moderate density which are black on the parafrontalia and pale on the parafacialia; *ia* long and thick, *ev* wanting, *oc* proclinate, lower part of parafrontalia with 6–7 pairs of *paf*. Antennae yellow, third segment about twice as long as the second, which shows a long black bristle, arista with long dorsal and ventral hairs. Antennal groove yellow pollinose, a median convexity is not developed. Bucca measures 2/5 of eye-length, densely pollinose like the parafacialium, hairs and setae pale, except the peristomal bristles, which are black, vibrissa long, facial ridge above it with 2 black setae. The small brown spot at the anterior eye-margin found in *T. neglectus*, is only weakly developed and ill-defined. Palpus yellow, terminally slightly dilated, greatest part of proboscis black.

Thorax greyish-cupreous, with an irregular white pollinosity, the pattern of which changes with the incidence of light. Pro- and poststigma brown. Chaetotaxy apparently as in *T. neglectus*, as far as it can be ascertained from the specimens, which are mounted on far too big pins. Wing hyaline, veins including basicosta yellow, stem-vein with black setae, base of r_{4+5} with 1–2 black setae, R_5 open, thoracic squama longer than broad, halter yellow. Legs dark-brown, fore-femora with a dense grey pollinosity; fore-tibia with 2 *ad* and 1 *pv*; mid-tibia with 2 *pd* and one *ad* and *pv*; hind-tibia with 2–3 *pd* and 2–3 *ad*, but *av* is wanting.

Abdomen with colouring and chaetotaxy as in *T. neglectus*, but hypopygium (Fig. 3) strikingly different.

length: 5–6 mm.

locality: Maiduguri, Nigeria, VIII–IX. 1942. 3 ♂♂ leg. F. Snyder (holotype and 1 paratype have been returned to the American Museum of Natural History, New York, the third male has been dissected and mounted on 4 slides, kept for the collection of the S.A.I.M.R., Johannesburg).

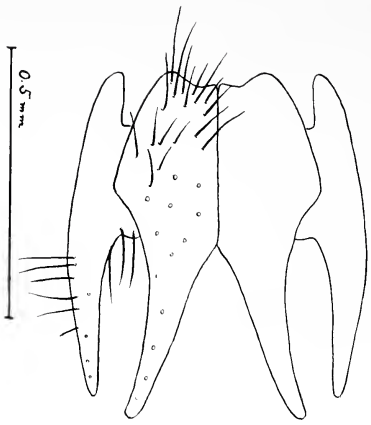

FIG. 4. *Thoracites cingulatus* Bezzi. Cerci with paralobi (specimen from Mozambique, after Zumpt, 1958).

Thoracites cingulatus Bezzi

Thoracites cingulatus Bezzi, Boll. Lab. Zool. gen. agr. Portici **8**, 1914, p. 290; Peris, An. Estac. exp. Aula Dei 3, 1952, p. 125; Zumpt, Explor. Parc natn. Albert Miss. G. F. de Witte **92**, 1958, p. 63 fig. 19.

This species has been based on a male from Thies, Senegal. Neither Peris nor I have seen the holotype, which should be located in Milano, Italy. Even if this specimen should become available, it is doubtful whether the dissection of the genitalia will be permitted. Peris mentioned a female specimen from Birmin Kebbi, Nigeria, in the collection of the British Museum, and said: "Etiquetada como tipo de la especie en el Museo Británico." Mr. A. C. Pont was kind enough to check this statement and informed me that this specimen was identified by Villeneuve and bears a characteristic blue label. The last line reads "sec. typ. Bezzi," but someone had incorrectly added a red label, which explains Peris' strange statement.

The status of *T. cingulatus* is therefore not satisfactorily cleared up. For the time being, the best solution should be to accept Peris' identification based on those specimens from Mozambique. The male genitalia (fig. 4) are characteristic, whereas the non-hypopygial features of the male do not allow a clear separation from *T. neglectus*, however, the only male specimen before me is in a very poor condition.

T. cingulatus sensu Peris is the only species from the Ethiopian geographical region, of which the female has been described. The specimen before me shows the following characteristics:

The frons measures at vertex nearly half of eye-length (frontal index = 0.47), it is strongly widened towards the antennal groove. Frontal stripe red-brown,

parafrontalia and -facialia densely white pollinose and with black setae, *iv, ev, oc, f,* 2 *fo* and 4 pairs of *paf* are well developed. Antennae yellow-brown. There is one bristle above the vibrissa, and the palpus is terminally more enlarged than in the male.

Colouring and chaetotaxy of the thorax as in the male. Wing hyaline, veins yellow, R_5 open. Only the right hind leg is present. Abdomen predominantly yellow, the black pattern consists of broad transverse bands on the last two tergites, whereas tergites III and I + II have these bands broadly interrupted in the middle. A longitudinal median stripe is not developed. The black pattern is therefore more reduced than in the male.

LENGTH: 7 mm.

LOCALITY: Mozambique, 1 ♂ ♀, leg. F. Muir (Sharp Coll. 1905–313). Peris saw another ♂ ♀ with the same labelling, British Museum (Nat. Hist.), London.

Literature Cited

Brauer, F., and J. E. Von Bergenstamm. 1891. Die Zweiflügler des Kaiserlichen Museums zu Wien. V.—Denkschr. Akad. Wiss. Wien **58**; pp. 305–446.

Peris, S. V. 1952. La subfamilia Rhiniinae (Dipt. Calliphoridae). An. Estac. exp. Aula Dei **3**; pp. 1–224.

Zumpt, F. 1958. Calliphoridae (Diptera Cyclorrhapha) Part II: Rhiniini. Explor. Parc natn. Albert Miss G. F. de Witte **92**; pp. 1–207.

BOOK REVIEWS

Introducing the Insect. F. A. Urquhart. Revised edition, 1966. Frederick Warne and Co., Ltd., London. 258 pp., numerous line drawings by E. B. S. Logier. $7.95.

This is a British edition of a book originally published in Canada in 1949. It has been revised only slightly, with some minor changes in the text to minimize confusion for users in the British Isles. However, as the publisher states, ". . . its appeal is worldwide. The author's intention was to provide a simple introduction to the study of insects generally. . . ." The book is a non-technical guide to the common orders and families of insects, with common group names emphasized; technical names are given parenthetically after the common names in text, but are omitted altogether in the keys. An especially useful feature of the keys to orders and families is the inclusion of a small line drawing immediately opposite each group name; this should appeal strongly to the beginner or layman who may be bewildered by the seeming intricacies of keys. The latter are, however, kept as simple and practical as possible. Following the family keys for each order is a brief but informative discussion of each family, accompanied by a more detailed figure. A chapter on making an insect collection and one on anatomy and life history are included. Only insects are treated; other arthropod groups sure to be encountered by the beginner are barely mentioned and quickly dismissed. The beginner may wonder at the arbitrary omission of anything "with more than three pairs of legs." The inclusion of a brief section on miscellaneous arthropods might have enhanced its appeal. Notwithstanding, its lack of pretension and of technical detail will appeal to many who seek an "introduction to the insect."

RICHARD W. FREDRICKSON
Saint Joseph's College,
Philadelphia

Bees: Their Vision, Chemical Senses, and Language. Karl von Frisch. Rev. edition 1971. Cornell University Press, Ithaca and London. xviii + 157 pp., 76 figs., photographs. $7.50.

More than twenty years ago, in his preface to the first edition of this volume, Karl von Frisch expressed his pleasure at being able to present to a wide audience through the medium of this little book, what had been given in three lectures to universities and scientific institutions during his lecture tour through the United States in 1949. It became an instant classic in the logical and clear reporting of his biological experimentation on bees.

Now, in this revised edition, von Frisch has updated his work by modifying the literal reproduction of the original lectures, by incorporating the additional research done by himself and other scientists in these intervening years, and by increasing the bibliography. Yet in so doing, he did not succumb to the temptation to expand his succinct book into an expensive reference tome. As a rseult, *Bees* remains in the author's words: "what it has been hitherto: an easily read introduction to one of the most fascinating areas of biology. It is designed to show the layman what sorts of problems are at issue here, and how they may be solved."

It is intended, therefore, as a semi-popular presentation to a mixed audience—an introduction for the untrained amateur, and a basic "must" reading for the professional entomologist. For both groups it should be a springboard for future in-depth studying of more detailed articles and books on the subject.

The same sequence of presentation has been retained in this revised edition, viz.— three chapters covering: the "color sense" (feeding card experiments, floral colors, beehive colors,

shape recognition); the "chemical sense" (flower odors, scent preferences, chemoreceptors and olfactory sense organs, chemical thresholds, scent training); and the "language" of the bees (the now-famous "round" and "tail-wagging" dance experiments, sound communication, bee vision and polarized light, evolution of the bees' language). In addition, twelve new photographs and eight new line drawings have been added, and some of the earlier drawings have been replaced.

It is von Frisch's intimate style of "thinking out loud" with the reader as listener which makes the logic of his hypotheses, experiments, successes and failures—such a delight. This book is not only a source of information on bees, but it is an excellent example in the proper use of the scientific method. Refinements of technique and recent research by others workers have enhanced rather than diminished most of the basic conclusions of von Frisch and his colleagues.

Daniel J. Sullivan, S.J.
Fordham University

BOOK NEWS

A Revision of *Actium* Casey and *Actiastes* Casey (Coleoptera: Psalaphidae). 1971. Albert A. Grigarick and Robert O. Schuster. University of California Press. Price $2.50. 56 pp.

During the 83 years between 1886 and 1969, 30 specific names were applied to *Actium* and it is now one of the largest genera of euplectine pselaphids in the Americas. In this paper the authors describe 19 new species of *Actium*, redescribing 14 species, considering 3 others species and removing 3 from the genus.

The authors redefine *Actiastes* and add 7 species, 3 of which were in *Actium*, and 4 are new.

Supplementary Studies on the Systematics of the genus *Perdita* (Hymenoptera: Andrenidae). 1971. P. H. Timberlake. University of California Press. Price $3.00. 63 pp.

The author states that since the completion of monographic revision of the genus *Perdita*, published in seven parts he finds it necessary to present this supplementary study. In this paper 64 species are treated, of which 32 are thought to be new and renewed study has revealed new synonymy involving four species and seven names.

The Classification, Evolution and Dispersal of the Winter Stonefly genus *Allocapnia*. 1971. Herbert H. Ross and William E. Ricker. Illinois Biological Monographs #45, University of Illinois Press, Urbana, Illinois, 61801. Price $8.95. 166 pp.

The Stonefly genus *Allocapnia* occurs only in western North America. It is associated with the temperate deciduous forest except for the species minima that reaches the northern tree line. All species emerge as adults during the winter or early spring.

The genus apparently evolved primarily in association with the Appalachian Mountain system, its neighboring ridges and areas northeast of them.

The authors state that the evidence suggests that all the phylogenetic developments of the genes started in the late Pliocene. They also suggest that the speciation pattern of *Allocapnia* is associated with the alternation of cold glacial and warm interglacial periods of the Pleistocene and comparable oscillations occurring in late Pliocene.

Proceedings of the New York Entomological Society

(Meetings held in Room 129 of the American Museum of Natural History unless otherwise indicated).

Meeting of April 6, 1971

President Dr. Lee Herman presided; 15 members and five guests were present. Elected to Active Membership were: Mr. Lucia S. Tompkins of New York City; Mr. Billy Pettit of London, England and Mr. Jeffrey N. L. Stibick of Papua and New Guinea.

PROGRAM. **Venezuela: From Caracas to Amazonas.** Mr. Jerzy Grabowski, a chemical engineer by profession is an ardent entomologist. He showed his very fine film in color of his last trip to South America—summer of 1970. He plans to make a similar trip in the summer of 1971.

Dr. Topoff announced that the last meeting of the year would be a so-called "free-for-all" in which members could participate in showing slides or demonstrations of general interest to the audience.

The meeting was adjourned at 9:40 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

Meeting of April 20, 1971

Vice-president Dr. Howard Topoff presided; 14 members and 9 guests were present. Dr. Linda H. Mantel of City College and Miss Bettina Bergh of Little Neck, N.Y., were proposed for Active Membership.

The Secretary read a letter of thanks from Roland R. McElvare in appreciation of the Society's resolution adopted at its Annual Meeting to send special greetings to the Honorary Members.

PROGRAM. **Arthropod Behavior: On the Land and in the Sea.** Dr. Edward Hodgson of Tufts College spoke on learning and special habituation in cockroaches. His research involved cockroach escape behavior and the neurophysiological processes involved in habituation when repeated stimuli such as air streams are directed at the cerci. The escape response was diminished and Dr. Hodgson explained the biochemistry of this kind of habituation.

The meeting was adjourned at 9:20 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

Meeting of May 4, 1971

President Dr. Lee Herman presided; 17 members and 5 guests were present.
Elected to Active Membership were: Dr. Linda H. Mantel of City College and Miss Bettina Bergh of Little Neck, N.Y.

Dr. Michael J. Abbatiello of the State University at Farmingdale, L.I., was proposed for Active Membership.

PROGRAM. **The Sensuous Butterfly—Coming of Age in Rhopalocera.** Dr. Arthur Shapiro of the Division of Science and Engineering of Richmond College, Staten Island, N.Y.,

discussed the relationship between population biology and sexual behavior on the basis of the epigamic behavior. "Territoriality" for instance, according to Dr. Shapiro, is probably not really a population-limiting factor. Instead, such epigamic behavior as "hill-topping" in some of the Lepidoptera he has studied, serves merely to bring the sexes together.
The meeting was adjourned at 9:15 P.M.

Daniel J. Sullivan, S.J., *Sec.*

Meeting of May 18, 1971

Vice-president Dr. Howard Topoff presided; 17 members and 5 guests were present.
Dr. Michael J. Abbatiello of the State University at Farmingdale, L.I., was elected to Active Membership.

Dr. David Sheby of Pratt Institute and the Rockefeller University was proposed for Student Membership. Because this was the last meeting of this academic year, the motion was made by Dr. Lucy Clausen and voted unanimously by the members present, that the By-Laws be suspended in order to permit the election of Mr. Sheby. Mr. Sheby was elected to Student Membership.

program. **Member Participation Night.** Dr. Howard Topoff introduced various members in attendance who displayed items and collections of entomological interest ranging from Chinese art to Egyptian scarabs. Live and dead specimens of various insects such as cockroaches, beetles, Gypsy Moth larvae, etc. were passed through the audience for closer scrutiny. Slides of ants carrying water in their jaws were also shown.

Finally a "honey-tasting" session, organized by Miss Helen McCarthy, afforded members the opportunity to taste representative types of honey from all over the world. These jars of honey were then raffled off to the various members.

The last meeting of the 1970–1971 academic year was adjourned at 9:30 P.M.

Daniel J. Sullivan, S.J., *Sec.*

Meeting of October 5, 1971

President Dr. Lee Herman presided; 18 members and 2 guests were present. Dr. Herman announced that Mr. Robert Buckbee would no longer be able to serve as the Society's "Business Manager" since he was retiring and moving to Florida. Mr. Dominick J. Pirone of Fordham University has agreed to succeed him.

Mr. Ephraim C. Shader of Stony Brook, N.Y., was proposed for Active Membership. Mr. David E. Foster of the University of Idaho and Mr. Felix J. Bocchino of Fordham University were proposed for Student Membership.

program. **The Smithsonian Expedition to Africa.** Dr. Karl V. Krombein, Senior Entomologist of the Smithsonian Institution, Washington, D.C., was accompanied on this expedition by Dr. and Mrs. Paul Spangler. Dr. Krombein explained that the reason for the trip was twofold: first, the opportunity to improve the Smithsonian's African insect collection by offering to share duplicates of such fauna which were in the museum in Kenya and to do on-the-spot collecting as well. Secondly, a visit to South Africa would provide insects for the Hall of Insects exhibit—especially individuals of a mound-building termite colony. Both objectives were met with about 17,500 insects sent to Washington comprising 9,000 species of which 60–80% were new to the museum. In addition, a representative termite

colony was excavated which was probably 75 years old, being 25 feet wide and over 5 feet high.

The meeting was adjourned at 9:20 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

Meeting of October 19, 1972

Vice-president Dr. Howard Topoff presided; 9 members and 5 guests were present. Mr. Ephriam C. Shader of Stony Brook, N.Y., was elected to Active Membership. Elected to Student Membership were: Mr. David E. Fpster of the University of Idaho and Mr. Felix J. Bocchino of Fordham University.

PROGRAM. **Enigma of Insect and Plant Diseases Caused by Mycoplasma-like Agents.** Dr. Karl Maramorosch of the Boyce Thompson Institute for Plant Research, Yonkers, New York, explained that initially these organisms were considered to be viruses. Since 1967 a better understanding of their mycoplasma-like nature has evolved. Systematically they seem to be close to bacteria and yet no actual relationship has been found. They differ from bacteria in not having a cell wall, but unlike viruses they contain both DNA and RNA. Mycoplasma-like agents cause at least 70 diseases in plants (such as aster yellows) and in such animals as sheep, dogs, chickens, turkeys and humans (PPLO). Insects such as leafhoppers are vectors of these mycoplasma-like organisms and are themselves sometimes killed in the process of transmission. They also have their own viruses.

The meeting was adjourned at 9:25 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

November 2, 1971—Election Day—No Meeting

Meeting of November 16, 1971

Vice-president Dr. Howard Topoff presided; 12 members and 4 guests were present. Dr. Mohammad Shadab of the American Museum of Natural History was proposed for Active Membership.

Mr. Louis Trombetta of Fordam University was proposed for Student Membership.

PROGRAM. **A World Nature Club Trip to Colombia, South America.** It was recalled that last February, Dr. Donald Messersmith of the Department of Entomology, University of Maryland, gave a lecture to the Society on his trip to Africa, Iceland and Greenland. Dr. Messersmith showed slides and many insect specimens which he collected on the Colombia trip. His special interest is Culicoides (Ceratopogonidae)—the Biting Midges. In three weeks he collected almost 4,000 specimens of many insect families which have been deposited with the U.S. National Museum.

The meeting was adjourned at 9:55 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

Meeting of December 7, 1971

Vice-president Dr. Howard Topoff presided; 17 members and 4 guests were present. Dr. Mohammad Shadab of the American Museum of Natural History was elected to Active Membership.

Mr. Louis Trombetta of Fordham University was elected to Student Membership.

PROGRAM. **Communication by Sound in Insects.** Dr. René Guy Busnel, Visiting Professor at the City College of New York discussed his research in the field of communication among insects. The role of acoustics in the behavior of insects, especially the Orthoptera, was studied by Dr. Busnela and his students for ten summers along the coast of southern France. Most of the recording on color film, with sound track and later a tape recorder was done near the city of Montpelier. The influence of sound on the mating behavior of these insects was shown in the film. The interesting phenomenon that various artificial and apparently unrelated noises such as whistles, bird calls, etc., induced was also shown.

The meeting was adjourned at 9:20 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

Meeting of December 21, 1971

In the absence of the President and the Vice-president the meeting was called to order by the Secretary, Dr. Sullivan; 13 members and 3 guests were present. There were no proposals for membership.

PROGRAM. **The Waika Indians of the Upper Orinoco.** Once again the members were treated to an excellent color film, narrated by the speaker of the evening, Mr. Jerzy Grabowski. In his introduction he recalled the fact that he had made several trips to this vast region of South America and had shown films to the society on previous occasions. This time his emphasis was on the Waika Indians and he described their customs and rituals.

The meeting was adjourned at 9:25 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

Meeting of January 4, 1972—The Annual Meeting

Vice-president Dr. Howard Topoff presided; 13 members and 3 guests were present. On behalf of the Nominating Committee, Dr. Topoff presented the list of candidates for office for the year 1972 as follows:

President—Dr. Howard Topoff
Vice-president—Father Daniel J. Sullivan
Secretary—Mrs. Joan DeWind
Assistant Secretary—Miss Betty White
Treasurer—Dr. Winifred B. Trakimas
Assistant Treasurer—Mrs. Patricia Vaurie
Trustees—Dr. James Forbes and Dr. David Miller

Upon motion made and duly seconded the candidates were unanimously elected to office. Mr. Martin Kolner of Arizona State University was proposed for Student Membership. Dr. Topoff explained to the membership the concern of the Executive Committee about various ways in which our Regular Meetings could be improved from the standpoint of wider publicity and better contact between members in attendance. He noted that financial considerations as well as union regulations restricted our use of other rooms and facilities for light refreshments such as coffee. Helpful suggestions from the audience were solicited.

PROGRAM. **Homing Behavior of Digger Wasps.** Mr. Matt Cormons used photographs from his Master's dissertation which he completed at the University of Wisconsin to illustrate his talk. He was concerned with what cues the wasp *Microbembex monodonta* (Hymenoptera: Sphecidae) in order to find her burrow which she had previously covered with sand. In general his results indicated that visual rather than olfactory cues were essential. In

future work he will refine his techniques to determine just how much cues influence the wasps homing behavior. (An abstract follows.)

The meeting was adjourned at 9:35 P.M.

DANIEL J. SULLIVAN, S.J., *Sec.*

HOMING BEHAVIOR OF DIGGER WASPS

The homing behavior of the digger wasp *Microbembex monodonta* was studied for three seasons at Spring Green, Wisconsin. This wasp nests in sandy, nearly barren areas. A provisioning female will leave and return to her nest, a burrow in the sand, many times during the day. Each time she leaves she kicks sand over the burrow entrance making it virtually undetectable to the human observer. The wasp, however, finds her burrow without hestitation upon each return.

This study investigated the potential cues used by a homing wasp. Various methods were used in attempts to disorient the wasp. These methods included: trampling the sand surface; covering the nest area with various materials; placing variously-sized and shaped objects around the burrow and then shifting them and masking potential distant visual and olfactory cues from the wasp.

The results suggest the following: *M. microdonta* uses distant cues to get into the general nest area. Local visual cues, including relief patterns on the sand surface enable the wasp to dig precisely at the nest entrance. Olfactory, auditory, tmperature and air current cues are apparently unimportant to a homing wasp since in the absence of these cues the wasp was apparently not disoriented. The results are basically similar to those obtained by investigators working with other species of sphecids.

MATT CORMON

Meeting of January 18, 1972

President Dr. Howard Topoff presided; 11 members and 4 guests were present. Presentation of the reports of the Treasurer and Publications Committees was postponed.
Mr. Martin Kolner of the Department of Zoology of Arizona State University was elected to Student Membership.

Miss Janice Gillespie of the Department of Entomology of the University of Idaho was proposed for Student Membership.

Subsequent to an earlier discussion on ways and means of attracting a wider audience to our meetings Dr. Topoff said that a review of past attendance showed some slacking off in the past year. Our Society has no institutional or other financial backing. The room is rented and the proposed refreshments would mandate union help and incur financial problems. Negotiations are in progress. He again solicited suggestions from the membership.

PROGRAM. **Numerical Taxonomy in Studying Cockroaches.** Dr. Ivan Huber of the Department of Biology of Fairleigh Dickinson University used photographs and two and three dimensional graphs to illustrate his talk. He compared phyletic classification of orthodox taxonomy and phenetic or numerical taxonomy of cockroaches and was of the opinion that the latter system indicated more highly refined relationships. (An abstract follows.)

The meeting was adjourned at 10:00 P.M.

JOAN M. DEWIND, *Sec.*

A TAXONOMIST'S VIEW OF THE COCKROACH

Taxonomy is currently undergoing both a resurgence and an upheaval. The availability of computers for processing large amounts of data about organisms and the appearance of new statistical techniques for analyzing the data have been principally responsible for this revolution.

The three main approaches to biological classification: phyletic, phenetic and cladistic, were briefly described and examples of each were shown.

The work discussed was a study of 37 species of cockroaches utilizing both adult and nymphal instars. McKittrick's phyletic classification was illustrated with slides of representative species, accompanied by an exposition of the reproductive biology of cockroaches, on which this classification is based. A phenetic (statistical) analysis of McKittrick's data produced taxonomic arrangements similar to the ones she produced using phyletic methods. Three-dimensional models of relationships among the species based on morphological similarities (computed from centroid component analyses of the author's data) were displayed. Such models help resolve taxonomic problems arising from unrelated species with similar morphological adaptations for occupying similar ecological niches.

Ivan Huber

Meeting of February 1, 1972

President Dr. Howard Topoff presided; 22 members and 24 guests were present. Janice Gillespie, Department of Entomology, University of Idaho was elected to Student Membership.

David A. Brody, Department of Entomology, American Museum of Natural History was proposed for Active Membership.

Dr. Winifred Trakimas Treasurer, reported on the state of the Society's treasury for 1971.

program. **Introduction to the World of Spiders.** Dr. John A. Cooke, Curator of Arachnids of the Department of Entomology of the American Museum of Natural History showed slides and three movies for which he acted as consultant. His discussion of spider behavior with splendid illustrative material was most enthusiastically received.

The meeting was adjourned at 9:40 P.M.

Joan M. DeWind, *Sec.*

Meeting of February 15, 1972

President Dr. Howard Topoff presided; 13 members and 13 guests were present. David A. Brody of the Department of Entomology of the American Museum of Natural History was elected to Active Membership.

Dr. Ivan Huber, Department of Biology, Fairleigh Dickinson University was proposed for Active Membership.

program. **Comparative Behavior of Army Ants.** Dr. Carl W. Rettenmeyer, Biological Sciences Group at the University of Connecticut, detailed the behavior of two species of army ants and illustrated his talk with slides.

The meeting was adjourned at 9:45 P.M.

Joan DeWind, *Sec.*

COMPARATIVE BEHAVIOR OF NEOTROPICAL ARMY ANTS

The Neotropical army ants include about 142 species, but our knowledge of their biology is based almost exclusively on four species in the genera *Eciton* and *Neivamyrmex*. One of the most specialized species, *Eciton hamatum*, is the best known, largely because it is primarily epigaeic. Its raid columns, emigrations, and nests or bivouacs are usually above ground where they can be observed and followed. Most army ant species are subterranean, and the meager information on their biology has been obtained mainly from chance encounters. *Labidus praedator* is one species that has bivouacs underground or in logs. It is a typical of most army ants because it has swarm raids. These are much smaller and more variable in duration, time of day, and direction than the swarm raids of *E. burchelli*. Captured prey is carried back to the bivouac along columns leading in different directions and disappearing into holes in the ground. These columns must be constantly changed and linked underground to keep up with the advancing swarm front. One emigration observed for about 16 hours in Costa Rica demonstrated that the brood has a much greater range in age than that of *Eciton* spp. The predominant type of brood (eggs, larvae, or cocoons) carried by the ants changed within the same emigration. That emigration also demonstrated that colonies of *L. praedator* can have over one million ants and a very large number of inquilines. Over 1,000 insect guests and 6,000 mites were taken from the single emigration, but those totals must be a small percent of the guests living within that colony.

CARL W. RETTENMEYER

INVITATION TO MEMBERSHIP

The New York Entomological Society was founded in 1892 and incorporated the following year. It holds a distinguished position among scientific and cultural organizations. The Society's **Journal** is one of the oldest of the leading entomological periodicals in the United States. Members and subscribers are drawn from all parts of the world, and they include distinguished professional naturalists, enthusiastic amateurs, and laymen for whom insects are only one among many interests.

You are cordially invited to apply for membership in the Society or to subscribe to its **Journal** which is published quarterly. Regular meetings are held at 8:00 P.M. on the first and third Tuesdays of each month from October through May at the American Museum of Natural History, the headquarters of the Society. A subject of general interest is discussed at each meeting by an invited speaker. No special training in biology or entomology is necessary for the enjoyment of these talks, most of which are illustrated. Candidates for membership are proposed at a regular meeting and are voted upon at the following meeting.

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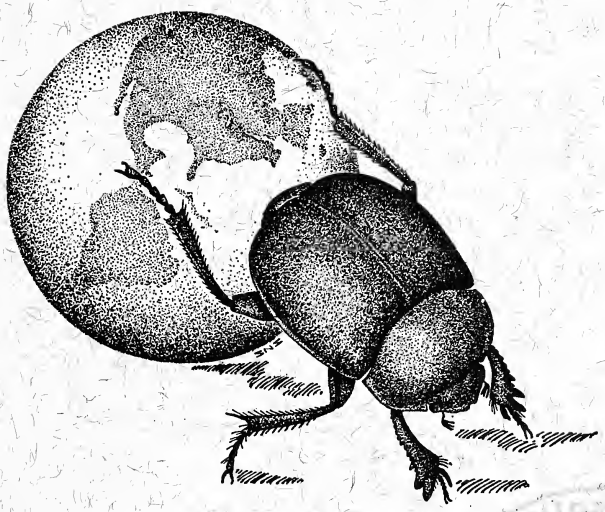

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CONTENTS

Adaptive Strategies of Feeding and Predator-Avoidance in the Larvae of the Neotropical Butterfly, *Morpho peleides limpida* (Lepidoptera: Morphidae)

ALLEN M. YOUNG
DEPARTMENT OF BIOLOGY, LAWRENCE UNIVERSITY, APPLETON, WISCONSIN 54911

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Abstract: The daily pattern of movement and feeding was studied for ten successive days in the larvae of the tropical butterfly, *Morpho peleides limpida* Butler, at a locality in central Costa Rica where this insect is unusually abundant. The major findings of these studies are: (1) larvae during all five instars are dawn-dusk feeders, with the average feeding time ranging between 20–35 minutes at each peak of activity, (2) movement is associated solely with commencement and termination of feeding since larvae have stable resting positions removed from feeding sites, and (3) the bimodal feeding activity is apparently under control of changes in light intensity. The adaptive significance of this larval feeding behavior is discussed in terms of the broad host plant specificity and apparent automimicry in this butterfly, and is interpreted as a mechanism for reducing predatory attack by visual vertebrate predators. Finally, it is hypothesized that only those species of *Morpho* which have experienced selective pressures molding them into successful second-growth forms evolve such feeding behavior, presumably as an additive measure for reducing predation from generalized visual vertebrate predators while exploiting a broad range of larval host plants. More highly specialized species of *Morpho* associated with primary-growth lowland tropical wet forests are predicted to lack such a behavioral pattern since (1) their larvae feed on fewer plant species, (2) the few local larval host plants are high in toxic secondary compounds, and (3) visual vertebrate predators in more stable tropical communities are themselves more specialized feeders and thus fewer species would consistently exploit *Morpho* larvae as a food source.

INTRODUCTION

This paper is one in a series concerning the evolutionary biology of New World neotropical butterflies belonging to the genus *Morpho* (Lepidoptera:

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Morphinae). Previous reports (Young, 1971a, b, c) have dealt primarily with adult ecology and behavior in selected species of *Morpho*, but this present paper describes a daily pattern of moving and feeding behavior in the larvae of a "brownish morpho" (Young, 1971b), *Morpho peleides limpida* Butler. This butterfly, which ranges from Venezuela to Mexico (Seitz, 1924; Le Moult and Real, 1962), is extremely widespread throughout the montane and lowland wet forests of Central America, occurring as at least 15 varieties. Zoogeographical studies (Seitz, 1924; Le Moult and Real, 1962; Blandin and Descimon, 1970) emphasize that *Morpho peleides* represents the major extension of the South American *achilles* group into Central America. A major aspect of this expansion has involved a long evolutionary history in members of the *achilles* group for adaptation to inhabiting less stable second-growth plant communities whereas most other species-groups of *Morpho* have remained associated with lowland primary-growth tropical wet forests. Therefore, taxonomic, behavioral, and ecological studies of *Morpho peleides* at different parts of its extensive geographical range should prove of interest in elucidating the widespread geographical expansion of the butterfly.

The studies herein reported concern *peleides limpida* at a montane wet forest site in central Costa Rica. The major findings of these descriptive studies are: (1) larvae of all instars exhibit a marked bimodal joint locomotor and feeding activity pattern over a 24-hour period, with peaks occurring at dawn and dusk; (2) younger larvae (instars 1–2) consistently begin to move and feed earlier in the evening and later in the morning than do older larvae (instars 3–5) on the same host plants. This displacement in daily activity pattern associated with instar is herein hypothesized to be a result of a change in resting position of larvae as they grow larger, causing temporal shifts in the registering of critical light intensities believed to initiate peak activity periods. The adaptive significance of such behavior in the larvae of *Morpho peleides* is also discussed in terms of an hypothesis which accounts for observed local broad host plant specificity, a defense strategy involving automimicry, and the local palatability spectrum for larvae. The adaptive significance of dawn-dusk feeding as related to marked differences in habitat selection exhibited by different species-groups is also discussed.

METHODS

In conjunction with studies of the life history and seasonal population structure of *Morpho peleides limpida* (Young and Muyshondt, 1972a), were observed on several different host plants at one locality in central Costa Rica. Observations on the feeding activity and related behavior of larvae were made at Cuesta Angel de Sarapiqui, a montane tropical wet forest (Holdridge, 1967) region of about 1000 meters elevation in the Alajuela Province. Observations were restricted to a narrow strip of early second-growth vegetation situated on

FIG. 1. Above: the second-growth habitat at Cuesta Angel, Heredia Province, Costa Rica (about 1000 m. elev.) where larval behavior in *Morpho peleides* was studied during June–September, 1971. Larvae were abundant on small seedlings of *Machaerium seemannii* (Leguminoseae) growing under a cover of tall grass on the steep slope directly to the left of the dirt road. Below: the typical seedling size of *Machaerium seemannii* in which eggs and larvae of *Morpho peleides* were most abundant. The tall grass has been cleared away to show the plant.

about a 25° slope and bordering a large coffee plantation on the west, and dropping off very steeply (about 60° incline) into virgin rain forest to the east. A one-lane dirt road (connecting San José with Puerto Viejo) ran along this strip of vegetation, (Fig. 1) giving access to this precarious study site situated about 5 miles south of Cariblanco de Sarapiqui. Due to the sloping terrain and soft earth, observations on larvae were made either by climbing these slopes, or by slowly working down sections of the slope on a rope harness.

A census of all life stages in a high density local population of *Morpho peleides* was started on June 25, 1971. The spatial distributions of eggs and larvae were examined in order to estimate rates of predation and parasitism. With associated data on the locations of larvae on different species of host plants, a study of diurnal feeding habits and other activities was begun on August 18, 1971. A series of ten successive days of observation on larval activity was obtained. On a day of observation, various instars were observed once every half-hour for 24 successive hours; data was recorded for individual larvae according to their instar, noting: position of the plant, resting periods, periods of movement, and periods of feeding. Movements of larvae between resting positions and feeding positions were also observed. By marking (with colored plastic tags) the individual host plants on which larvae were found, the same larvae were observed throughout the study period. Larval densities per individual host plant usually varied from one to four, often having first, second, and third instars together on a plant. This made it possible to determine the activities of different age-classes of larvae, on the same host plant, as well as on different individual host plants; this permitted variations in 24 hour activity patterns with respect to the microgeographic distribution of host plants (i.e., relative exposure of individual plants to shading effects of the undergrowth canopy). Unlike certain species of Brazilian *Morpho* (Seitz, 1924; Luis Otero, pers. comm.), the larvae of *Morpho peleides* are not gregarious and the movements of individual larvae on a plant are independent of one another.

Since females of *Morpho peleides* oviposit heavily on various host plants less than 2 meters tall observations of larval activity were restricted to plants less than this height. The most abundant larval host plant was *Machaerium seemannii* (Leguminoseae), with larvae most frequently on plants less than one meter in height (Fig. 1). The low distribution of larvae facilitated their examination with minimal mechanical disturbance resulting from jarring host plants, especially considering the sloping nature of the terrain at the study site.

RESULTS

Despite high rates of parasitism on larval *Morpho peleides* the long developmental time (about 110 days) of this butterfly relative to the short study period (10 days) permitted study of activity patterns for a relatively unchanging number of larvae. Numbers of larvae relative to the abundance of

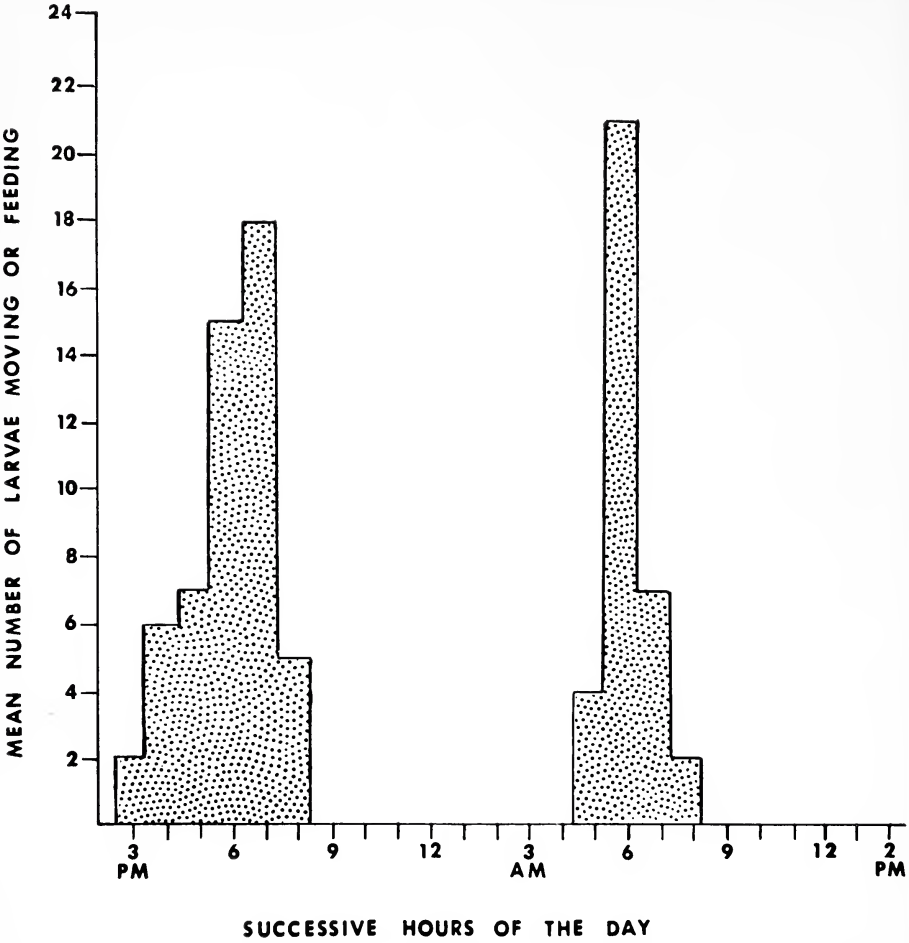


FIG. 2. The bimodal "dawn-dusk" daily pattern of movement and feeding exhibited by larvae of *Morpho peleides* at Cuesta Angel. Given are the mean numbers of larvae, all instars combined, seen at half-hour intervals, over a ten-day period. Measurements of activity patterns were made on the same larvae.

different host plants are summarized for the study period in Table 1. Of interest here is the fact that this butterfly undergoes successful development on several different host plants (listed in Table 1) in one locality. Since larvae were most abundant on *Machaerium seemannii* (Table 1), the bulk of observations on daily movement and feeding were limited to this plant species.

Larval feeding in *Morpho peleides* is markedly bimodal (Fig. 2), with peaks of feeding activity occurring during early morning and early evening hours. During the intervening hours of day and night, larvae are completely inactive

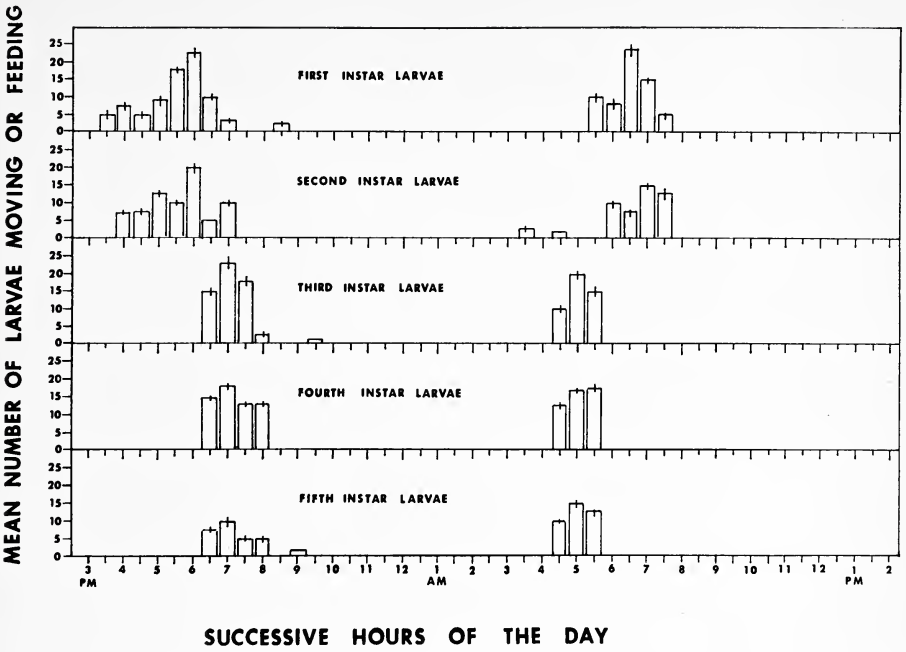


Fig. 3. Bimodal "dawn-dusk" daily pattern of movement and feeding in different instars of larval *Morpho peleides* at Cuesta Angel whose activity patterns are summarized in Fig. 1. The small vertical bars on each histogram unit are standard errors for the mean numbers of larvae moving and feeding during a given half-hour interval. There is a statistically significant shift (see text) in peak activity period occurring between second and third instar larvae.

and do not move at all. Movement appears to be associated exclusively with feeding activity and larvae crawl from resting positions to other sites for feeding. There is a marked temporal displacement in peak feeding periods at the beginning of the third instar of larval development (Fig. 3) resulting in third, fourth, and fifth instar larvae feeding later in the evening and earlier in the morning, relative to feeding peaks for first and second instars. A one-way analysis of variance for unequal sample sizes (Dixon and Massey, 1969) was employed to test the null hypothesis that there is no significant shift (temporal displacement) in feeding times among different instars. This hypothesis was rejected at $P < 0.05$ (F value for "right side" of Fig. 3 is 9.62; for left side, $F = 7.48$), with a significant shift in feeding times seen only between second and third instar larvae of *Morpho peleides*. The assumption of an infinite food supply necessary to use this test is justified since larvae do not experience crowding on individual host plants (Young and Muyshondt, 1972a). This pattern of temporal shift during ontogeny of *Morpho* is extremely consistent in

TABLE 1. Numbers of eggs and larvae of *Morpho peleides limpida*[a] on various host plants, from Cuesta Angel on the Caribbean slopes of Costa Rica.

Host plant[b]	Ranked[c] abundance	Eggs	Larval instar 1	2	3	4	5
Machaerium seemanii	1	82	51	43	20	19	9
Mucuna urens	2	52	33	21	15	10	4
Inga sp-1	3	30	26	19	14	0	2
Machaerium donnell-smithii	4	20	11	7	3	0	0
Pithecolobium sp-1	5	10	6	1	0	1	0
Inga sp-2	6	6	4	0	2	0	0

[a] Given are the numbers of immature *Morpho* seen daily for ten successive days, August 22 through September 1, 1971. With few exceptions, numbers of immatures did not change during this period.

[b] Two other host plants, *Pterocarpus* sp-2 and *Lonchocarpus* sp-1, are not shown here since larval numbers were low.

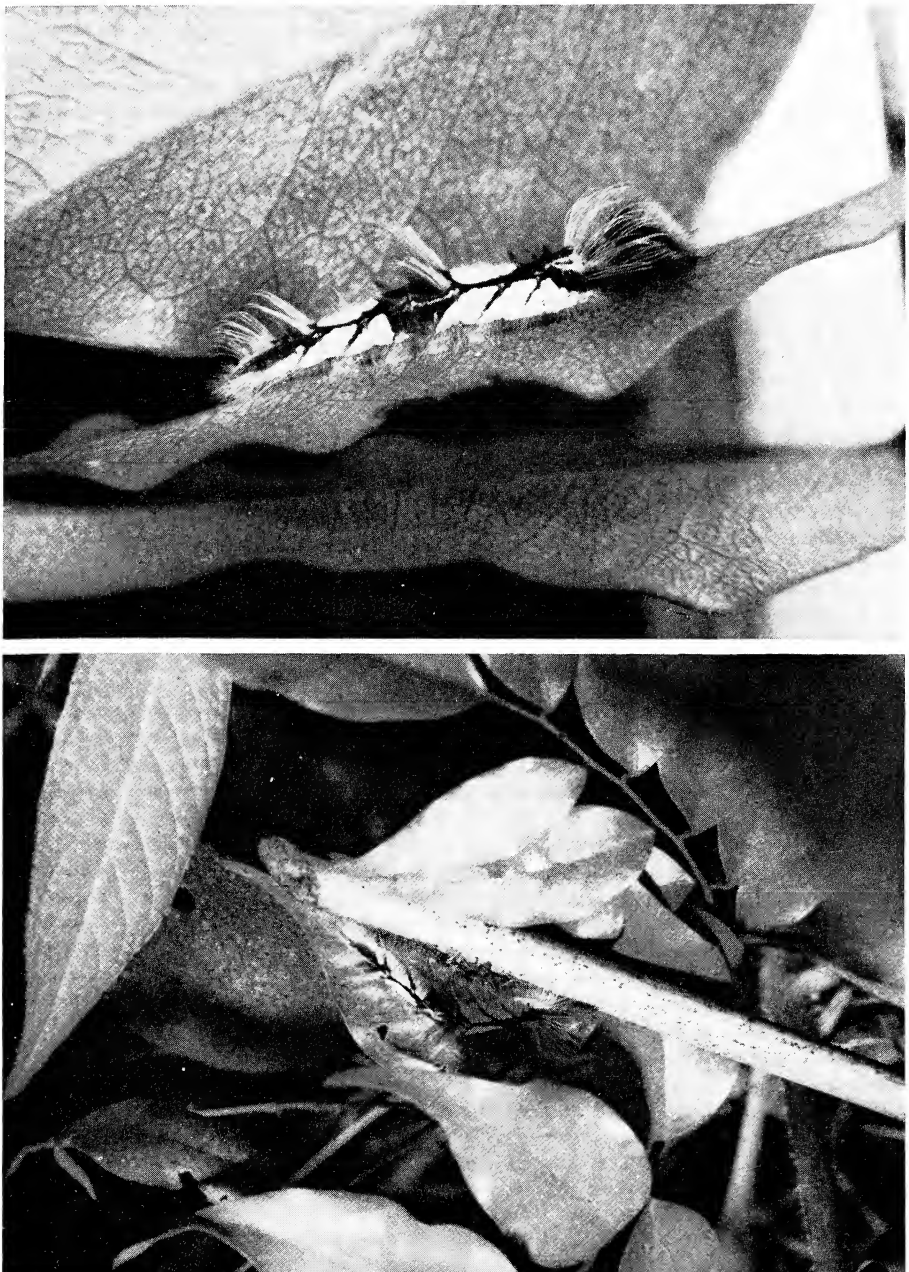
[c] In this ranking, 1 corresponds to the most abundant (population density) plant species exploited by *Morpho*.

field samples at Cuesta Angel, and has also been observed for larvae from a different locality, Bajo la Hondura, San Jose Province (also montane wet forest of about the same elevation as Cuesta Angel).

Regardless of instar, larvae of *Morpho peleides* separate their resting and feeding sites on *Machaerium*. This is essentially a vertical separation in later instars, while it is limited to adjacent leaves in younger instars. Younger larvae (first and second instars) always rest on the undersides of old leaves (Fig. 4) these being the leaves on which the eggs were deposited. Females lay their eggs singly, although as many as five eggs may be deposited on an individual plant by the same female on the same day. Eggs are laid on dorsal surfaces of older leaves (never on young leaves) and the first instar larvae, upon hatching, immediately crawl to undersides of these leaves. It is important to point out that females generally select leaves for egg deposition which are heavily shaded by the host plant—eggs are never laid on apical leaves exposed to direct sunlight. First instar larvae rest on the undersides of these well shaded leaves (Fig. 4), where they individually build small silken mats, and retain these resting sites through the second instar. Feeding takes place by movement to adjacent leaves, and seldom is the same leaf used as a resting site and a feeding site. Between late second instar and late third instar larvae acquire new resting positions on larger leaves near the exposed periphery of the host plant (Fig. 4).

→

FIG. 4. Resting positions of the larvae of *Morpho peleides* on *Machaerium seemannii*. Right: early third instar larva resting on silken mat woven on the ventral surface of a leaf of the host plant. Larvae rest with head directed upward and the weight of the body causes the leaf to hang vertically. Until the middle of the third instar, larvae may rest on leaves, but become increasingly exposed to direct sunlight resulting from moving towards the periphery of the host plant (see text). Left: late fourth instar larva resting on a grass



stem at the base of the host plant. Larvae during the late third instar, and throughout the fourth and fifth instars become exposed to direct sunlight through the acquisition of resting positions not heavily-shaded by leaves of *Machaerium*.

By the time of the late third instar, larvae change their resting sites, now preferring to rest on even larger leaves near the ground, or else on branches of the host plant near the ground, or occasionally on branches of other plants in intimate contact with the host plant (Fig. 4). Barring any major disturbances, larvae retain these new resting sites until pupation. The dramatic lowering of resting sites on the host plant results in the development of a major and pronounced vertical movement associated with feeding. Third, fourth, and fifth instar larvae move from their individual resting sites near the ground to leafy regions in the uppermost one-third of the host plant, during feeding period (Fig. 3). As with younger larvae, older larvae individually construct thin silken mats for resting sites and always return to the same resting site upon termination of a feeding period. The changing of resting sites is apparently associated with increased size and weight of third instar larvae. They appear very awkward and remain only partially concealed on the smaller leaves associated with upper regions of the host plant, and owing to their extremely bright red and yellow patch work coloration, become noticeable targets for predator attack. The resting sites for all instars appear to function to conceal larvae when not feeding. The resting positions of larvae from the late third instar onwards are usually exposed to direct sunlight, despite the fact that fourth and fifth instars usually rest very close to the ground. This is attributed to the highly exposed plant growth form of *Machaerium* in which leaves do not form a small canopy over the seedlings. Furthermore, the seedlings are most abundant on exposed grassy slopes (Fig. 1). There is always a choice of a resting site (usually an older leaf or section of branch or stem—Fig. 4) that offers either a partial or completely unobstructed view of the sky, through the canopy of the undergrowth. Since individual larvae always return to the same resting sites after feeding, larvae during resting periods (Fig. 3) are always in direct contact with a general intensity of illumination which is not reduced from shadow effects of undergrowth. Relative to these older larvae, first and second-instar larvae, on the other hand, will register lower intensities of illumination *at any hour* during resting periods, since their resting sites are usually heavily shadowed by the undersides of *Machaerium* leaves. Such differences in resting site preference will in turn result in temporal shifts in the initiation of feeding activity (Fig. 3), assuming the latter to be under partial control of light intensity.

DISCUSSION

The data on the dawn-dusk locomotor and feeding activity pattern in larval *Morpho peleides* are discussed from three major standpoints: (1) A proposed mechanism for dawn-dusk feeding, (2) the adaptive significance of dawn-dusk feeding in larval *Morpho peleides*, and (3) dawn-dusk feeding as an adaptive strategy for the genus *Morpho*.

A PROPOSED MECHANISM FOR DAWN-DUSK FEEDING: The mechanism responsible for the bimodal feeding activity in larval *Morpho peleides* is undetermined, although it is suspected to involve an endogenous rhythm that can be modified by environmental factors such as heavy rainfall, strong winds, etc. Evidence suggesting such effects on the feeding rhythm comes from direct observation of larvae in the field under different environmental conditions: during heavy rainfall, larval feeding is postponed or halted. This also occurs during strong gusts of winds. Larvae that are feeding on individual host plants situated in heavily-shaded vegetation exhibit displaced feeding periods, *regardless of instar number*: in general, larvae in such shaded places begin feeding earlier (between 30–50 minutes) in the evening than larvae located on host plants in open, exposed places; the same larvae also begin to feed later in the morning (between 30 and 60 minutes later) than do larvae on exposed plants. However, no significant difference in larval numbers on shaded versus exposed plants was found—suggesting that oviposition occurs in both places in about equal frequency (assuming no differential rates of predation and parasitism between the two microhabitats). Again, this pattern resulting from microgeographic differences in larvae is consistent from day to day, and all instars exhibit such a difference in the commencement of feeding. These observations are interpreted as responses to changing intensity of illumination during the evening and dawn hours—larvae living on shaded plants register a lower intensity of illumination earlier than larvae on exposed plants in the same area. Larvae on exposed plants begin to feed earlier than those on shaded plants and the reverse pattern occurs for the dusk feeding period. Therefore, it appears that initiation of the two feeding periods is a response to changes in light intensity associated with the transition between day and night and vice-versa. It is less likely a response to temperature change since this would probably be less varying among different microhabitats than would light intensity resulting from the varied natures of vegetation cover in early second-growth habitats. However, temperature cannot be ruled out as a factor contributing to the regulation of bimodal feeding of larval *Morpho peleides* at this time; experiments are now underway with laboratory cultures of *Morpho* to study the mechanism of feeding regulation. The difference with respect to microhabitats seen in the field suggest a photoperiodic response within 24-hour periods.

The variations in peak feeding periods seen for different instars of *Morpho peleides* (Fig. 3) is further evidence that feeding behavior is initiated by changes in light intensity. These varations may be accountable in terms of the resting positions of larvae, relative to their exposure to unobstructed sky. While the resting positions of third, fourth, and fifth-instar larvae are generally lower on individual host plants than resting positions of younger larvae, these older larvae are invariably exposed directly to the sky and this direct sunlight—an important observation in interpreting the shift in peak feeding periods of older

larvae. Thus while such larvae are generally concealed in shaded places, where they rest on branches (Fig. 4), they have unobstructed visual contact with the sky and the changes in light intensity occurring throughout the day. Younger larvae, on the other hand, being confined to resting positions on the undersides of leaves (Fig. 4), while physiologically capable of responding to the same light intensities of older larvae, do not register the same intensities of light as do older larvae, at the precise same time of day—there will be a displacement of their time of response which is proportional to the degree of shading they are experiencing under leaf cover. Assuming that larval activity is triggered by temporal changes in light intensity, first and second-instar larvae should begin to feed earlier in the afternoon than older larvae, and later in the morning than older larvae as seen in the data on feeding activity of different instars (Fig. 3).

It is unlikely that the mechanism for this feeding activity pattern involves rhythmic changes in sugar levels and other metabolites within host plant tissues since the level of desired nutrient substances such as sugars would be minimal during the dawn hours. Other environmental influences such as diurnal temperature and humidity changes, known to act as sensory cues in the feeding behavior of some lepidopterous species (Dethier and Schoonhoven, 1968), cannot be ruled out here, but it appears that diurnal change in light intensity is the major factor intiating dawn-dusk feeding.

THE ADAPTIVE SIGNIFICANCE OF DAWN-DUSK FEEDING: In light of the high species density associated with tropical wet forest habitats (e.g., MacArthur, 1969), it is interesting to consider the possible adaptive significance of "dawn-dusk" feeding behavior as a specialized defense strategy in larval *Morpho peleides*. With the exception of the fifth-instar, the larvae are gaudily-colored in a mosaic of bright yellow and red patches and lines. At the fifth-instar, larvae become a dark brown, loose the large yellow patches, and appear more cryptic than younger larvae. By the time larvae become late third instars, they are too large to stay on the undersides of *Machaerium* leaves during long resting periods, and conceal themselves on branches near the ground, in heavy shade, (Fig. 4). I interpret this behavior as a means of escape from birds and other small insectivorous vertebrates (lizards and frogs) which are active at different times of the day and night. Concealment of first and second instar larvae on the undersides of leaves functions in the same manner as resting on low branches in heavy shade. The question as to whether or not *Morpho peleides* is palatable to potential vertebrate predators is somewhat puzzling. I documented substantial adult mortality in this butterfly species, presumably the result of avian predation. Dr. Alexander F. Skutch since tells me that the Rufous-tailed Jacamar, *Galbula ruficauda*, captures many butterflies, including species of the genus *Morpho*, at various elevations of wet forest in Costa Rica. The bright coloration of the larvae suggests unpalatability, as indicated by lab-

oratory studies of other groups of unpalatable adult butterflies (Brower and Brower, 1964). Apparently such phytophagous insects receive their protection (unpalatability) from their own predators by storing within their bodies phenolic and other classes of secondary plant compounds (Von Euw, Reichstein, and Rothschild, 1969; Brower, Brower, and Corvino, 1967). Since feeding experiments using *Morpho* as prey for caged birds have not been performed, it cannot be said conclusively that larvae are unpalatable. Indirect evidence of unpalatability has been observed when larvae of *Morpho peleides* disturbed in the laboratory, produce a volatile substance that has a strong vinegar odor. This substance is secreted by a small orange gland situated between the first pair of true legs. During emission, the larva raises itself so that the gland becomes exposed; this is accompanied by a waving motion of the anterior end of the body, presumably as a means of aiming the gland in the direction of potential danger. The entire event lasts about 10 seconds. This behavior and the irritating sensations produced by the dorsal tufts of hairs have been observed in two subspecies of *Morpho peleides* (*limpida* in Costa Rica and *hyacinthus* in El Salvador) and at least one subspecies of *Morpho polyphemus* from El Salvador (Young and Muyshondt, 1972c).

Studies on papilionidae (Eisner 1970; Eisner et al., 1971) indicate that such properties of *Morpho* larvae may function as defense mechanisms rendering them undesirable as prey for vertebrate predators. Parasitism of larvae is common in natural populations (Young and Muyshondt, 1972a) and presumably such substances do not deter attack by hymenopterous or dipterous parasites. Attack by predatory insects, such as ants, has not been observed. *Morpho peleides* larvae may obtain defensive compounds directly from foliage (i.e., volatile turpines or other phenols) or else synthesize these compounds using precursors obtained from foliage. If larvae are unpalatable, then the striking bright coloration can be interpreted as aposematic, although direct evidence for this is lacking at the present.

Assuming that larvae are protected against their predators, the existence of high predation rates on adult *Morpho peleides* suggest palatability. If it is assumed further that adults retain the palatable properties of their larvae, a plausible explanation of such predation could reside either in the feeding behavior of the predators, or through automimetic complexes in which such predators encounter palatable individuals. For the first explanation, it is known that some species of tropical birds feed selectively on certain parts of the bodies of lepidopterous larvae and adults (i.e., some birds pull out the intact digestive tract by the head of unidentified larvae and apparently devour only the remaining body tissues) (Young, pers. obs.). However, there is no evidence of such selective feeding on *Morpho* larvae. A more reasonable explanation is concerned with the apparent broad local larval host plant specificity exhibited by *Morpho peleides* (Table 1) and the possible occurrence of local complexes of

automimicry within this butterfly. Automimicry has been previously studied for a single species of butterfly (the Monarch) in which it was found that this species occurred as several geographical varieties, exhibiting a broad spectrum of palatability (Brower, Brower, and Corvino, 1967; Brower, 1970). Brower, Pough, and Meck (1970) discuss the adaptive significance of automimicry for butterfly populations with respect to avain predation. Unlike the automimicry discovered in the Monarch Butterfly, *Danaus plexippus*, (Brower, Brower, and Corvino, 1967; Brower, 1970), in *Morpho peleides*, such an advantage is defined within local populations, rather than among different geographically separated populations. In terms of the model presented by Brower, Pough, and Meck (1970), their parameter *m* (the number of prey per predator) may be large for local populations of *Morpho peleides* since the distribution of this species may be less patchy than that of other species possessing a narrower host plant specificity. Localized increase in *m* should enhance the effects of automimicry as a mechanism for lowering predation rate. Assuming the existence of automimicry in *Morpho peleides*, the adaptive significance of dawn-dusk feeding in the aposematically-colored larvae of this butterfly becomes accountable.

The most plausible explanation for the evolution of distinct bimodal "dawn-dusk" feeding strategy in an aposematic species is that local larval populations consist of a series of palatable and unpalatable varieties in which frequencies of the varieties are so similar that would-be vertebrate predators encounter unpalatable and palatable individuals equally. In this hypothesis, the dawn-dusk feeding activity pattern ensures survivorship of both palatable and unpalatable larvae from predation by vertebrates. It is known that the cardiac glycoside content of various species of Asclepiad plants varies qualitatively and quantitatively and the palatability of Monarch butterflies whose larvae feed on them comprise a spectrum of palatability ranging from completely acceptable to completely unacceptable (Brower, 1970). It is also known that most plants have complex mixtures of phenols that vary among related species, and even among different populations of a single plant species (Levin, 1971). While the function of phenols actually isolated from the wings of certain butterflies (Ford, 1941; Morris and Thomson, 1963; 1964) is unknown, it is possible that some species obtain defensive properties, similar to those demonstrated for cardiac glycosides, alkaloids, and other secondary plant substances taken up by other insects (Brower, Brower, and Corvino, 1967; Von Euw, Reichstein, and Rothschild, 1969). It it plausible that the host plants of *Morpho peleides* (Table 1), while all members of the Leguminoseae, represent different ensembles of secondary plant substances (probably phenols) that endow their herbivores with different degrees of palatability. Careful searching would probably reveal additional host plants of this butterfly, on a local basis, lending further support to this hypothesis of automimicry. Experimental feeding studies involving larvae placed on different host plant species must be done. In El Salvador, *Morpho polyphemus*

feeds on *Paullinia pinnata* (Sapindaceae), in addition to a variety of legumes, including *Inga* sp. and *Machaerium salvadorensis* (Young and Muyshondt, 1972b). Natives of El Salvador use crushed leaves of *Paullinia* as a fish poison ("Barbasco").

Substantial evidence of predation on adult *Morpho peleides* in Costa Rica was found in automimetic assemblages it is possible that a substantial portion of the adult butterflies would be acceptable as prey and therefore such a population could in fact experience extensive avian predation, depending to a large extent upon foraging habits of the birds (i.e., Jacamars) involved. Unlike larvae of *Morpho peleides* which can evolve a daily feeding strategy adjusted so that maximal activity occurs at times of the day when vertebrate (visual) predators would be least likely to detect them, adults of this species are least active when many insectivorous birds forage. Substantial predation on adults is predicted in localities where the species is common and exploits different larval host plants. An alternate explanation for high adult mortality would be that individuals become more acceptable as prey as they complete ontogeny. Perhaps only the first four larval instars are unpalatable, with the fifth instar becoming palatable and resulting in a palatable adult. It is known that the fifth instar larva of *Morpho peleides* is cryptic in appearance, unlike the earlier instars which are very gaudily-colored (Fig. 4; Young and Muyshondt, 1972a). Such a change in coloration may be associated with an increase in palatability during this instar since selection would favor the development of crypsis with increased acceptability as prey during ontogeny.

The local abundance of the unpalatable variety of *Morpho peleides* is a function of the relative numbers of unpalatable host plants in the area, the strategy of oviposition of female morphos, and the degree of adult population cohesiveness at breeding sites. Young (in prep.) found that adult populations of *Morpho peleides* at Cuesta Angel and Bajo la Hondura tend to be stable during periods of high recruitment and that females wander farther than males. Females presumably wander more than males as they search for suitable oviposition sites. This permits exploitation of many different kinds of host plants by the species.

DAWN-DUSK FEEDING AS AN ADAPTIVE STRATEGY IN MORPHO: Observations on the natural history of various Brazilian species of *Morpho* (L. S. Otero, pers. comms.) indicate that different species-groups exhibit marked differences in: host plant specificity at the family level, type of oviposition, and degree of larval gregariousness on host plants. However, unlike other groups of tropical butterflies (e.g., Alexander, 1961), distinct larval feeding patterns have not yet been studied in the genus *Morpho* and it is predicted that very different daily activity patterns of peak feeding exist in this group. From recent observations of both Brazilian and Central American *Morpho* (L. S. Otero, pers. comm.; Young and

Muyshondt, 1972a, b, c) several predictions on various adaptive ecological and behavioral traits for different species-groups of the genus *Morpho* have been summarized (Young and Muyshondt, 1972c). Of major interest here are contrasts in some of these traits predicted for Central American species of dazzling blue morphos" (*rhetenor, cypris* groups) and the "brownish morphos" (*achilles* group) discussed elsewhere in terms of adult behavior (Young, 1971b). Species of dazzling blue morphos are generally confined to the canopy of primary-growth lowland tropical wet forests, while species of brownish morphos (i.e., *Morpho peleides*) are highly distributed in both primary and second-growth wet forests along altitudinal gradients (Young and Muyshondt, 1972c). Dazzling blue morphos are specialized forest species in which local larval host plant specificity is narrow, females exhibit cluster oviposition, and larvae are usually gregarious. Brownish morphos are capable of exploiting second-growth plant communities, possess broad local larval host plant specificity (Table 1), single oviposition, and single (non-gregarious) larvae. Such ecological and behavioral traits of species in the *achilles* group are interpreted as being components of an adaptive strategy for successful colonization of less stable plant communities (early successional stages) in the wet tropics (Young and Muyshondt, 1972a, b, c).

The adaptive significance of dawn-dusk feeding in the larvae of *Morpho* can be predicted in terms of habitat selection by member species of the genus. It is hypothesized that only species with broad host plant specificity, encompassing a spectrum of palatability, will evolve such a feeding strategy. Thus, virtually all species in the *achilles* group should possess dawn-dusk feeding, since all of these species have broad local larval host plant specificities (Costa Lima, 1936; Seitz, 1924; Otero, 1971; L. S. Otero, pers. comm.). In species of *Morpho* having broad host plant specificity, and experiencing colonizing episodes into less stable tropical communities, such a behavioral trait, while possibly prolonging developmental time (egg-adult), serves to minimize encounters between larvae and their vertebrate predators depending upon vision as a means of locating prey. More specialized species-groups of *Morpho*, such as the dazzling blue and glossy white morphos typically associated with more stable tropical communities, are predicted to experience selection pressures disfavoring the development of dawn-dusk feeding in their larvae. While their larvae are also gaudily-colored, many of them not only possess narrow larval host plant specificities, but these host plants may be unpalatable. Being more specialized feeders, larvae of these species would not be dawn-dusk foragers since automimicry would be lacking in local populations. Therefore, larvae could complete development faster and thus stand less risk of attack by parasitic and predatory species of insects and other arthropods. The daily pattern of larval feeding in more specialized species of *Morpho* may therefore be erratic, completely diurnal, or perhaps completely nocturnal. All of these patterns have

been casually noted in various species of the genus (L. S. Otero, M. Barcant, pers. comms.). It is therefore predicted that species belonging to specialized groups such as the dazzling blue morphos, would experience lower predation rates, both as adults and larvae. Preliminary evidence supporting this view has been obtained for *Morpho amathonte*, a dazzling blue morpho, a species generally restricted to lowland wet forests. It is hypothesized that dawn-dusk feeding in the larvae of *Morpho peleides* and other members of the *achilles* group has evolved as an adaptive strategy in response to high predation rates from insectivorous vertebrates in second-growth plant communities, where oviposition is on a wide range of plant species. Predation rates from insectivorous vertebrates are predicted to be higher on potential prey species such as *Morpho peleides* in second-growth habitats since predators possess more generalized feeding preferences in less stable communities. Such a strategy would be less adaptive in species associated with more stable plant communities since they possess specialized host plant preferences and may be unacceptable as prey. Potential vertebrate predators in more stable communities would be more specialized feeders (e.g., Cain, 1969) and thus predation rates may consistently be lower on larvae irrespective of the palatability of the species. Clearly, experimental field and laboratory studies are needed to test these ideas.

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The *Penenirmus* (Mallophaga: Ischnocera) of the Picidae (Aves: Piciformes)

Robert C. Dalgleish

Department of Biological Sciences, Union College, Schenectady, New York, 12308

and

Biological Research Station, Edmund Niles Huyck Preserve, Rensselaerville, New York

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Abstract: Eight species of *Penenirmus* from the Picidae are recognized and discussed. Neotypes are established from *P. serrilimbus* (Burmeister, 1838) and *P. heteroscelis* (Nitzsch, 1866). *Paranirmus* Zlotorzycka, 1964, is considered congeneric with *Penenirmus*. New synonymies include: *P. macrotrichus* (Kolenati, 1858) and *P. tuktola* (Ansari, 1947) (=*P. pici* (Fabricius, 1798)); *P. fiebrigi* Eichler, 1953, *P. serrilimbus asyndesmus* Emerson and Johnson, 1961, *P. s. pileatus* Emerson and Johnson, 1961, *P. pici rivolii* (Carriker, 1963), *P. p. caurensis* (Carriker, 1963) and *P. silesiacus* Zlotorzycka, 1966 (=*P. auritus* (Scopoli, 1763)); *P. accuratus* Zlotorzycka, 1964 (=*P. heteroscelis* (Nitzsch)); *P. villosus* Emerson and Johnson, 1961 (=*P. jungens* (Kellogg, 1896)). Species from 18 genera and 60 species of Picidae were examined. A key is given, and all species are illustrated and or re-described.

Penenirmus Clay and Meinertzhagen, 1938

Penenirmus Clay and Meinertzhagen, 1938, Entomologist **71**: 73.

Type species: *Pediculus albiventris* Scopoli, 1763

Picophilopterus Ansari, 1947, Proc. natl. Inst. Sci., India **13**: 265.

Type species: *Picophilopterus tuktola* Ansari, 1947. (Erected for species found on the Picidae).

Paranirmus Zlotorzycka, 1964, Acta Parasitologica Polonica 12: 275.

Type species: *Nirmus heteroscelis* Nitzsch, 1866. NEW SYNONYMY.

Penenirmus is known from the Passeriformes and Piciformes. Its distribution among these orders is poorly known, though it would appear that all of the Picidae are infested. This genus is more commonly collected than any of the other Mallophaga found on the Picidae. Species included herein are, for the present, considered congeneric with those known from the passerines and other families of Piciformes. These species do however form a well defined group which is recognized by the absence of a postantennal suture, the presence of anterior median notches on tergites II–III, and basal sclerites on the penis.

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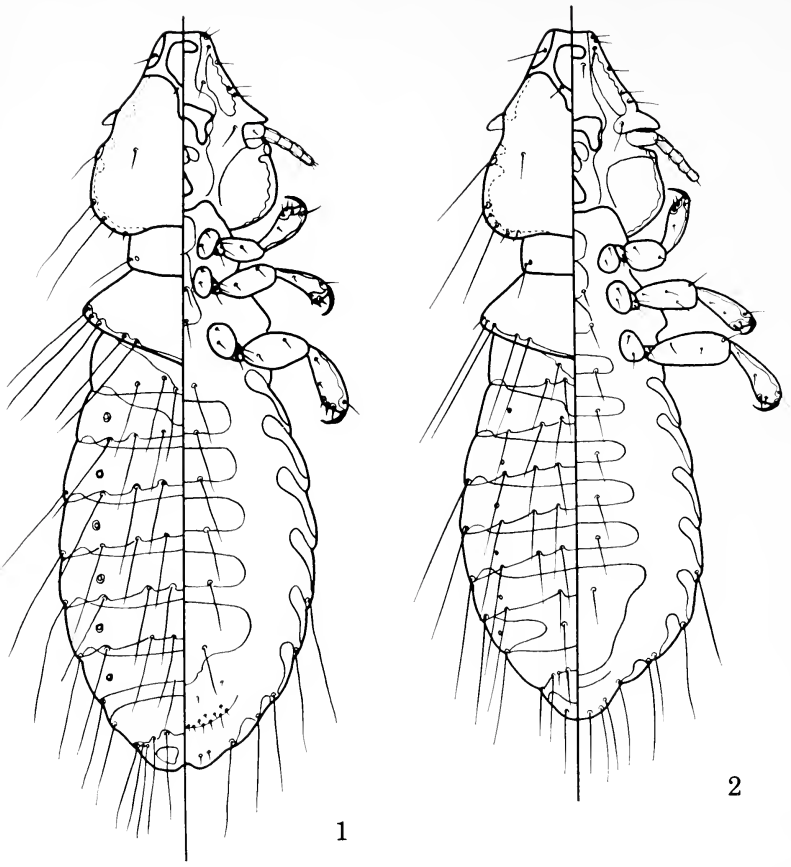


FIGS. 1 & 2. *Penenirmus auritus* (Scopoli), dorsal and ventral views of (1) female and (2) male. Drawn to the same scale.

Carriker (1963: 33) recommended that *Picophilopterus* Ansari, 1947, be re-erected for this group. This action, in my opinion, in the absence of well defined generic limits and the great amount of undescribed "*Penenirmus*," was premature and I prefer to withhold any decision on the taxonomic placement of this and other *Penenirmus* species groups until these deficiencies are removed.

All specimens examined were mounted on slides. Descriptions, illustrations and measurements are based on specimens macerated in hydroxide, cleared, and mounted in Canada Balsam. The nomenclature of the hosts follows that of Peters (1948).

Identification of the species discussed herein is based for the most part on chaetotaxy. It is necessary, in the case of abdominal chaetotaxy, to consider the total or the mean number of centroposterior setae of the sternites or tergites III–VI, rather than the number on any one segment. The chaetotaxy of the

head is more reliable, though occasional specimens with an abnormal number of setae will be encountered. It is, however, possible to recognize the atypical, in almost every case, by position of adjacent setae. The number of centroposterior setae on the dorsal margin of the pterothorax is a reliable character, though the position of these setae is not. This central group of setae on the pterothorax is usually widely separated from the lateral groups, though an almost continuous row of evenly spaced setae is not uncommon.

Many species and subspecies erected by previous authors are based, in part, on differences in the shape of the dorsal anterior plate of the forehead. During this study, this structure was routinely outlined and its proportions compared with those of the head. The variation in this plate as found in *P. auritus* from two hosts is presented graphically (Figs. 15, 16). It would appear that this structure is readily altered by different techniques in mounting, probably depending upon the degree of maceration, though it may also exhibit considerable "natural" variation; in either case it is too variable to be of taxonomic use.

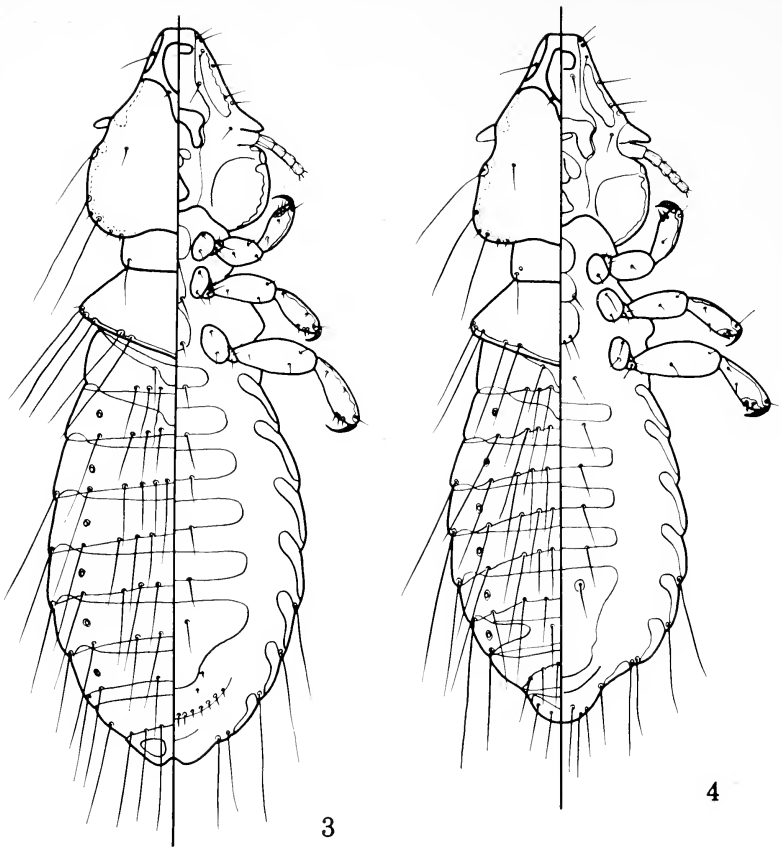
Key to the species of *Penenirmus* from the picidae

1. Temporal setae 1, 2 and 3 elongate, others short and inconspicuous (Figs. 9, 10). 2
– Temporal setae 1 and 3 elongate, seta 2 and others short and inconspicuous (Figs. 11–14). 3
2. Temporal seta 2 slender, basal diameter less than that of 1 or 3; preantennal region short (Fig. 10). ..... *arcticus*
– Basal diameter of temporal seta 2 equal to that of 1 and 3; preantennal region as long as postantennal region. (Fig. 9). ..... *serrilimbus*
3. Pterothorax with 4 centroposterior setae (Figs. 1–4). 4
– Pterothorax with 6 or more centroposterior setae (Figs. 5–8). 5
4. Centroposterior setae of tergites IV, V and VI total less than 16 (Figs. 1, 2). ..... *auritus*
– Centroposterior setae of tergites IV, V and VI total 16 or more (Figs. 3–4). ..... *pici*
5. Anterior dorsal setae of forehead longer than the distance between them (Fig. 14). ..... *heteroscelis*
– Anterior dorsal setae of forehead shorter than the distance between them (Fig. 13). 6
6. Sternites with an average of 4 centroposterior setae; segments IV and V each with 2 pairs of pleural setae. ..... *campephili*
– Sternites with an average of 2 centroposterior setae; segments IV and V each with 1 pair of pleural setae. 7
7. Centroposterior setae of tergites IV, V and VI total less than 16. ..... *jungens*
– Centroposterior setae of tergites IV, V and VI total 16 or more. ..... *maculipes*

Penenirmus arcticus Carriker, 1958
(Fig. 10)

Type host: *Picoides arcticus* (Swainson)

Penenirmus arcticus Carriker, 1958, Proc. ent. Soc. Washington **60:** 168, Figs. 1, 2. Type host: *Picoides arcticus.*



FIGS. 3 & 4. *Penenirmus pici* (Fabricius), dorsal and ventral views of (3) female and (4) male. Drawn to the same scale.

Penenirmus californiensis arcticus Carriker; Emerson and Johnson, 1961 J. Kansas ent. Soc. **34:** 39, Figs. 10, 17, 27. Hosts: *Picoides arcticus* and *P. tridactylus bacatus* Bangs.

The short, broad head (Fig. 10), with temporal seta 2 slender and elongate, distinguishes this species from all others known from the Picidae.

The preantennal length is conspicuously shorter than the postantennal length of the head. Lateral margins of forehead are convex rather than straight or concave as in other species. Temporal setae 1, 2 and 3 elongate, 2 approximately half the basal diameter of either 1 or 3. Pterothorax with 4 centroposterior setae. Centroposterior setae of tergites IV–VI total less than 16 ($\bar{x}$ 4/tergites. Centroposterior setae of sternites IV–VI total less than 9 ($\bar{x}$ 2/sternite). Abdomen similar in proportions to that of *P. auritus*.

The original description is based on a series of 4 pairs, reported as being

left too long in hydroxide. The type series is not mounted in Canada Balsam and the medium is vacuolated. The types have been compared with better prepared material and differ only in features attributable to the excessive maceration.

Dimensions in mm.: Total length, male 1.70, female 1.78–1.87; head length, male 0.51, female 0.52–0.56; head width, male 0.45, female 0.46–0.53; prothorax width, male 0.29, female 0.26–0.30; pterothorax width, male 0.45, female 0.45–0.49; abdominal width, male 0.60, female 0.64–0.70.

Material examined: 3 males, 2 females from *Picoides arcticus* (Swainson) from Canada and U. S. A.; 2 females from *Picoides tridactylus crissoleucus* (Reichenbach) from Siberia.

Penenirmus serrilimbus (Burmeister, 1838)
(Fig. 9)

Type-host: *Jynx torquilla* Linn.

Docophorus serrilimbus Burmeister, 1838, Handb. Ent. **2**(2): 427. Host: *Yjnx* (sic) *torquilla.*

Docophorus serrilimbus N.; Giebel, 1866, Z. ges. Nat. Wiss. **28:** 360. Host: *Yunx* (sic) *torquilla.*

Philopterus serrilimbus Nitzsch; Harrison, 1916, Parasitology **9:** 104. Host: *Iynx* (sic) *torquilla.*

Philopterus serrilimbus (Nitzsch); Seguy, 1944, Faune de France **43:** 238, Figs. 354, 355. Host: *Jynx torquilla.*

Penenirmus serrilimbus (Burmeister); Hopkins and Clay, 1952, Check list of genera and species of Mallophaga: 276. Host: *Jynx torquilla.*

Penenirmus serrilimbus serrilimbus (Burmeister); Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 39, Figs. 9, 19, 28. Host: *Jynx torquilla.*

This species is readily distinguished from others of this group by the 3 pairs of equally robust, elongate temporal setae. The elongate forehead (Fig. 9) distinguishes *P. arcticus* for which the abdominal chaetotaxy is identical.

Dr. Clay has examined 27 males and 53 females from the type host from Spain, United Kingdom, Czechoslovakia, India and Afghanistan, and 1 male and 2 females from *Jynx rufficollis* Wagler, and found them all to agree with this diagnosis.

The Burmeister types are lost and there has been no subsequent neotype designation for *Docophorus serrilimbus* Burmeister, 1838. The male on slide No. 11121 from a *Jynx torquilla torquilla* from Norfolk, England, June, 1938, Meinertzhagen, British Museum, is hereby designated Neotype and the 5 females on that slide are Neoparatypes. This slide has been so labeled and deposited in the British Museum (Natural History). The neotype agrees with the original description and preserves the identity of this species, about which there has been no disagreement.

Dimensions in mm.: Total length, male 1.76–1.96, female 2.00–2.39; head length, male 0.50–0.55, female 0.55–0.57; head width, male 0.43–0.46, female 0.46–0.52; prothorax width, male 0.25–0.28, female 0.28–0.30; pterothorax width, male 0.39–0.45, female 0.43–0.50; abdominal width, male 0.55–0.62, female 0.64–0.73.

Material examined: 1 male, 4 females from *Jynx torquilla* from Thailand and Spain; 1 male, 13 females from *Jynx torquilla torquilla* from England, India and Pakistan.

Penenirmus auritus (Scopoli, 1763)
(Figs. 1, 2, 11)

Type host: *Dendrocopos major pinetorum* (Brehm)

Pediculus auritus Scopoli, 1763, Ent. carniolica: 383. Hosts: *Pico Majore* and *Martio*. (in part)

Philopterus auritus Scopoli; Harrison, 1916, Parasitology **9:** 11, 88. Host: *Picus* spp. (*superciliosus* Nitzsch placed as a synonym)

Philopterus auritus (Scopoli); Seguy, 1944, Faune de France **43:** 238, Figs. 350, 351, 352, 353. Hosts: *Picus viridis*, *Dryobates major*, *D. medius*, *Picus canus*. (in part; *pici* Fabr., *scalaris* Nitzsch, and *superciliosus* Burmeister, placed as synonyms)

Penenirmus auritus (Scopoli); Clay and Hopkins, 1951, British Mus. (Nat. Hist.), Bull ent. **2:** 14, Figs. 19, 20, Pl. 1, Fig. 4. (Neotype selected, *superciliosus* Burmeister placed as a synonym)

Penenirmus auritus auritus (Scopoli); Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 35, Figs. 5, 20, 23. Host: *Dendrocopos major pinetorum* (C. L. Brehm).

Docophorus superciliosus Burmeister, 1838. Handb. Ent. **2**(2): 427. Host: *Pic. major*.

Docophorus superciliosus N.; Giebel, 1861, Z. ges. Nat. Wiss. **18:** 305. Host: *Picus major*.

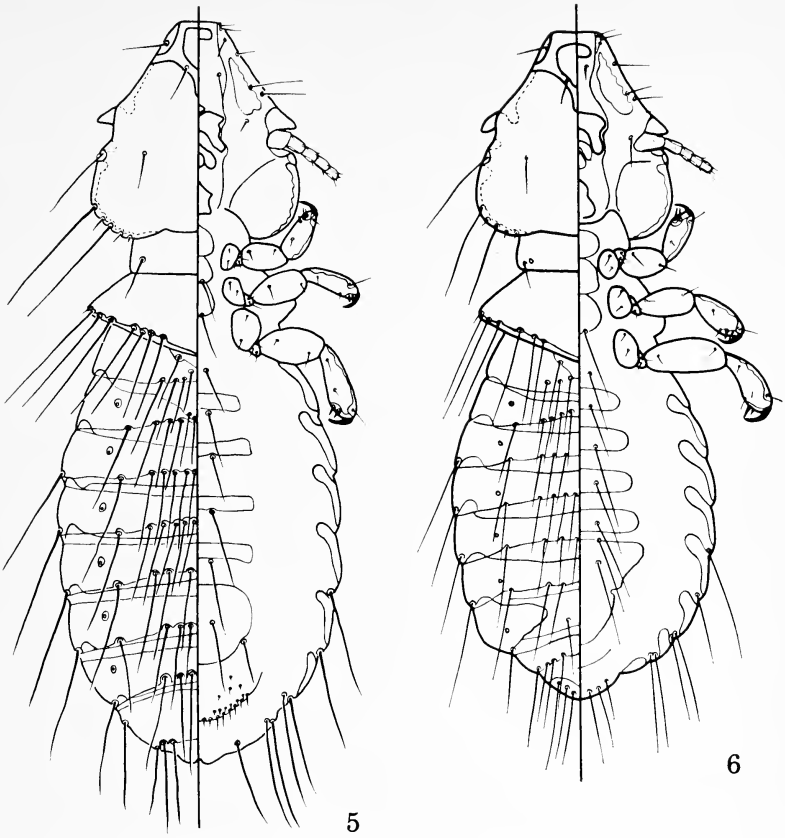
Penenirmus superciliosus (Burmeister); Clay and Hopkins, 1951, British Mus. (Nat. Hist.), Bull ent. **2:** 15. Type host: *Dendrocopos major major* Linn. (Neotype selected, placed as a synonym of *auritus* Scopoli)

Docophorus californiensis Kellogg, 1896, Occ. Pap. California Acad. Sci. (2), **6:** 483, Pl. 66, Fig. 6. Host: *Melanerpes formicivorus bairdi* Ridgway.

Philopterus californiensis Kellogg; Harrison, 1916, Parasitology **9:** 90. Host: *Melanerpes* spp.

Penenirmus californiensis (Kellogg); Hopkins and Clay, 1952, Check list of genera and species of Mallophaga: 274. Host: *Melanerpes formicivorus bairdi* Ridgway.

Penenirmus auritus californiensis (Kellogg); Carriker, 1956, Florida ent. **39:**



Figs. 5 & 6. *Penenirmus heteroscelis* (Nitzsch), dorsal and ventral views of (5) female and (6) male. Drawn to the same scale.

34, Figs. 30, 31. Hosts: *Melanerpes f. formicivorus* (Swainson), *Melanerpes formicivorus flavigula* (Malherbe).

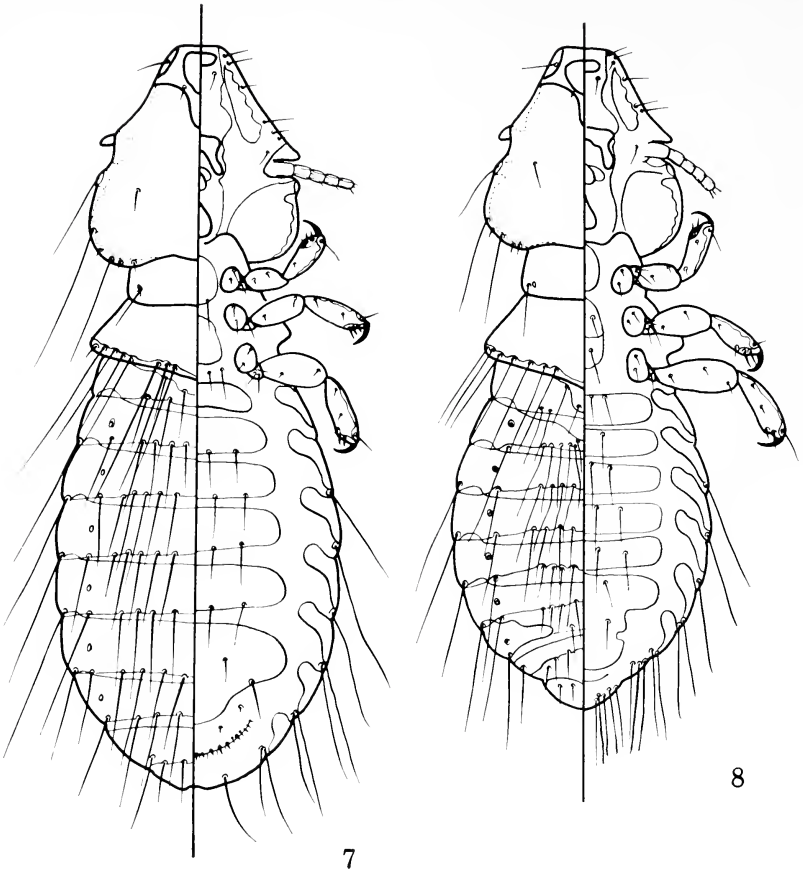
Penenirmus californiensis californiensis (Kellogg); Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 36, Figs. 7, 16, 25. Hosts: *Melanerpes formicivorus, Melanerpes erythrocephalus* (Linn.).

Docophorus evagans Kellogg, 1896, Occ. Pap. California Acad. Sci. (2),**6:** 480, Pl. 66, Fig. 2. Host: *Dendrocopos pubescens* (Linn.).

Penenirmus evagans (Kellogg); Hopkins and Clay, 1952, Check list of genera and species of Mallophaga: 274. Host: *Dendrocopos pubescens* (Linn.)

Penenirmus auritus evagans (Kellogg); Carriker, 1956, Florida ent. **39:** 35, Fig. 32. Hosts: *Dendrocopos pubescens, Dendrocopos scalaris giraudi* (Stone).

Penenirmus varius Emerson, 1953, J. Kansas ent. Soc. **26:** 134, Figs. 6, 8. Hosts: *Sphyrapicus v. varius* (Linn.), *Sphyrapicus v. nuchalis* Baird.



FIGS. 7 & 8. *Penenirmus campephili* Eichler, dorsal and ventral views of (7) female and (8) male. Drawn to the same scale.

Penenirmus auritus varius Emerson; Carriker, 1956, Florida ent. **39:** 37, Fig. 33. Host: *Sphyrapicus v. varius.*

Penenirmus californiensis varius Emerson; Emerson and Johnson, 1961 J. Kansas ent. Soc. **34:** 38, Figs. 8, 22, 26. Host: *Sphyrapicus varius varius, Sphyrapicus v. appalachiensis* Ganier, *Sphyrapicus v. nuchalis* Baird, *Sphyrapicus v. ruber* (Gmelin), *Sphyrapicus v. daggetti* Grinnell.

Penenirmus fiebrigi Eichler, 1953, Zool. anz. **150:** 240, Figs. 2, 7, 11. Host: *Colaptes campestris campestroides* (Malherbe). NEW SYNONYMY.

Penenirmus serrilimbus fiebrigi Eichler; Emerson and Johnson, 1961 J. Kansas ent. Soc. **34:** 40.

Penenirmus peusi Eichler, 1953, Zool. anz. **150:** 242, Figs. 4, 9, 11, 18. Host: *Dendrocopos syriacus balianicus* (Gengler and Stresemann).

Penenirmus auritus peusi Eichler; Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 36.

Penenirmus auritus aurifrons Carriker, 1956, Florida ent. **39:** 37, Figs. 34, 35. Host: *Melanerpes aurifrons grateloupensis* (Lesson).

Penenirmus serrilimbus aurifrons Carriker; Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 39, Figs. 9, 19, 29. Hosts: *Melanerpes a. aurifrons* (Wagler), *Melanerpes c. carolinus* (Linn.)

Penenirmus serrilimbus asyndesmus Emerson and Johnson, 1961, l.c.: 40, Figs. 12, 21, 31. Host: *Asyndesmus lewis* (Gray). NEW SYNONYMY.

Penenirmus serrilimbus pileatus Emerson and Johnson, 1961, l.c.: 40, Figs. 11, 18, 30. Hosts: *Dryocopus pileatus abieticola* (Bangs), *Dryocopus pileatus pileatus* (Linn.). NEW SYNONYMY.

Picophilopterus pici rivolii Carriker, 1963, Mem de la soc Ciencias Naturales la Salle **23** (63): 35, pl. 9, Figs. 1, 3. Host: *Piculus rivolii meridae* (Chapman). NEW SYNONYMY.

Picophilopterus pici caurensis Carriker, 1963, l.c.: 35, pl. 9, Fig. 2. Host: *Veniliornis passerinus modestus* Zimmer. NEW SYNONYMY.

Penenirmus silesiacus Zlotorzycka, 1964, Acta Parasit. Polonica **12**(24): 273, Figs. 9F, 9G. Host: *Dryobates medius* (L.) NEW SYNONYMY.

Penenirmus auritus (Figs. 1, 2) is distinguished from others known from the Picidae by the 4 elongate setae on the temples, 2 short anterior dorsal setae of the forehead, fewer than a total of 16 centroposterior setae on tergites IV–VI ($\bar{x} = 4$/tergite) and less than a total of 9 centroposterior setae on sternites IV–VI ($\bar{x} = 2$/sternite).

The preantennal length of the head (Fig. 11) approximates the postantennal length. Anterior dorsal setae of forehead short and stout. Temporal setae 1 and 3 elongate, 2, 4 and 5 short and inconspicuous. Pterothorax and tergites III–VI each with an average of 4 elongate centroposterior setae. Sternites III–VI each with 2–3 centroposterior setae.

Carriker (1957: 96) selected the male on slide No. 361a as the lectotype of *P. californiensis* Kellogg. This designation was made while the specimen was in the original mountant of gelatin, which had darkened and vacuolated, thus obscuring the specimen. Upon remounting, 1 female and 2 immatures were found, not 1 male, 1 female and 1 immature as reported by Carriker. In that there is no male on slide 361a, Carriker's lectotype designation is emended to read: the female on slide 361a is selected as lectotype and the slide is so labeled. Paralectotypes are recorded from the Snow Museum, University of Kansas; Cornell University; University of California at Berkeley; and the United States National Museum.

The female lectotype of *P. evagans* Kellogg, selected by Carriker (1957: 96) on slide No. 307a, was not available for study. Slide No. 311a, labeled "*Dryobates pubescens, Docoph. evagans* K. n.sp., (near *P. superciliosus*), N.M.

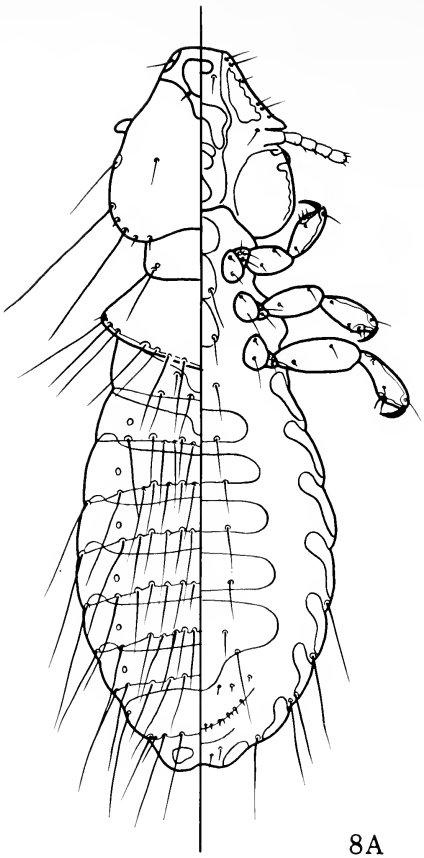


FIG. 8A. *Penenirmus maculipes* (Piaget), dorsal and ventral views of holotype female.

II., fig'd" has been remounted, examined and labeled paralectotype. Slides 361a, 307a and 311a are in the Kellogg Collection of the University of California at Berkeley.

The subspecies of *P. auritus*, *P. californiensis* and *P. surrilimbus*, recognized by Emerson and Johnson (1961), are based on the shape of the dorsal anterior plate of the forehead and chaetotaxy of the pterothorax and vulva. These characters are not reliable as considerably overlapping inter- and intra-population variation is evident in large series. The outlines of dorsal anterior plates are given (Figs. 15, 16) for specimens taken from 2 species of hosts. With the exception of *P. serrilimbus serrilimbus* and *P. californiensis arcticus*, these subspecies are considered to be conspecific with *P. auritus*.

Likewise the erection of *P. silesiacus* Zlotorzycka, 1964, for a single female and one immature is both unwarranted and unsupported. The features dis-

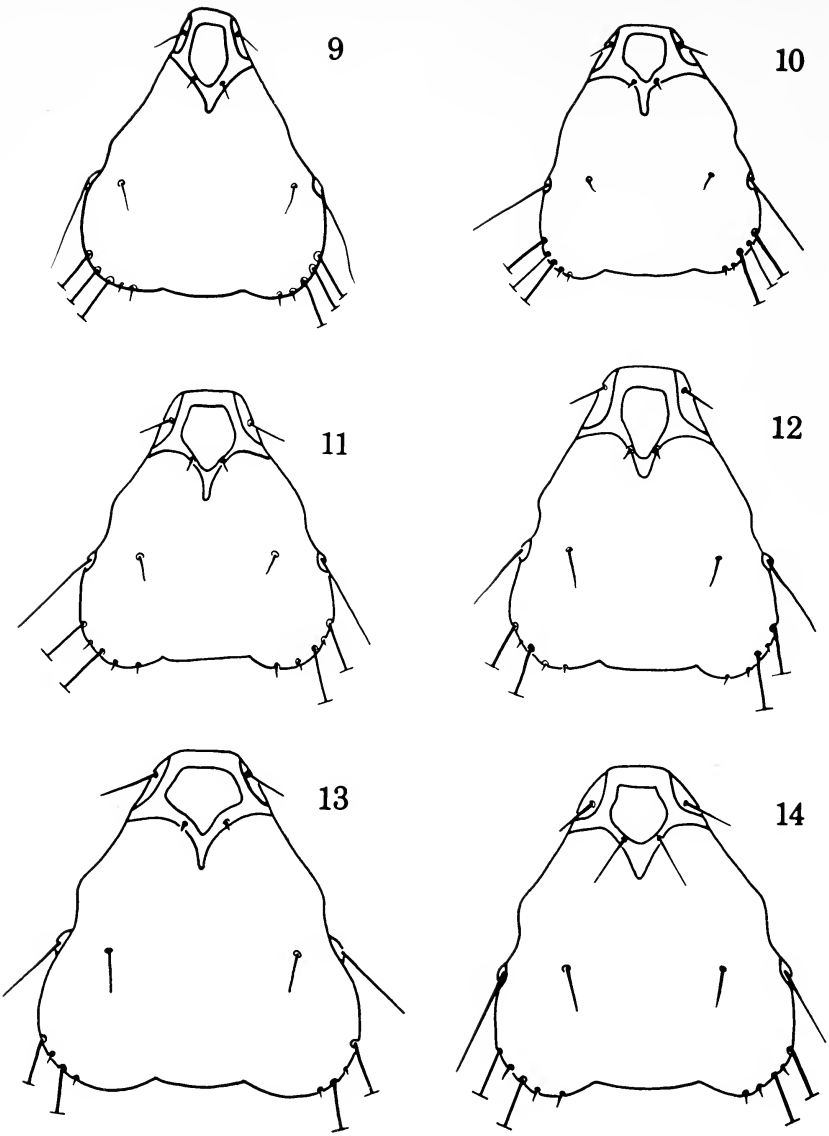
cernible from the drawing and photograph and those of the brief description, fall within the range of variation of *P. auritus*, which appears to infest all *Dendrocopos* species.

Neither the original descriptions nor specimens examined from the type hosts of *P. fiebrigi* Eichler, 1953, *P. pici rivolii* (Carriker, 1963) and *P. pici caurensis* (Carriker, 1963), contained characters, which in my opinion, warrant the erection of these new taxa.

Prior to 1963 Carriker considered *Penenirmus* from the new world Picidae to be subspecies of *P. auritus*. In his study of the Mallophaga from Venezuelan birds (Carriker, 1963:34) however, he places them all as subspecies of *P. pici* and re-erects *Picophilopterus* Ansari, 1947, for the *Penenirmus* from the Picidae.

Dimensions in mm.: Total length, male 1.39–2.08, female 1.63–2.36; head length, male 0.42–0.59, female 0.48–0.64; head width, male 0.30–0.55, female 0.41–0.59; prothorax width, male 0.20–0.35, female 0.24–0.40; pterothorax width, male 0.34–0.56, female 0.35–0.63; abdominal width, male 0.41–0.79, female 0.50–0.92.

Material examined: 1 male from *Picummus cinnamomeus* Wagler from Colombia; 2 males, 1 female from *Picummus olivaceus* Lafresnaye from Colombia; 1 female from *Picummus innominatus* Burton from Thailand; 1 male, 2 females from *Colaptes campestris* (Vieillot) from Paraguay; 2 males, 3 females from *Colaptes campestris campestroides* (Malherbe) from Paraguay; 1 male, 1 female from *Chrysoptilus punctigula striatigularis* Chapman from Colombia; 1 female from *Chrysoptilus punctigula ujhelyi* Madarasz from Colombia; 2 males, 2 females from *Chrysoptilus atricollis peruvianus* Rlichenbach from Peru; 9 males, 9 females from *Piculus rivolii rivolii* (Boissonneau) from Colombia; 10 males, 11 females from *Piculus rivolii brevirostris* (Taczanowski) from Colombia and Peru; 4 males, 4 females from *Piculus rivolii atriceps* (Sclater and Salvin) from Peru; 1 female from *Piculus rubiginosus alleni* (Bangs) from Colombia; 6 males, 5 females from *Piculus rubiginosus uropygialis* (Cabanis) from Costa Rica; 1 male, 1 female from *Piculus rubiginosus yucatanensis* (Cabot) from Yucatan; 4 males, 4 females from *Micropternus brachyurus phaioceps* (Blyth) from Thailand; 3 males, 7 females from *Micropternus brachyurus squamigularis* (Sundevall) from Thailand; 1 male, 1 female from *Picus chlorolophus* Vieillot from Thailand; 1 male from *Picus mineaceus* Pennant from Malaya; 2 males, 3 females from *Picus mineaceus malaccensis* Latham from North Borneo; 1 male from *Dryocopus pileatus* (Linn.) from U.S.A.; 2 females from *Dryocopus pileatus pileatus* (Linn.) from U.S.A.; 5 males, 8 females from *Dryocopus pileatus abieticola* (Bangs) from U.S.A.; 3 males, 5 females from *Dryocopus lineatus* (Linn.) from Yucatan and Trinidad; 1 male, 3 females from *Dryocopus lineatus petersi* (van Rossem) from Mexico; 5 males, 10 females from



FIGS. 9–14. Dorsal view of heads drawn to the same scale. (9) *P. serrilimbus*, (10) *P. arcticus*, (11) *P. auritus*, (12) *P. pici*, (13) *P. campephili*, (14) *P. heteroscelis*.

Asyndesmus lewis (Gray) from U.S.A.; 35 males, 28 females from *Melanerpes erythrocephalus* (Linn.) from Canada and U.S.A.; 4 males, 11 females from *Melanerpes formicivorus* (Swainson) from U.S.A.; 5 males, 5 females from *Melanerpes formicivorus formicivorus* (Swainson) from U.S.A.; 7 males, 6 females from *Melanerpes formicivorus bairdi* Ridgway from U.S.A.; 5 males,

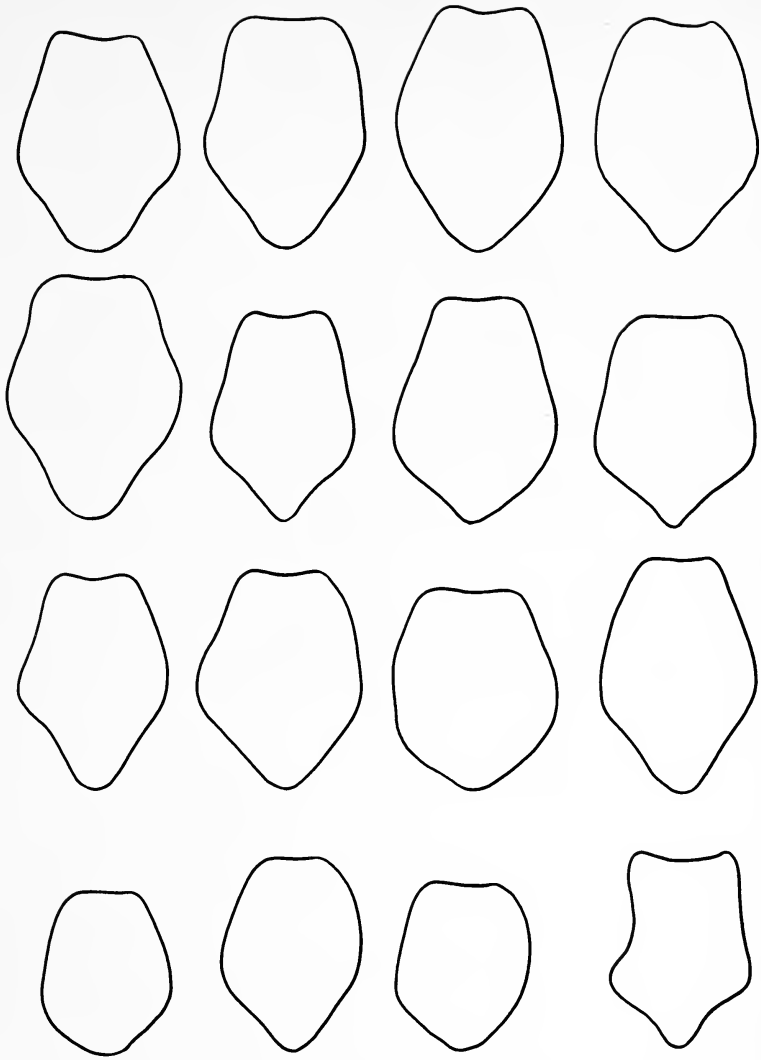


Fig. 15. Outline of dorsal anterior plate of foreheads of *P. auritus* from *Melanerpes erythrocephalus* from various localities. Scale adjusted so that the head width is the same in each case.

8 females from *Melanerpes formicivorus flavigula* (Malherbe) from Colombia; 4 males, 6 females from *Melanerpes formicivorus striatipectus* (Ridgway) from Costa Rica; 4 males, 8 females from *Melanerpes hypopolius albescens* (van Rossem) from U.S.A.; 9 males, 15 females from *Melanerpes carolinus* (Linn.) from U.S.A.; 2 males, 9 females from *Melanerpes aurifrons* (Wagler) from U.S.A.; 4 males, 6 females from *Melanerpes aurifrons grateloupensis* (Lesson)

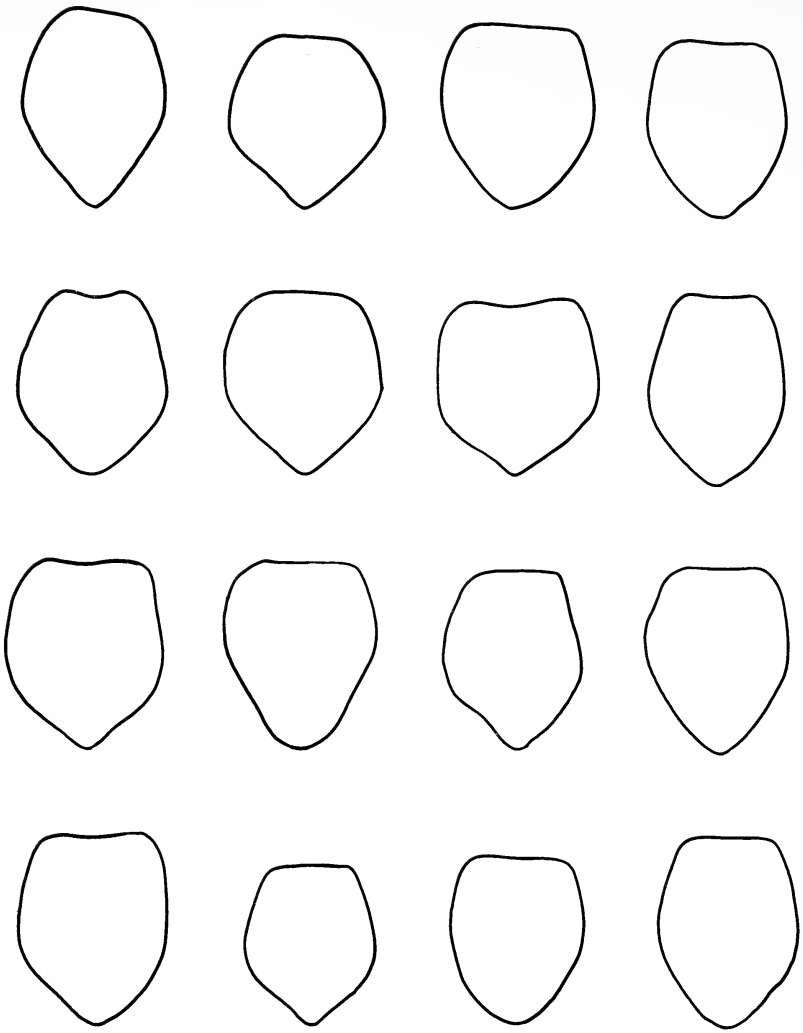


FIG. 16. Outline of dorsal anterior plates of foreheads of *P. auritus* from *Sphyrapicus varius* from various localities. Scale adjusted so that the head width is the same in each case.

from Mexico; 8 males, 8 females from *Melanerpes superciliaris nyeanus* (Ridgway) from Bahama Islands; 2 males, 2 females from *Melanerpes cruentatus cruentatus* (Boddaert) from Peru, Bolivia and Colombia; 37 males, 46 females from *Sphyrapicus varius* (Linn.) from Canada and U.S.A.; 22 males, 29 females from *Sphyrapicus varius varius* (Linn.) from Canada and U.S.A.; 19 males, 16 females from *Sphyrapicus varius nuchalis* Baird from U.S.A.; 2 males, 2 females from *Sphyrapicus varius ruber* (Gmelin) from

U.S.A.; 5 males, 5 females from *Sphyrapicus thyroideus* (Cassin) from Mexico and U.S.A.; 1 male from *Veniliornis fumigatus* (d'Orbigny) from Mexico; 1 male from *Veniliornis kirkii cecilii* (Malherbe) from Colombia; 2 males, 9 females from *Veniliornis callonotus major* (Berlepsch and Taczanowski) from Peru; 2 males, 1 female from *Veniliornis dignus* (Sclater and Salvin) from Colombia; 19 male and 24 female Neoparatypes from *Dendrocopos major major* (Linn.) from Estonia; Neotype male and 3 male and 4 female Neoparatypes from *Dendrocopos major pinetorum* (C. L. Brehm) from Poland; 6 males, 8 females from *Dendrocopos darjellensis* (Blyth) from Sikkim; 6 males, 4 females from *Dendrocopos leucotos* (Bechstein) from Formosa; 3 males, 5 females from *Dendrocopos hyperythrus hyperythrus* (Vigors) from Nepal; 1 male, 1 female from *Dendrocopos atratus* (Blyth) from Thailand; 2 males, 2 females from *Dendrocopos macei macei* (Vieillot) from India; 3 males, 5 females from *Dendrocopos minor minor* (Linn.) from Estonia; 2 females from *Dendrocopos kizuki* (Temminck) from Korea; 3 males, 12 females from *Dendrocopos albolarvatus* (Cassin) from U.S.A.; 7 males, 21 females from *Dendrocopos villosus* (Linn.) from Bahama Is., Canada and U.S.A.; 6 males, 4 females from *Dendrocopos villosus hyloscopus* (Cabanis and Heine) from U.S.A.; 2 males, 1 female from *Dendrocopos villosus harrisii* (Audubom) from U.S.A.; 3 males, 8 females from *Dendrocopos villosus extimus* (Bangs) from Costa Rica; 9 males, 11 females from *Dendrocopos pubescens* from U.S.A.; 1 female from *Dendrocopos pubescens medianus* (Swainson) from U.S.A.; 8 females from *Dendrocopos scalaris* (Wagler) from Mexico and U.S.A.; 3 females from *Dendrocopos scalaris giraudi* (Stone) from Mexico; 1 male from *Dendrocopos scalaris symplectus* (Oberholser) from U.S.A.; 1 male, 3 females from *Dendrocopos arizonae* (Hargitt) from Mexico;

Penenirmus pici (Fabricius, 1798)
(Figs. 3, 4, 12)

Type host: *Picus viridis* Linnaeus

Pediculus pici Fabricius, J. C., 1798, Ent. Syst. Suppl.: 571. Host: *Pico viridi.*

Philopterus pici Fabr.: Harrison, 1916, Parasitology **9:** 17, 102. Host: *Picus* spp. (*scalaris* Nitzsch, placed as a synonym)

Penenirmus pici (J. C. Fabricius); Hopkins and Clay, 1952, Check list of general and species of Mallophaga: 275. Host: *Picus viridis* Linn. (*scalaris* Burmeister, placed as a synonym)

Docophorus scalaris Burmeister, 1838, Handb. Ent. **2**(2): 427. Hosts: *Pic. viridis, canus, medius.*

Docophorus scalaris N.; Giebel, 1866, Z. ges. Nat. Wiss. **28:** 360. Host: *Picus minor.*

Docophorus macrotrichus Kolenati, 1858, S. B. Akad. Wiss. Wien **29:** 248, Pl. 1, Fig. 5. Host: *Chrysophlegma flavinucha.* NEW SYNONYMY.

Penenirmus macrotrichus (Kolenati); Hopkins and Clay, 1952, check list of general and species of Mallophaga: 275. Host: *Picus flavinucha* Gould.

Picophilopterus tuktola Ansari, 1947, Proc. natl. Inst. Sci., India **13:** 265, Fig. 4. Host: *Picus s. squamatus* Vigors. NEW SYNONYMY.

Penenirmus tuktola (Ansari); Hopkins and Clay, 1952, Check list of genera and species of Mallophaga: 276. Host: *Picus s. squamatus.* NEW SYNONYMY.

In general appearance this species closely resembles *P. auritus* from which it is distinguished by the greater number of centroposterior setae on tergites and the elongate forehead.

The head (Fig. 12) is produced in front as in *P. serrilimbus,* though it has only 2 pairs of elongate temporal setae. The stout anterior dorsal setae of the forehead are short. The proportions of the thorax and abdomen (Figs. 3, 4) are similar to *P. auritus.* Centroposterior of tergites IV–VI total more than 16 ($\bar{x}$ 8/tergite). Sternites IV–VI with less than 9 centroposterior setae ($\bar{x}$ 2/sternites).

Neoparatypes of *P. pici,* selected by Clay and Hopkins (1960: 7), have been examined. The paratypes of *P. tuktola* examined are not significantly different from either *P. pici* or *P. macrotrichus,* though specimens from the type host of the latter were consistently larger than the series from other hosts.

Dimensions in mm.: Total length, male 1.72–2.18, female 2.18–2.64; head length, male 0.53–0.67, female 0.61–0.74; head width, male 0.47–0.58, female 0.52–0.66; prothorax width, male 0.28–0.37, female 0.31–0.40; pterothorax width, male 0.43–0.62, female 0.54–0.67; abdominal width, male 0.54–0.82, female 0.70–0.90.

Material examined: Neotype and 5 males, 5 females from *Picus viridis* Linn. from England, Sweden and Yugoslavia; 9 males, 15 females from *Picus vaillantii* (Malherbe) from Morocco; 1 male, 1 female from *Picus s. squamatus* Vigors from Pakistan; 3 males, 6 females from *Picus vittatus* Vieillot from Thailand; 7 males, 9 females from *Picus vittatus eisenhoferi* Gyldenstolpe from Thailand; 4 males, 4 females from *Picus canus* Gmelin from Thailand; 4 males, 1 female from *Picus c. canus* Gmelin from Estonia; 2 males, 2 females from *Picus canus gyldenstolpei* S. Baker from Nepal; 1 male, 4 females from *Picus canus hessei* Gyldenstolpe from Thailand; 6 males, 8 females from *Picus erythropygius* (Elliot) from Thailand; 2 males, 3 females from *Picus flavinucha* Gould from Thailand; 1 male, 1 female from *Picus flavinucha archon* Deignan from Thailand; 1 male, 1 female from *Picus flavinucha lylei* (Kloss) from Thailand; 5 males, 5 females from *Picus flavinucha pierrei* Oustalet from Thailand; 4 males, 4 females from *Picus chlorolophus laotianus* Delacour from Thailand; 1 female from *Picus mentalis humii* (Hargitt) from

Thailand; 8 males, 14 females from *Dinopium b. benghalense* (Linn.) from India; 8 males, 8 females from *Dinopium b. punticolle* (Malherbe) from India; 8 males, 8 females from *Dinopium javanense* (Ljungh) from Philippine Islands and Thailand; 1 female from *Dinopium j. javanense* (Ljungh) from Thailand; 2 males, 2 females from *Dinopium j. intermedium* (Blyth) from Thailand; 1 male, 4 females from *Gecinulus grantia grantia* (McClelland) from Thailand; 2 females from *Gecinulus grantia viridanus* Sclater from Burma; 1 male from *Mulleripicus pulverulentus harterti* Hesse from Thailand; 1 male, 1 female from *Mullericpicus p. pulverulentus* (Temminck) from Thailand; 4 males, 4 females from *Dryocopus javensis feddeni* (Blyth) from Thailand; 6 males, 10 females from *Blythipicus p. pyrrhotis* (Hodgson) from Nepal; 2 females from *Chrysocolaptes lucidus guttacristatus* (Tickell) from Thailand.

Penenirmus heteroscelis (Nitzsch, 1866)
(Figs. 5, 6, 14)

Type host: *Dryocopus martius martius* (Linn.)

Nirmus heteroscelis Nitzsch, 1866, Z. ges. Nat. Wiss. **27:** 118. Host: *Pico martio.*

Degeeriella heteroscelis (Nitzsch); Seguy, 1944, Faune de France **43:** 310. Host: *Picus martius.*

Penenirmus heteroscelis (Nitzsch); Hopkins and Clay, 1952, Check list of general and species of Mallophaga: 274. Host: *Dryocopus m. martius.* (*pici* Schrank and *kumagera* Uchida placed as synonyms)

Paranirmus heteroscelis (Nitzsch); Zlotorzycka, 1964, Acta Parasit. Polonica **12**(24): 275, photo 20. Host: *Dryocopus martius.*

Pediculus pici Schrank, 1803, (nec Fabricius, 1798), Fauna boica: 188. Host: Schwarzspecht.

Philopterus kumagera Uchida, 1949, Jap. Med. J. **1:** 544, Fig. 12. Host: *Dryocopus m. martius.*

Penenirmus accuratus Zlotorzycka, 1964, Acta Parasit. Polonica **12**(24): 271, Figs. 9a, 9b. photo. 16. Host: *Dryocopus m. martius.* NEW SYNONYMY.

This distinctive species is identified by the elongate dorsal anterior setae of the forehead.

The head (Fig. 14) is similar in proportions to *P. arcticus* though significantly larger. The preantennal length is noticeably shorter than the postantennal length of the head.

The single female examined had more thoracic and abdominal setae than either of the 2 males. Pterothorax with a centroposterior group of 3 (male) or 4 (female) elongate setae on each side. General form (Figs. 5, 6) similar to *P. campephili,* though lacking the broad pleural thickenings of the latter

species. Tergites III–VI each with 6–8 (male) or 6–10 (female) elongate centroposterior setae and 2 shorter centroposterior setae on sternites III–VI.

The Nitzsch collection was destroyed during World War II. There has been no subsequent neotype selected for *Nirmus heteroscelis* Nitzsch, 1866. The pair examined from the type host; *Dryocopus martius* are hereby designated as Neotypes. They are in good condition and agree with the original description and the concept in common use during the last hundred years. The Neotype male and neoparatype female, from *Dryocopus martius* (Linn.) from Nischninovgorad, U.S.S.R., Apr., 1926, W. W. Karpoff, Col. No. 34., are deposited in the British Museum (Natural History). Figures are of these specimens.

Through the kindness of Dr. Göllner-Scheiding of the Zoologisches Museum der Humboldt-Universitat, I have been able to examine the single male on which *Paranirmus* Zlotorzycka, 1964, is based. It differs from the neotype of *P. heteroscelis* only in features perhaps best attributed to the techniques of mounting. It resembles specimens which have been preserved in alcohol for a considerable time, then only partially macerated and placed in a thick mount of Canada balsam. The discernible chaetotaxy does not differ from that for Figure 6.

The description of *P. accuratus* Zlotorzycka, 1964, is neither adequate nor diagnostic. In the absence of any evidence to the contrary, I have therefore considered it to be conspecific with *P. heteroscelis*.

Dimensions in mm.: Total length, male 1.70, female 2.11–2.15; head length, male 0.55–0.59, female 0.61–0.62; head width, male 0.52–0.56, female 0.58–0.61; prothorax width, male 0.30–0.32, female 0.32–0.36; pterothorax width, male 0.52–0.56, female 0.56–0.62; abdominal width, male 0.72–0.75, female 0.80–0.82.

Material examined: 3 males, 2 females from *Dryocopus martius* (Linn.) from Poland and U.S.S.R.

Penenirmus jungens (Kellogg, 1896)

Type host: *Colaptes auratus luteus* Bangs

Docophorus jungens Kellogg, 1896, Occ. Pap. Calif. Acad. Sci. (2),**6:** 481, Pl. 66, Fig. 4. Host: *Colaptes auratus* (Linn.).

Philopterus jungens Kellogg; Harrison, 1916, Parasitology **9:** 97. Host: *Colaptes auratus*.

Penenirmus jungens (Kellogg); Hopkins and Clay, 1952, Check list of genera and species of Mallophaga: 275. Host: *Colaptes auratus luteus* Bangs.

Penenirmus villosus Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 41, Figs. 13, 15, 32. Host: *Dendrocopos v. villosus* (Linn.) (probable error). NEW SYNONYMY.

This species is somewhat intermediate between *P. auritus* and *P. pici* and

can be distinguished from them only by the 3 pairs of elongate centroposterior setae on the pterothorax.

The proportions of the head and abdomen are similar to *P. auritus*, as is the abdominal chaetotaxy, except that in *P. jungens* tergites III–VI typically have 3 pairs of centroposterior setae.

Carriker (1957:97) selected ". . . the female (in best condition) on slide No. 309a as lectotype." Slide 309a has 1 male and 2 females. It has been remounted and the female on the right is designated as lectotype, the others thus becoming paralectotypes. One male and 2 females on a second slide numbered 310a and otherwise labeled as 309a, have been remounted and labeled as paralectotypes. The above types have been returned to the Kellogg Collection, at the University of California, at Berkeley.

Penenirmus villosus is based on a mixed series. The holotype, allotype and 2 paratypes are indistinguishable from *P. jungens*, whereas 10 male and 7 female paratypes examined are identical to *P. auritus*. It is likely that the series including the holotype and 3 paratypes are stragglers off *Colaptes auratus*; all other paratypes will likely prove to be *P. auritus*, which normally infests *Dendrocopos villosus*.

Dimensions in mm.: Total length, male 1.54–2.08, female 1.80–2.32; head length, male 0.52–0.61, female 0.56–0.64; head width, male 0.47–0.56, female 0.49–0.62; prothorax width, male 0.26–0.33, female 0.27–0.34; pterothorax width, male 0.40–0.58, female 0.44–0.63; abdominal width, male 0.54–0.74, female 0.68–0.85.

Material examined: 6 males, 5 females from *Colaptes cafer* (Gmelin) from Mexico and U.S.A.; 3 males, 6 females from *Colaptes cafer collaris* Vigors from U.S.A.; 35 males, 54 females from *Colaptes auratus* (Linn.) from Canada and U.S.A.; 5 males, 15 females from *Colaptes auratus luteus* Bangs from U.S.A.; 1 female from *Colaptes chrysoides mearnsi* Ridgeway, from U.S.A.; 2 males, 2 females from *Dendrocopos villosus* (Linn.) (probable error) from U.S.A.

Penenirmus campephili Eichler, 1953
(Figs. 7, 8, 13)

Type host: *Campephilus magellanicus* (King)

Penenirmus campephili Eichler, 1953, Zool. anz. **150:** 239, figs. 16, 17. Host: *Campephilus magellanicus*.

This species (Figs. 7, 8) is readily distinguished from others known from the Picidae by the presence of 2 pairs of pleural setae on segments IV–V and 4 sternocentral setae on each abdominal segment.

The preantennal length of the head (Fig. 13) is approximately equal to the postantennal length. Dorsal anterior setae of forehead short. Pterothorax with 3 pairs of elongate centroposterior setae, as in *P. jungens*. Tergites III–VI

each with 8–10 centroposterior setae and sternites III–VI each with an average of centroposterior setae.

Dimensions in mm.: Total length, male 1.90, female 1.96–2.27; head length, male 0.59, female 0.62–0.66; head width, male 0.58, female 0.62–0.64; prothorax width, male 0.36, female 0.35–0.38; pterothorax width, male 0.61, female 0.61–0.70; abdominal width, male 0.77, female 0.79–0.88.

Material examined: 2 male, 4 female paratypes from *Campephilus magellanicus* from Chile.

Penenirmus maculipes (Piaget, 1880)
(Fig. 8A)

Type host: "Picus from Bangka"

Docophorus maculipes Piaget, 1880, Pediculines: 661, Pl. 54, Fig. 54, Fig. 3. Host: *Picus* from Bangka.

Philopterus maculipes Piaget; Harrison, 1916, Parasitology **9:** 98. Host: *Picus* sp.

Penenirmus maculipes (Piaget); Hopkins and Clay, 1952, Check list of genera and species of Mallophaga: 275. Host: *Picus* from Bangka.

Penenirmus maculipes (Piaget); Emerson and Johnson, 1961, J. Kansas ent. Soc. **34:** 42. Host: *Picus* from Bangka.

This species is based on a single female, in good condition, reportedly from a *Picus* from Bangka.

This species is readily distinguished from others known from the Picidae by the 4 pairs of centroposterior setae on the pterothorax, 10 elongate centroposterior setae on tergites III–V, and 9 on tergites VI–VII. Dorsally it resembles *P. campephili* from which it is distinguished by its 2, as opposed to 4, centroposterior setae on sternites III–VI, and single pair of pleural setae on segments IV–V.

Dr. H. G. Deignan, U. S. National Museum, (*in* Emerson and Johnson, 1961:43) cites the following species as possibly being the "*Picus* from Bangka": *Picus puniceus observandus* (Hartert), *Picus mineaceus malaccensis* Latham, *Picus mentalis humii* (Hargitt), *Dinopium rafflesii rafflesii* (Vigors and Harsfield), *Micropternus brachyurus badius* (Raffles), *Hemicircus concretus coccomentopus* (Reichenbach), and *Dryocopus javensis javensis* (Horsfield). Specimens examined from *Picus mineaceus*, *Picus mentalis*, *Micropternus brachyurus* and *Dryocopus javensis* are not conspecific with the type and should not be considered as possible type host of *P. maculipes*. It is tempting to therefore conclude that the type host is either *Picus puniceus*, *Dinopium rafflesii* or *Hemicircus concretus* and furthermore, *Penenirmus pici* or *P. auritus* are known to infest *Picus* spp. and *Dinopium* spp., thus *Memicircus concretus* appears to be the most probable type host of *P. maculipes*. This speculation however rests on the reliability of the original collection data. Hopkins and Clay

(1954) list the 496 species described by Piaget and cite 96 host records as being in error with another 15 listed as probable host errors. With approximately 20% of the Piaget host records known to be wrong it is neither prudent nor profitable to rely too heavily on a type host identified through such a process of elimination. The type host designation must await the collection of conspecific specimens which most likely will come from some southeast asian woodpecker.

Material examined: 1 female Holotype from *Picus* from Bangka (B.M. natural history).

Index to the *Penenirmus* from the picidae

Host	*Penenirmus* species
Piciformes	
Suborder Pici	
Picidae	
Jynginae	
Jynx torquilla Linn.	***serrilimbus* (Burmeister, 1838)
Jynx ruficollis Wagler	*serrilimbus* (Burmeister, 1838)
Picumninae	
Picumnus cinnamomeus Wagler	*auritus* (Scopoli, 1763)
Picumnus olivaceus Lafresnaye	" "
Picumnus innominatus Burton	" "
Picinae	
Colaptes cafer (Gmelin)	*jungens* (Kellogg, 1896)
Colaptes auratus (Linn.)	** " "
Colaptes chrysoides (Malherbe)	" "
Colaptes campestris (Viellot)	*auritus* (Scopoli, 1763)
Chrysoptilus punctigula (Boddaert)	" "
Chrysoptilus atricollis (Malherbe)	" "
Piculus rivolii (Boissonneau)	" "
Piculus rubiginosus (Swainson)	" "
Micropternus brachyurus (Vieillot)	" "
Picus viridis Linn.	***pici* (Fabricius, 1798)
Picus vaillantii (Malherbe)	" "
Picus squamatus Vigors	" "
Picus vittatus Vieillot	" "
Picus canus Gmelin	" "
Picus erythropygius (Elliot)	" "
Picus flavinucha Gould	" "
Picus chlorolophus Vieillot	*auritus* (Scopoli, 1763) *pici* (Fabricius, 1798)
Picus mentalis Temminck	*pici* (Fabricius, 1798)
Picus mineaceus Pennant	*auritus* (Scopoli, 1763)
Dinopium benghalense (Linn.)	*pici* (Fabricius, 1798)
Dinopium javanense (Ljungh)	" "
Gecinulus grantia (McClelland)	" "
Dryocopus martius (Linn.)	***heteroscelis* (Nitzsch, 1866)
Dryocopus pileatus (Linn.)	*auritus* (Scopoli, 1763)

Dryocopus lineatus (Linn.)	" "
Asyndesmus lewis (G. R. Gray)	" "
Melanerpes erythrocephalus (Linn.)	" "
Melanerpes formicivorus (Swainson)	" "
Melanerpes hypolius (Wagler)	" "
Melanerpes carolinus (Linn.)	" "
Melanerpes aurifrons (Wagler)	" "
Melanerpes superciliaris (Temminck)	" "
Melanerpes cruentatus (Boddaert)	" "
Sphyrapicus varius (Linn.)	" "
Sphyrapicus throideus (Cassin)	" "
Veniliornis fumigatus (d'Orbigny)	" "
Veniliornis kirkii (Malherbe)	" "
Veniliornis callonotus (Waterhouse)	" "
Veniliornis dignus (Sclater & Salvin)	" "
Dendrocopos major (Linn.)	***auritus* (Scopoli, 1763)
Dendrocopos darjellensis (Blyth)	" "
Dendrocopos leucotos (Bechstein)	" "
Dendrocopos hyperythrus (Vigors)	" "
Dendrocopos atratus (Blyth)	" "
Dendrocopos macei (Viellot)	" "
Dendrocopos minor (Linn.)	" "
Dendrocopos kizuki (Temminck)	" "
Dendrocopos albolarvatus (Cassin)	" "
Dendrocopos villosus (Linn.)	" "
Dendrocopos pubescens (Linn.)	" "
Dendrocopos scalaris (Wagler)	" "
Dendrocopos arizonae (Hargitt)	" "
Picoides tridactylus (Linn.)	*arcticus* (Carriker, 1958)
Picoides arcticus (Swainson)	***arcticus* (Carriker, 1958)
Blythipicus pyrrhotis (Hodgson)	*pici* (Fabricius, 1798)
Campephilus magellanicus (King)	*campephili* (Eichler, 1953)

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Hibernation Sites and Temperature Tolerance of Two Species of *Vespula* and One Species of *Polistes* (Hymenoptera: Vespidae)

David L. Gibo
Erindale College, University of Toronto, Mississauga, Ontario.

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Abstract: The range of temperatures encountered at hibernation sites of *Vespula maculata* (Linnaeus), *Vespula arenaria* (Fabricieus), and *Polistes fuscatus* (Fabricius) during the winter and spring of 1971–72 are presented. The tolerance of each species to temperatures below freezing was determined. All individuals of both *Vespula* species tested were killed by −10°C, while all *Polistes fuscatus* tested were killed at −20°C. These lethal temperatures were lower than the minimum temperatures observed at the hibernation sites.

INTRODUCTION

In temperate regions overwintering queens of the genus *Vespula* frequently hibernate in rotting logs and similar situations (Evans, 1963; Rau, 1929), while wasps of the genus *Polistes* hibernate in walls of buildings, under shingles, and in cracks in boards (Eberhard, 1969). Rau (1934) found that the queens of *Vespula maculata* (Linnaeus) constructed individual cells within the wood, and speculated that temperatures at the hibernation site were lower than in the surrounding area. The present paper reports the range of temperatures encountered during the winter and spring at a hibernation site of *Vespula maculata* (Linnaeus) and *Vespula arenaria* (Fabricius), and the tolerance of these two species and of *Polistes fuscatus* (Fabricius) to temperatures below freezing.

During October and November of 1971, a total of 86 *Vespula maculata* queens, 64 *Vespula arenaria* queens, and 88 *Polistes fuscatus* queens were found hibernating on the grounds of the Erindale campus of the University of Toronto in Ontario, Canada. The *Vespula* queens were located on the floor of the forest near the base of a stump in litter composed almost entirely of chips of decaying wood. The hibernating queens were found at depths ranging from one to twelve centimeters and were often found in individual cells of the type described by Rau (1934). The *Polistes* queens were collected around buildings, and most were taken near the window frame of an old shed.

Because both *Vespula* species construct distinctive aerial nests (Miller, 1961), it was possible to count the number of nests of each species in the forest. After an extensive search, only six nests of *Vespula arenaria* were found.

Acknowledgments: I would like to thank Donald Davis who helped collect the *Vespula* queens, Anne Culpeper and Guy Latimer who helped locate the *Vespula* nests, P. J. Pointing for valuable suggestions, and Glenn Morris who criticized the manuscript.

However, ten nests of *Vespula maculata* and four additional nests of *Vespula arenaria* were found on the college grounds adjacent to the forest. Apparently, the queens of *Vespula maculata* found at the hibernation sites had come from areas outside the forest.

MATERIALS AND METHODS

Readings of the temperature of the litter at two *Vespula* hibernation sites were taken from early November to May. These sites were only two meters apart and had accounted for about one third of the total number of queens captured; they were assumed to be preferred locations. One of the sites had litter 12 cm. deep and temperature probes were placed at the surface, at 6 cm. and at 12 cm. At the second site, the litter was only 6 cm. deep, and the probes were placed at the surface and at 6 cm.

Reading of litter temperatures and the air temperature at a height of 1 m. were taken several times a month. Care was taken to obtain readings during periods of unusually cold weather. Occasionally, throughout the winter, temperatures were taken at the *Polistes fuscatus* hibernation sites in the shed.

An attempt was made to determine if a detectable daily litter temperature cycle occurred during the months of complete snow cover. During one 24-hour period in late winter, when the snow depth was 15 cm., readings were taken every 6 hours. The air temperature varied from –.5°C. to 7.5°C. while litter temperatures remained constant at 0.0°C. Consequently, since daily temperature fluctuations were apparently absent in the litter during the months of complete snow cover, no attempt was made to take temperature at a standard time. A reading in the morning is assumed to give the same litter temperature as an afternoon reading.

When snow cover was absent, large fluctuations in temperature (21°C.) were observed in the litter during the course of a day. During these periods, temperature readings were taken mainly during the afternoon, and no attempt was made to determine the minimum and the maximum for any one day. Consequently, litter temperatures taken in the absence of snow cover are used only as a conservative indicator of the earliest and latest date for the occurrence of freezing temperatures.

The temperature tolerance of the queens of *Vespula maculata*, *Vespula arenaria*, and *Polistes fuscatus* was determined by exposing groups of wasps to specific temperatures for 48 hours and then noting how many had died. These temperatures were 0.0°C., –5.0°C., –15°C. and –20°C. ± .5°C. Prior to the temperature tolerance experiments, the wasps had been maintained at +5°C. for two to three months during which time death rates of 3% for *Vespula maculata*, 11% for *Vespula arenaria*, and 8% for *Polistes fuscatus* were observed. The individuals of each species of wasps were divided into four groups of ten, and each group was exposed to one of the test temperatures for 48 hours.

Table 1. Maximum and minimum temperatures observed at a hibernation site of both *Vespula arenaria* and *Vespula maculata* during the period of complete snow cover, (December 31, to March 31) based on readings taken several times per month (total = 14).

Location of Probe	Maximum	Minimum	Range
Air	+7.5°C.	−13.5°C.	21.0°C.
Surface	1.0	− 6.5	7.5
6 cm.	1.0	− 2.5	3.5
12 cm.	1.5	− 1.5	3.0

After the test, the groups were returned to +5°C. and examined for movement. *Polistes fuscatus* was the only species exposed to −20°C.

RESULTS

Freezing temperatures were first observed at the surface of the litter on December 18, at 6 cm. on January 15, and at 12 cm. on January 26. Freezing temperatures were last recorded at the surface of the litter on March 31, and at 6 cm. and 12 cm. on April 11. The litter was an effective insulator. On December 18, when there was no snow cover and the air temperature was −12.5°C., the temperatures of the litter were −5.0°C. at the surface, 0.0°C. at 6 cm., and 2.0°C. at 12 cm. The effect of snow cover was to damp out daily temperature fluctuations.

The litter was completely covered with snow from about December 31 to March 31. Table I shows the maximum and minimum temperatures observed during this period. The temperature of the litter showed much less variation than the air temperature, and the observed temperature range decreased with depth. The lowest air temperature observed occurred on the night of January 26, 1972, and was −13.5°C. The corresponding temperatures for the litter were −6.5°C. at the surface, −2.5°C. at 6 cm., and 0.0°C. at 12 cm. At this date the snow cover was about 10 cm. The temperature of the hibernation sites in the shed was found to be similar to the air temperature.

Table 2. Survival of queens of *Vespula arenaria*, *Vespula maculata*, and *Polistes fuscatus* after exposure for 48 hours to various temperatures, based on 10 individuals of each species for each temperature.

	Percent survival at each temperature		
Temperature	Vespula arenaria	Vespula maculata	Polistes fuscatus
0.0°C.	100%	100%	100%
−5.0	80	100	100
−10.0	0	0	100
−15.0	0	0	90
−20.0	−	−	0

The results of the temperature tolerance experiments are shown in Table II. Between –5°C. and –10°C., the survival of both species of *Vespula* went from 80% in *Vespula arenaria* and 100% in *Vespula maculata* to 0.0% for both species. In comparison, *Polistes fuscatus* queens had 100% survival at –10.0%C. and 90% at –15.0°C. None of the *Polistes fuscatus* survived –20.0°C.

DISCUSSION

The difference between a temperature that could be tolerated by most individuals and a temperature that killed all the individuals was only 5°C. for the three species. These tolerance ranges corresponded closely to the minimum temperatures observed at the hibernation sites. In the litter, the lowest temperature, –6.5°C., was observed at the surface, and temperatures increased with depth. At 12 cm., the temperature was never below –1.5°C. Since temperatures as low as –10°C. did not occur in the litter, any *Vespula maculata* and *Vespula arenaria* present should have had a low winter mortality.

In contrast to the relatively warm hibernation sites required by the *Vespula* species, *Polistes fuscatus* can withstand temperatures as low as –15.0°C. and can survive in far less sheltered above ground situations. However, since air temperatures of –20°C. usually occur in Southern Ontario each winter, some protection from the weather is required. During cold winters, structures such as the shed would be unsuitable as a hibernation site, and winter survival may be restricted to those *Polistes fuscatus* that hibernate in buildings.

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European Pseudoscorpions from New England

William B. Muchmore
Department of Biology, University of Rochester
Rochester, New York 14627

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Abstract: The occurrence of *Cheiridium museorum* (Leach) and *Allochernes peregrinus* Lohmander in North America is recorded for the first time.

Over the years a small number of European pseudoscorpions have been identified in the fauna of North America (cf. Hoff, 1958; Muchmore, 1969). This note is to report two additional species collected in New England and presumably established there.

Cheiridium museorum (Leach)

Three male specimens were found at Pepperell, Middlesex County, Massachusetts, in September, 1966 by P. Weygoldt (collection of Museum of Comparative Zoology, Harvard University). These specimens have been prepared for microscopic study, examined in detail, then compared both with Beier's description of the species (1963, p. 244) and with representatives of the species from Herefordshire, England (on loan from the British Museum, Natural History). They are similar in all details of size and proportion, and there is no doubt that they are *C. museorum*. This species is easily distinguished from the known American forms; *C. insperatum* Hoff and Clawson (1952) is significantly larger and has more slender appendages, while *C. firmum* Hoff (1953) is much smaller and has more robust appendages.

Even though Beier (1932, p. 8) considered that *C. museorum* was almost cosmopolitan in distribution, the species has never been definitely reported from the Western Hemisphere. It certainly might be expected that a species which is so common around homes and farms in Europe would have been introduced into America on many occasions; but, if so, it has either failed to establish itself here, or else has not been noticed because of its very small size and cryptic habits.

Allochernes peregrinus Lohmander

A single male, apparently referable to this species, was taken by S. B. Peck at Monadnock State Park, Marlboro, Cheshire County, New Hampshire, on

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14 June 1970. It was recovered by Berlese separation of a 42 liter sample of beech leaf-log litter, and was accompanied by many specimens of *Microbisium confusum* Hoff, other arthropods, etc. The specimen has been mounted on a slide, studied in detail, and compared with the descriptions of species of *Allochernes* provided by Beier (1963, p. 262) and with specimens of *A. dubius* (Cambridge), kindly supplied by P. D. Gabbutt of the University of Manchester, England. According to all morphological criteria, it appears to be a representative of *A. peregrinus*, a form which has been known only from Sweden. In particular, the eleventh tergites possess tactile setae; the palps are attenuated; and the fourth pedal tarsus bears no real tactile seta, but rather an elongated, dentate seta just distad of the middle.

On the basis of the single specimen, it cannot be decided indisputably that it belongs to this species; it might possibly be an individual variant of some other species of the genus. However, it is certainly a representative of *Allochernes*, a European and Asian genus never previously reported from America. It is hoped that further collecting in the area and elsewhere will turn up additional specimens of this interesting species.

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Analogous Prey Escape Mechanisms in a Pulmonate Mollusk and Lepidopterous Larvae

William H. Gotwald, Jr.
Department of Biology, Utica College of Syracuse University, Utica, New York 13502

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Abstract: Analogous mechanisms to escape predation by *Anomma* driver ants are employed by a terrestrial pulmonate mollusk and by lepidopterous larvae. Each involves dropping on the end of a thin cord of secreted material that the ants cannot traverse. Theoretically, this mechanism could be used by diverse organisms having the ability to secret or form such cords.

The evolutionary refinement of predatory mechanisms, i.e. prey detection and capture, has been accompanied by the elaboration of progressively more sophisticated means of defense and escape in prey species. Many potential prey organisms, such as the skunks (*Mephitis* spp.) and spitting cobras (*Naja* spp.), have concentrated on the elaboration of repellent chemical products (such chemicals were classified as defensive allomones by Brown et al., 1970), while others, such as the porcupine [*Erethizon dorsatum* (L.)], have effectively exploited structural deterrents. Of all phyla, arthropods have probably gone furthest in evolving complex defense mechanisms. Spraying glands, "reactor" glands (in which the chemical precursors of a defensive secretion are not mixed until the moment of extrusion), and enteric discharges are among the general categories for such mechanisms (Eisner, 1971). Although successful defense against a predator usually precedes escape, adaptation in some organisms appears to have emphasized escape alone, to the neglect of preliminary defensive systems. The escape flight patterns employed by certain noctuid moths to escape capture by bats (Roeder and Treat, 1961) and tail autotomy in certain lizards, such as geckos (Gekkonidae), are but two examples.

During investigations of *Anomma* driver ants in Ghana and Kenya (May–August 1971), I frequently observed organisms reacting to *Anomma* foraging attacks. Two observations involved phylogenetically widely separated organisms employing analogous escape mechanisms. One of these organisms was the terrestrial mollusk commonly referred to as a slug (Order Pulmonata), the others were caterpillars of the lepidopterous family Noctuidae (Catocalinae-Erebinae complex of Hampson).

Acknowledgments: I am grateful to Dr. David Barr, Royal Ontario Museum, Toronto, for critically reading the manuscript and to Dr. John G. Franclemont, Cornell University, for identifying the lepidopterous larvae. My field work in Ghana was greatly facilitated by Mr. Dennis Leston, Department of Zoology, University of Ghana, and in Kenya by Mr. G. R. Cunningham-van Someren, East African Research Unit of Chesterford Park Research Station. The research was supported by National Science Foundation Grant GB 22856.

Driver ants belong to the subgenus *Anomma*, genus *Dorylus*, and are important tropical Old World predators. These ants forage in swarms containing millions of workers and drive before them those organisms, invertebrates and vertebrates, whose mobility permits escape. Their foraging patterns are well documented in the literature (Cohic, 1948; Raignier and van Boven, 1955; Savage, 1847, 1849; Schneirla, 1971; Wheeler, 1910).

OBSERVATIONS AND DISCUSSION

The first observation (8 July 1971) occurred near Legon in the coastal scrub and grassland region of Ghana. A swarm of *D.* (*Anomma*) *nigricans* Illiger was foraging in an area of high grasses and small leguminous trees bordering on a dirt road, and was first detected as a few small columns of workers moving along the edge of the road. Individuals foraged on the grasses and the trees, climbing the grasses to the tips of the leaves (1 to 1.5 meters high) and the trees to a height of about 3 meters. They did not forage on the leaves of the trees.

A slug, 8 cm. long, was trapped by the foraging workers at the tip of a blade of grass, 1.5 meters above the ground. A cluster of foraging workers accumulated behind the slug. A number of workers attempted to bite it but may have been prevented from doing so by the slug's coating of integumental slime. The ant mandibles did not penetrate the integument, and the mouthparts became entangled with the slime. Eisner (1971) reported that integumental slime in slugs does serve as a defensive mechanism against arthropod predators. A small mass of slime collected on the blade of grass, immediately behind the slug, and an increasing number of workers became ensnared in it. Eventually, as the leaf tip bent with the weight of ants and slug, the slug slid from the leaf, suspended posteriorly by a thread of slime. This cord of slime slowly (over a period of about 10 minutes) stretched to a length of approximately 20 cm., at which point it broke. The snail fell to the substrate. Before the cord broke, the slime-mired worker ants had tried unsuccessfully to climb down the cord.

Approximately 40 struggling worker ants remained glued to the leaf tip but most dropped from the leaf, one by one, over a period of 45 minutes. At the end of this period, 3 workers were still glued in place.

Thickly matted ground cover obscured the fate of the slug. However, the foraging front of an *Anomma* swarm advances (almost "flows") into adjacent areas and the entire swarm follows behind. A swarm remains in one area for only a short period of time. By the time the slug dropped to the substrate, most of the swarm had moved on.

A second observation (10 August 1971) was made at Kakamega Forest Station in Kenya. Kakamega is a relict forest including both West and East African faunal and floral elements. Again a *D.* (*Anomma*) *nigricans* swarm,

about 20 meters wide, was under observation. The workers foraged on low vegetation to heights of about 1.5 meters and in trees, particularly those covered with mosses, to heights of at least 3 meters. A total of 6 larval lepidoptera escaped attack by dropping from the leaves of low vegetation on threads of silk. Each remained dangling from the under surface of its leaf during the raid. Eventually all dropped to the ground, but again, because of the ground cover, their fate was not observed. However, the nucleus of the swarm had already passed at the time they began dropping.

CONCLUSIONS

Many organisms escape *Anomma* driver ant foraging raids by running, jumping, or flying. Others, with limited mobility must utilize alternative means of escape. One method, observed for both a pulmonate mollusk and lepidopterous larvae, effectively separates predator and prey by means of a slender cord. The predators are unable to negotiate this "bridge." After the swarm has passed, the prey organism drops to the substrate. Swynnerton (1915) also reported such escape from *D.* (*Anomma*) *nigricans* by larvae (presumably Lepidoptera) and spiders. Theoretically, the mechanism could be used by a number of diverse organisms having the ability to secrete or form such cords, and may, in fact, be a commonly employed method of escape.

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The Systematics of the Tribe Plectoderini in America North of Mexico (Homoptera: Fulgoroidea, Achillidae). 1971. Lois Breimeier O'Brien. University of California Press. 80 pp. $3.00.

The author states that this revision of the tribe Plectoderini in America north of Mexico is based on an evaluation of morphological characters and host associations. The 32 previously known species from this area have been referred to the genus *Catonia*. Eleven of these species are found east of the 100th meridian and 21 are described from California and Arizona. Eight new species are described.

A comparison made with the known West Indian and Central American faunas show that 3 of the United States species belong in the genera *Opsiplanom* or *Momar*. Three new genera, predominantly western (*Juniperia*, *Synecdoche*, and *Xerbus*) are established in this paper. Eight of the eastern species plus 2 western ones are retained in the genus *Catonia*. Thus the 40 species belong to 6 genera.

A Field Guide to the Butterflies and Burnets of Spain. W. B. L. Manley and H. G. Allard. Hampton, Middlesex, England, E. W. Classey, Ltd., pp. 1–192, col. pls. 1 + 1–40. Obtainable in the U. S. A. from Entomological Reprint Specialists, P. O. Box 77971, Dockweiler Sta., Los Angeles, California, 90007. $37.50.

At first glance anyone accustomed to the more or less pocket-sized books called Field Guides and Field Books that have proliferated in recent years will wonder why this book is called a "field guide." Certainly its $8\frac{3}{4} \times 10\frac{1}{2}$ inch size will not fit very well into a collecting bag; and its sumptuous appearance, with hundreds of beautifully accurate color illustrations, would seems to fit it better for the role of a cocktail-table conversation piece. However, it is truly a field guide, among its other virtues, because of the enormous amount of detailed information given about exact localities, environments, food plants and dates which will guide the collector to his quarry. It would be even more useful if a few maps had been included. But it is sure to prove one of the most useful of collecting aids; and I suspect that it will greatly increase the numbers of collectors visiting the Iberian Peninsula, and that most of them will carry copies.

In addition to Spain, which is covered in great detail, Madeira and the Balearic and Canary Islands are treated in separate sections; and records and other details about Portugal are included in the main text. (Readers of this review will be interested to learn that the chief reference for Portuguese butterflies is that of Zerkowitz, 1946, Journal of the New York Entomological Society, vol. 54.)

The Burnets, by the way, are a most unusual group of Old World day-flying moths (Zygaenidae) with bold patterns mostly of iridescent green and red. We have none in North America. They have long been special favorites with collectors (I have heard this called zygaenomania) who industriously catalogue every variation of color and pattern and name these by the hundreds as "subspecies," varieties, forms or aberrations at, we might venture, the drop of a bonnet. This was the sort of excess that led the International Code of Zoological Nomenclature to bar infrasubspecific names from formal scientific nomenclature; and this in turn has stimulated the naming of a great deal of nonsense as "subspecies."

The Iberian Peninsula is a happy hunting ground for students of variation, having great climatic diversity and a very varied, largely mountainous terrain. It has many alpine species, relics from the Pleistocene glaciations, and also many Mediterranean and African elements. This has led to a proliferation of "subspecies" names that often seems

exaggerated to a North American student, and, in fact, often is. The authors have questioned or omitted many names of dubious status, and have exposed others. Their work may encourage further irresponsible naming by making things easier for the ignorant; but it will most certainly be a great aid to all serious students of population variation and evolution everywhere.

The colour reproductions, made from more than 1100 specimens, are incredibly good. I have been told that the work was done with a very special, room-sized, electronic scanner, the complexity of which is quite baffling to a layman—and this I can well believe, for the results are extraordinarily fine. Perhaps "space-age" electronics are of value even to the bug hunter.

The authors have organized their work very thoroughly and with meticulous regard for taxonomy and bibliography. A synonymic checklist gives references to the original descriptions, locality and other data are well documented, and an extensive bibliography (compiled by someone who knows how to write a proper bibliographic reference) lists the publications chiefly concerned. This sort of thing alone will make the book extremely useful to the scientist as well as to the amateur.

Alexander B. Klots
The American Museum of Natural History

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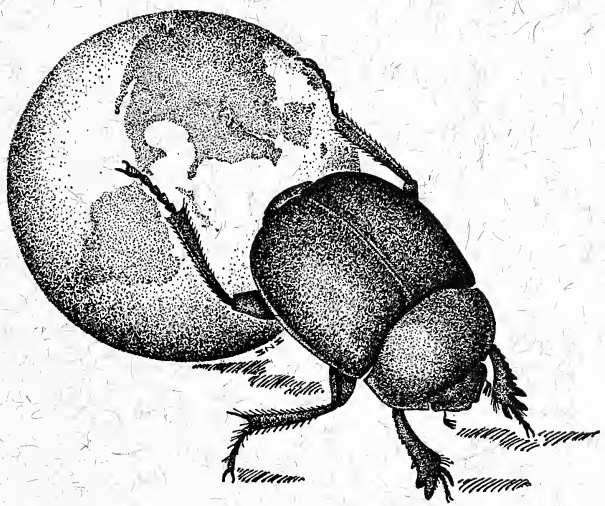

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CONTENTS

Observations on *Exaerete* spp. and their hosts *Eulaema terminata* and *Euplusia surinamensis* (Hymen., Apidae, Euglossinae) in Trinidad

FRED D. BENNETT
COMMONWEALTH INSTITUTE OF BIOLOGICAL CONTROL, GORDON STREET, CUREPE, TRINIDAD

RECEIVED FOR PUBLICATION APRIL 5, 1972

Abstract: In Trinidad the parasitic *Exaerete dentata* (Linn.) develops in the cells of *Euplusia surinamensis* (Linn.) and a second species in the cells of *Eulaema terminata* Smith. The female of *E. dentata* opens the recently sealed cell and removes the host's egg and after ovipositing reseals the cell. Females of *Exaerete* sp. were observed to enter a nest of *E. terminata* but activities within the nest could not be observed. In the discussion the behavior of *Exaerete* spp. is compared with other parasitic bees.

The appearance of the recent review on the evolution of parasitism among bees (Bohart, 1970) has prompted the preparation of the following notes on my somewhat limited observations on *Exaerete* spp. in Trinidad. In his review Bohart refers to the two parasitic Euglossine genera *Exaerete* and *Aglae* and states that little is known of the biology of these parasites, although he speculates that their habits are probably intermediate between those of *Psithyrus*, which invades nests of *Bombus* and after an initial struggle is accepted by the original queen and her workers, and those of most parasites of solitary bees in other families which surreptitiously insert their eggs in the partially provisioned or sealed cells when the host bees are absent.

Zucchi et al. (1969) in their comprehensive review of the biology of the Euglossinae also refer to the dearth of observations on the behavior of the parasitic members, although they cite most of the instances where definite host-parasite associations are known. In one other reference (Dodson and Frymire, 1961), *Exaerete smaragdina* Guer. is mentioned as a parasite of *Euplusia surinamensis* (Linn.) in Ecuador. Accordingly, the following observations may be of interest.

ASSOCIATION WITH *Eulaema terminata*

In Trinidad where three species of *Exaerete*, i.e., *dentata* (Linn.), *smaragdina* Guer., and an undescribed species near *frontalis* Guer. occur (J. G. Rozen, pers. comm., 1966; J. S. Moure, CMF, pers. comm., 1972), a female of this genus was observed on several occasions hovering near and entering a nest of *Eulaema terminata* Smith within a hollow tree.

The nest was discovered on April 9, 1964, by D. Bharath, who had earlier located another nest of this species (Bennett, 1965). While we were walking along a pathway in the Nariva Swamp he noted a female of *E. terminata*

enter a small opening in a tree trunk. The opening, oval-shaped, approx. 6 cm. × 5.4 cm., situated 1.3 mm. from ground level, had been closed with mud except for a circular 1.5 cm. hole near the top. Arrangements were made for Mr. Bharath to make continual observations on activities near the entrance of the nest from early morning until late afternoon on April 15 and 16, and again from 10:30 A.M., April 21, until activity ceased on the afternoon of April 25.

(a) Activities of *E. terminata*: The pertinent observations are summarized in Table 1. When leaving the nest, females of *E. terminata* frequently disappear rapidly with little or no orientation flight, while returning bees usually hover momentarily before entering and hence the number of entries recorded for the day was usually greater than the number of departures, although on two occasions there were more observed departures than entries. It was discovered during the first day that returning females approached the nest entrance but retreated if the observer was close enough to attempt to determine whether nesting material or pollen was being carried. Accordingly, on only a few occasions was the nature of the load determined, although it was ascertained that either pollen or mud (nesting material) (never both) could be collected on the first morning trip. Frequently on an afternoon flight adults returned unladen and it is assumed that they had left the nest to collect nectar for their own use, a habit observed earlier in *Euglossa cordata* (author's unpubl. data). If laden in the afternoon, the load was invariably identified as pollen. Although the number of bees in the nest was not determined, an analysis of the departure and return times suggests that three or at most four females were active; for example, three females departed in rapid succession on the morning of April 16. There were two well-defined periods of flight activity, i.e., the first part of the morning and late afternoon. The time of first departure varied from 5:30 to 6:05 A.M., i.e., usually as the sky brightened in the east but before sunrise. The duration of the first afternoon flight varied from 25 minutes to almost two hours. The afternoon flights usually terminated well before sunset, although in the forest light had begun to fade. Although the nest entrance was examined after dark in the evening and before sunrise in the morning it was never closed, although *Euglossa cordata* (Linn.) and *E. variabilis* Friese usually close the entrances to their nests at night (Bennett, 1966).

(b) Observations on *Exaerete*: During the days that the nest was under close observation one *Exaerete* adult was frequently observed resting on foliage one to three meters from the nest entrance. On one day two adults were present. On three separate occasions a *Eulaema* female, returning when an *Exaerete* was flying near the entrance, attempted to drive it away and failing to do so flew away thereafter. Observed entries into the nest are noted in

TABLE 1. Summary of flight activity of *Eulaema terminata* and *Exaerete* sp., April 1964

Date	15	16	21	22	23	24	25
Eulaema							
A.M.							
(1) 1st ♀ departed	n.r.	5:30	n.r.	5:45	5:40	5:45	6:05
1st ♀ returned	5:51	5:55	n.r.	5:55	6:02	6:01	7:10
(3) Activity terminated	10:10	11:10	11:35	11:34	11:26	11:21	11:31
(4) Total no. of trips**	(12)15	(19)20	n.r.	(15)15	(9)9	(6)6	(10)11
P.M.							
(5) 1st ♀ departed	2:21	3:15	3:05	3:10	3:11	4:09	3:12
(6) 1st ♀ returned	4:20	3:31	3:30	3:26	3:41	4:23	3:41
(7) Flight activity terminated	5:33	6:18	5:21	5:56	6:04	6:49	5:55
(8) Total no. of trips**	(5)5	(8)8	(9)7	(7)8	(11)9	(6)5	(6)8
Exaerete							
(9) Entered nest	8:45	—	7:01	6:30*	6:25	6:10*	11:02
(10) Left nest	8:47	—	7:02		6:26		11:44

* Approached but did not enter.
** Recorded departures and arrivals of all bees (figures in brackets are departures; unbracketed are return trips).
n.r. Not recorded.

Table 1. It seems unlikely in view of observations reported below that oviposition could have occurred except on the final visit when the *Exaerete* female remained in the nest for 45 minutes. Unfortunately the specific identity of the *Exaerete* females was not determined.

Observations were suspended while I was absent from Trinidad and I was not able to visit the site again until September 3. During this period the top of the tree was snapped off when a larger neighboring tree was uprooted during a tropical storm. When the standing trunk of the tree was felled the center proved to be rotten with a somewhat irregular cavity, ca. 8 cm. in diameter, extending 20 cm. below the nest opening and upward about 40 cm. The group of cells that had been attached to the side of the trunk about 2 m. from ground level, i.e., above the entrance hole, had become dislodged and the cell mass broken into several pieces. These, although partially reconstructed (fig. 1), were not in a suitable condition for analysis. Bees had apparently emerged from some, whereas smaller irregular holes in others suggested that predation by ants may have occurred. One cell contained the cocoon of a Mutillid wasp, apparently the first record of the family from a species of *Eulaema*, although Dodson (1966) records an unidentified species from *Euglossa* spp.

ASSOCIATION WITH *Euplusia surinamensis*

Adults of *Exaerete dentata* have been reared from cells of *Euplusia surinamensis* obtained from diverse nesting sites on a number of occasions. As most of these nesting sites were located in crevices between stacked lumber or in

Fig. 1. Cells of *Eulaema terminata* removed from nest in hollow tree.

cracks between joists and floor boards beneath houses elevated on pillars, the activities of neither of the bees could be readily observed. Similarly, the occasional cells of *Euplusia* found in abandoned galleries of *Xylocopa frontalis* or in the *Euglossa* nesting boxes described briefly by Bennett (1965) have never been encountered when provisioning was under way.

The discovery that *Euplusia surinamensis* frequently nests in crevices in eroded shale sea cliffs near Balandra offered an opportunity to make limited observations on its parasite, *Exaerete dentata.*

(a) Description of the *Euplusia* nesting site: Owing to the gradual encroachment of the sea, sections of the shale comprising the seacliffs periodically topple into the sea as the bases of the cliffs are undermined. When this occurs a series of crevices 1 cm. or more in depth and frequently 15 to 20 cm. in width and length is formed. These crevices are at varying slopes, depending on the angle at which the rock strata came to rest after the last major geological upheaval. The crevices most frequently occupied are those sloping upward into the cliff. Crevices on relatively open, exposed cliffs are exploited as nesting sites less frequently than those in sheltered bays or those in small caves.

The cave where observations were made was quite small, the entrance ca. 1.3 m. high and 1.8 m. wide opening into a small chamber about 1.8 m. high,

2 m. wide, and 2 m. deep. At high tide the waves break against the cliff and the resulting spray frequently moistens the cells. However, adults of both *Euplusia surinamensis* and *Exaerete dentata* have been frequently reared from badly weathered groups of cells taken from this cave.

As the cells of *Euplusia* spp., including those of *E. surinamensis* (Dodson, 1966; Zucchi et al., 1969) and of *E. violaceae* (Blanchard; Sakagami and Michener, 1965) have been described, they will not be redescribed in detail. Constructed of resin and pieces of bark in linear series, each cell after it is formed is provisioned, and after an egg is deposited, sealed with smaller pieces of bark held together by resin.

(b) Notes on *Exaerete*: At 9:05 A.M. on May 2, 1966, when observations were commenced, a female of *E. dentata* was already examining a recently sealed cell. Although apparently quite nervous initially (evidenced by the rapid alternate telescoping and expansion of the abdomen), she examined the slightly concave end of the cell with both antennae and mandibles and began to remove bits of bark from the cell cap. Although some bits of the bark fell to the ground, most were attached by the female to the inside of the partially formed cell next in sequence. By 9:19 A.M. the cell cap was opened sufficiently to permit insertion of the head and part of the thorax into the cell. On one occasion during this period of opening the cell the female lost her footing and fell almost to the floor of the cave before taking wing and returning to the cell. At 9:20 the bee removed the egg of *Euplusia* which had previously reposed on the surface of the cell provisions and crushed it with her mandibles. Following a short period of activity during which the head remained within the cell, possibly rearranging the provisions slightly, the female reversed her position and inserted the tip of the abdomen into the cell (9:22). She remained motionless for several seconds; then, extending the tip of the abdomen slightly further, deposited an egg (9:24). She then commenced the resealing of the cell, utilizing the bits of chewed wood and resin removed a few minutes earlier. At 9:40 the female "lost her footing," dropped from the cell, and flew away. She returned at 9:42 and after several seconds' search relocated the cell, alighted, and continued her activities. When she alighted the female had a bit of chewed wood in her mandibles; this was probably present when she dropped from the cell. When the cell was almost sealed the bee again "fell off" at 10:05, flew about the face of the cliff, approached a partially provisioned *Euplusia* cell about 3 meters from the one she had been sealing, but did not alight. Returning to the original cell a few seconds later, she spent another ten minutes packing and smoothing the cell cap before again falling from the cell and alighting on my shirt where she rested for almost a minute. She still had bits of chewed wood and resin between her mandibles. Leaving my shirt she flew out of the cave, hovered

in front of the partially provisioned cell visited earlier, alighted, explored the cell contents, and deposited the chewed wood at the cell entrance. She stayed in the cell for almost one minute, flew off, and entered another crevice quite close to the cell which had been recently sealed and where a *Euplusia* female had entered with bits of bark earlier in the morning. She spent only a few seconds before again taking flight. After flying in an exploratory fashion about the face of the cliff, the bee flew around the point into the next small bay and after moving back and forth along the face of the cliff flew upward over the cliff and disappeared.

Somewhat similar although less detailed observations were made at another site in company with E. Kjellesvig-Waering on August 2, 1966, at a small seaside hotel at Mayaro, Trinidad. Three *Exaerete* females were observed near a nesting site of *E. surinamensis* where several individuals were nesting in hollow clay tiles at the top of the end wall of the porch. One end of the tiles was open, the other embedded in the wall of the building. Although there were numerous cells, the adults of *Euplusia* and *Exaerete* could be observed only indistinctly from a distance of 1.5 m. because a concrete beam projecting downward only few centimeters from the open end of the tiles prevented closer scrutiny. Over a two-hour period one female of *E. dentata* remained stationary at the entrance of a cell; she appeared to be resting and her behavior was quite unlike that of the female observed at the Balandra site. Two females collected at this site, as well as several adults that emerged from the Balandra site, were determined as *E. dentata*.

DISCUSSION

Although a female of an unidentified species of *Exaerete* was observed to enter the nesting site of *Eulaema terminata* on several occasions, there was no indication that she was readily accepted or lived in harmony with the females of *E. terminata*. Similarly, observations on *Exaerete dentata* parasitic on *Euplusia surinamensis* indicate that the habits of members of the genus are more like those of parasites of solitary bees than to those of *Psithyrus* (discussed by Bohart, 1970).

It is of interest to note that the habit of opening a recently completed host cell, removing the host's egg, and then after depositing its own egg resealing the cell is very similar to that reported for *Stelis* (*Odontostelis*) *bilineolata* (Spinola), the only other bee parasitic on a Euglossine for which details of the biology are known (Bennett, 1966). Unlike *S. binotata*, which is unrelated to its hosts, *Euglossa cordata* and *E. variabilis* Friese, and drives the host bee permanently from the nest, the attack by *Exaerete dentata*, as determined subsequently by the emergence pattern from series of cells, does not deter the *Euplusia* female from constructing additional cells in the same series on top of one opened and resealed by *Exaerete*.

The only other parasitic bees whose females open host cells, presumably destroy the host egg, and then presumably reseal the cells are the Halictid parasites such as *Sphecodes*. Details of behavior have not been observed, but closed cells containing no host egg or young are well known. In some cases the host (or hosts) is killed or leaves the nest, while in others they remain (see Bohart, 1970).

Acknowledgments: I am indebted to my field collector Mr. D. Bharath, who located the nest of *Eualema terminata* and at great personal discomfort spent several days and nights in the Nariva Swamp carrying out many of the observations reported for this species. The *Euplusia* nesting site at Balandra was the joint discovery of my wife Betty and my son Philip. Dr. J. G. Rozen and J. S. Moure, CMF identified the specimens of *Exaerete* and reported the occurrence of three species of the genus in Trinidad.

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The Microsporidian *Octosporea muscaedomesticae* as a Pathogen of Larval and Pupal *Phormia regina* (Diptera: Calliphoridae)[1]

John Paul Kramer
Department of Entomology, Cornell University, Ithaca, New York 14850

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Abstract: The microsporidian *Octosporea muscaedomesticae* Flu can successfully parasitize larval *Phormia regina*. The protozoan appears to attack only the epithelium of the proximal intestine. The disease generated by the protozoan is often complicated by a secondary bacterial infection which becomes systemic. About 90% of the larvae exposed to the pathogen died as larvae or pupae. The few adults produced from the larval cultures exposed to the pathogen were disease-free.

INTRODUCTION

Fantham and Porter (1958) briefly described a microsporidian infection in larval *Musca domestica* and refer to the parasite as *Octosporea muscaedomesticae* Flu. Since no description of the parasite accompanies this observation, the identity of their microsporidian remains uncertain. Hence the present report may be the first to treat this cytozoic parasite in subimaginal hosts. *O. muscaedomesticae* does produce changes in adult *Phormia regina* (Meigen) recognizable as disease by destroying or severely deforming host cells in the posterior portion of the proximal intestine (Kramer, 1966). In the present report we will see that *O. muscaedomesticae* generates disease in subimaginal stages of *P. regina* as well. That the larva and the adult of *P. regina* are both readily infected *per os* by *O. muscaedomesticae* is a noteworthy sidelight since many species of microsporidians that successfully invade holometabolous insects by the oral route attack only one stage or the other.

MATERIALS AND METHODS

About 130 newly hatched *P. regina* larvae were placed on a chunk of pork liver that had been dipped into an aqueous suspension of fresh *O. muscaedomesticae* spores recovered from diseased adults. A control group of newly hatched larvae was placed on a chunk of liver that had been dipped into tap water. Both groups of larvae were obtained from the same disease-free stock culture. After about 70 hours both groups were transferred to fresh liver. Beginning on the sixth day of the experiment dead specimens were

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TABLE 1. Mortality and post-mortem findings in *Phormia regina* populations: One exposed to *Octosporea muscaedomesticae* (=Omd.) as first-instar larvae and the other not so exposed.

Stage at Death	Experimentals				Controls		
		Pathogen				Pathogen	
	% Mortality	Omd. only	Omd. & Bacteria	Not det.*	% Mortality	Bacteria only	Not det.*
Immature Larva	12(16/130)**	—	—	12	11(14/130)**	—	11
Mature Larva	33(38/114)	11	25	2	5(6/116)	4	2
Pupa	87(66/76)	2	51	13	19(21/110)	—	21
Larva—Pupa	92(120/130)	13	76	27	32(41/130)	4	34

* Not determined; ** proportion of specimens dying at given stage.

removed daily from each group and each cadaver was studied individually. The mortality and post-mortem findings for subimaginal stages are summarized in Table 1. Post-eclosion findings in adults from both groups are given in Table 2.

RESULTS AND INTERPRETATIONS

Post-Mortem Changes in Larvae. Dead mature larvae were divided into two categories on the basis of their gross appearance: those that were firm of flesh and whitish in color versus those that were soft, elongate, and dark brown. The chyle stomach, proximal intestine, hind intestine, and rectum of specimens in the "white" category were packed with spores of the parasite. Actual growth and multiplication of the parasite appeared to be restricted to the epithelium of the proximal intestine in these specimens (see Figs. 1 and 2). The hemocoel contained few bacteria and no *O. muscaedomesticae*. The internal organs of larvae in the brown category were in varying degrees disorganized or decomposed and putrifying bacteria were found in association with spores of the protozoan in these cadavers. About one-third of the dead mature larvae had succumbed to octosporeosis alone and about two-thirds of them to a combination of octosporeosis and a bacterial infection.

Post-Mortem Changes in Pupae. Individuals dying in the pupal stage were almost always reduced to an amorphous liquefied mass containing both the

TABLE 2. Post-eclosion findings in adult *Phormia regina*: one group from a population exposed to *Octosporea muscaedomesticae* as first-instar larvae and the other from a population not so exposed.

Source	Findings		
	Gross Appearance Normal	Omd. Spores in Meconia	Omd. in Intestines
Exposed Population	10/10*	7/10	0/10**
Unexposed Population	89/89	0/28	not tested

* Proportion of sample positive; ** flies dissected on post-eclosion day 9.

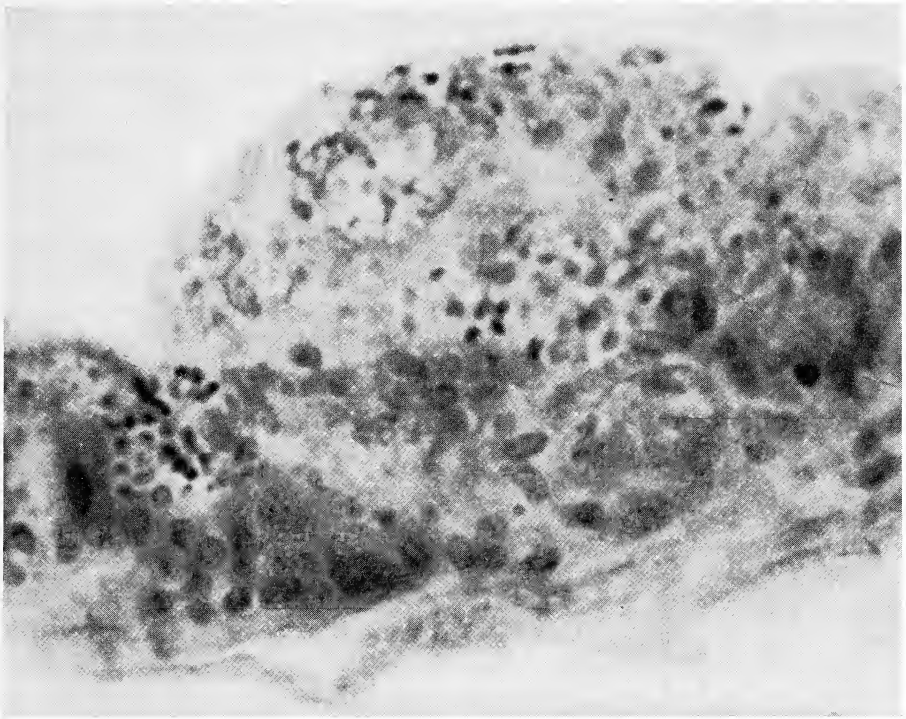

Fig. 1. Portion of a transverse section of the proximal intestine of a diseased *P. regina* larva. Note schizogonic stages of *O. muscaedomesticae* in cell cytoplasm.

protozoan and putrifying bacteria. Two puparial cases contained partly formed flies and octosporeosis alone appeared to be responsible for these deaths.

Observations on Adults. Ten flies were produced from the population exposed to *O. muscaedomesticae.* Seven of these flies produced meconia containing spores of the protozoan. The spores from these meconia were fed to other flies but produced no infection. Apparently the spores had been deactivated in some unknown manner prior to their discharge from the exposed individuals. On post-eclosion day nine all flies in the exposed group were dissected and they proved to be uniformly parasite-free.

DISCUSSION

Whether the octosporeosis generated by *Octosporea muscaedomesticae* occurs in natural populations of larvae has not been demonstrated. Since some subacutely infected flies are highly mobile, they probably do contaminate larval foodstuffs with their spore-filled feces (Kramer, 1965). The extent to which these spores retain their infectivity in decaying organic matter is

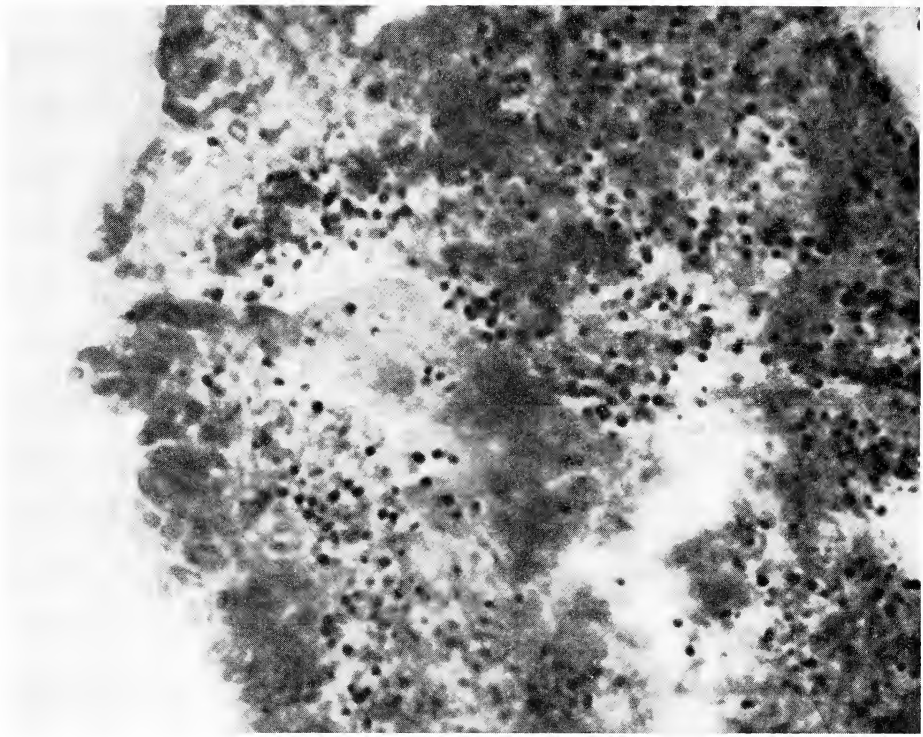

FIG. 2. Portion of a transverse section of the proximal intestine of a diseased *P. regina* larva. Note spores of *O. muscaedomesticae* in cell cytoplasm.

problematical since microsporidian spores can be deactivated in a liquid medium by dense populations of bacteria or fungi (see Kramer, 1970).

The results of this study clearly indicate that *O. muscaedomesticae* can cause a fatal disease in subimaginal *P. regina*. More often than not the disease is complicated by a secondary bacterial infection which becomes systemic. Those adults that developed from an infected culture in the present study were disease-free. Hence there is no evidence to suggest that the parasite can be transmitted from larva to adult via the pupa.

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Four New Species of *Prodidomus* (Araneae: Prodidomidae) from South India

J. A. L. Cooke
American Museum of Natural History, New York 10024

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Abstract: *Prodidomus* **tirumalai** sp. n., *P.* **palkai** sp. n., *P.* **venkateswarai** sp. n., and *P.* **papavanasanemensis** sp. n. are described from the State of Andrah Pradesh.

INTRODUCTION

The Prodidomidae are a small and rather obscure family of spiders of predominantly tropical and subtropical distribution. Generally placed near the Gnaphosidae, the problem of their affinities is complex and the subject of a separate study, and hence will not be considered here.

First revised by Dalmas (1918), the Prodidomidae received little attention until Cooke (1964) added three new genera and a further fourteen species. Since then Suman (1967) has added a further species of *Prodidomus* from Hawaii. The present paper describes four species collected near Tirupati, about 100 miles northwest of Madras, and brings the number of nominal species in *Prodidomus* to forty. Most *Prodidomus* species are associated with hot, arid desert habitats, and it is therefore of interest to note that three of the new species described here were taken from extremely humid locations.

Prodidomus **tirumalai**, new species

DIAGNOSIS

This species is unlikely to be confused with any other at present known. The epigynum is somewhat reminiscent of *P. rodolphianus* Dalmas from E. Africa, but the two species differ markedly in size and spination.

DESCRIPTION OF HOLOTYPE

Body length (excluding chelicerae and spinnerets), 4.4 mm.; carapace length, 1.4 mm.; carapace width, 1.1 mm.; sternum length, 1.1 mm.; sternum width, 0.7 mm.; diameter of AME, 0.09 mm.; eye group width, 0.4 mm.; eye group depth, 0.3 mm.

Carapace, pale yellow-brown without pattern, with recumbent hairs directed toward midline. AME (anterior median eyes), separated by one-third their diameter, PME (posterior median eyes), separated by half their major diameter, PLE (posterior lateral eyes), contiguous with ALE (anterior lateral eyes) and PME. Clypeus width, slightly more than half diameter of AME, with numerous forward-pointing hairs. Abdomen, pale-pinkish without pattern, paler beneath and clothed in recumbent hairs. Sternum, yellowish with dark border, with scattered hairs recumbent centrally but erect marginally and with tuft between coxae IV. Labium, broad as long, slightly narrowed anteriorly with some erect hairs. Chelicerae neither geniculate, divergent, nor projecting. Palps, truncated and somewhat tumid. Legs, same color as carapace with pair of fine dorsal spines on all femora; otherwise spineless except for apical ventral pair on tibia III and

tibia and metatarsus IV. Epigynum (fig. 1) of Group I type (cf. Cooke, 1964) with fertilization pores close to epigastric furrow and without median septum.

MATERIAL

Holotype female, collector's field number 191664; India, Andrah Pradesh, near Tirupati, Tirumala; January 19, 1966 (J. A. L. Cooke); paratype female, collector's field number 171662, same locality as holotype, January 17, 1966 (J. A. L. Cooke); paratype female, collector's field number 1516615A, same locality as holotype, January 15, 1966 (J. A. L. Cooke). Types deposited in the American Museum of Natural History.

ETYMOLOGY

The species is named for the temple community at Tirumala in the hills above Tirupati (A. P.), South India.

ECOLOGY

In litter and under stones in deep, humid forested valleys at 2,400 ft. The habitat in each case was similar although the three valleys were several miles apart. The capture of *Prodidomus* species in humid situations is noteworthy as most other members of the genus appear to be associated with arid desert conditions.

Prodidomus **palkai**, new species

DIAGNOSIS

The distinctive epigynum sets this species clearly apart from other members of the genus. There is some resemblance to the published figure of the epigynum of *P. aurantiacus* Simon (Dalmas, 1918), but the two species differ significantly in size and spination.

DESCRIPTION OF HOLOTYPE

Body length (excluding chelicerae and spinnerets), 3.4 mm.; carapace length, 1.28 mm.; carapace width, 0.95 mm.; sternum length, 0.85 mm.; sternum width, 0.7 mm.; diameter of AME, 0.07 mm.; eye group width, 0.32 mm.; eye group depth, 0.29 mm.

Carapace, yellow-brown with dark reticulations and dark border, with long recumbent hairs directed toward midline. AME separated by half their diameter, PME separated by one-third of their minor diameter, PLE almost contiguous with ALE and PME. Clypeus, width slightly greater than diameter of AME, with approximately twenty-five inconspicuous projecting hairs. Abdomen, pale yellowish with faint pinkish wash, covered in recumbent hairs. Sternum, yellow with dark border, with erect hairs marginally and between coxae IV. Labium, longer than broad, slightly narrowed anteriorly. Chelicerae, not geniculate, projecting or divergent. Palps, truncated and somewhat tumid. Legs, yellowish with pair of fine dorsal spines on all femora; otherwise spineless except for apical ventral pair on tibia III and on tibia and metatarsus IV. Epigynum (fig. 2), appearing as a pair of sclerotized rings arising from a plate overhanging the epigastric furrow. In the absence of males it is not possible to determine with certainty which group *P.* **palkai** belongs to.

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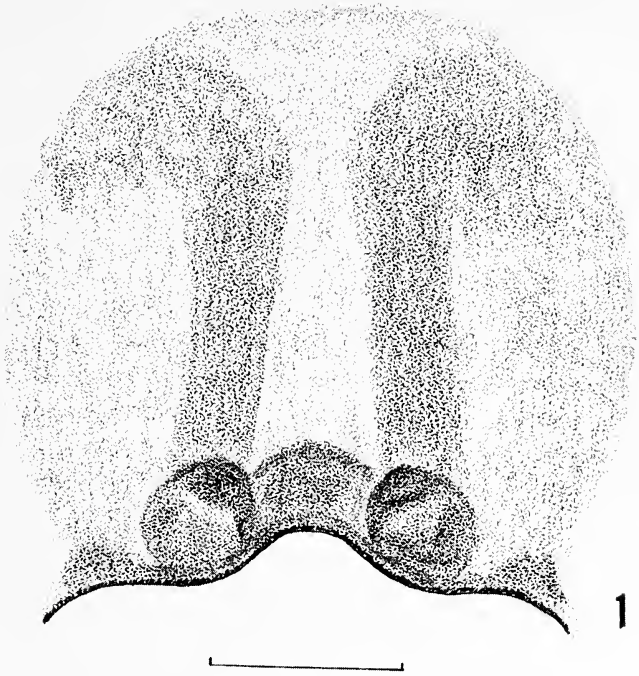
FIGS. 1–2. 1. *Prodidomus* **tirumalai**, new species. Epigynum. 2. *Prodidomus* **palkai**, new species. Epigynum. Scale line equals 0.1 mm.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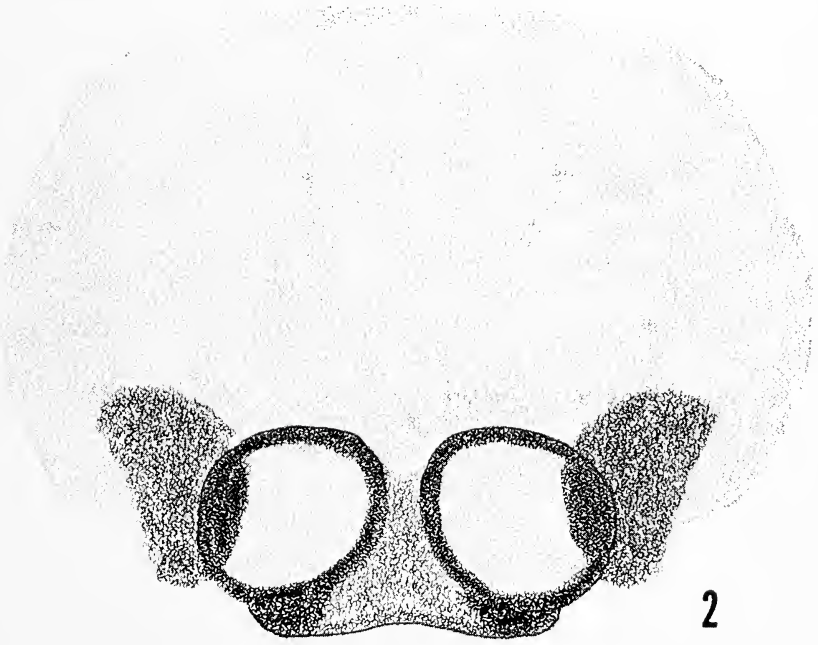
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MATERIAL

Holotype female, collector's field number 1516615B; India, Andrah Pradesh, near Tirupati, Tirumala; 2,400 ft., January 15, 1966 (J. A. L. Cooke); paratype female, same number, date, and locality. Types deposited in the American Museum of Natural History.

ETYMOLOGY

The species is named for Dr. John Palka, at the time attached to Sri Venkateswara University, Tirupati.

ECOLOGY

Both specimens were taken under stones in a deep, humid forested valley, in company with *P.* **tirumalai**. They were immature at the time of capture but moulted to maturity some three months later.

Prodidomus **venkateswarai**, new species

DIAGNOSIS

The epigynum of this small species is quite characteristic and cannot be confused with any other member of the genus.

DESCRIPTION OF FEMALE HOLOTYPE

Body length (excluding chelicerae and spinnerets), 2.5 mm.; carapace length, 1.1 mm.; carapace width, 0.82 mm.; sternum length, 0.75 mm.; sternum width, 0.06 mm.; diameter of AME, 0.07 mm.; eye group width, 0.29 mm.; eye group depth, 0.24 mm.

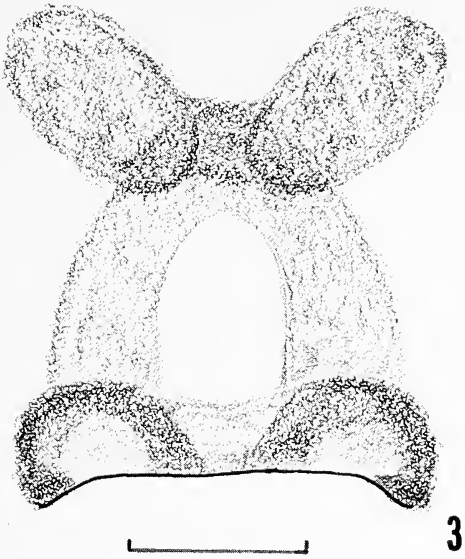
Carapace, pale yellow-brown, with recumbent hairs directed toward midline. AME separated by one-third of their diameter and touching ALE, PME separated by one-third of their minor diameter, PLE touching PME and ALE. Clypeus, width one-half diameter of AME, with fringe of long forward-pointing hairs. Abdomen, with faint pinkish wash and slightly darker median stripe anteriorly, ventrally paler, clothed in recumbent hairs. Sternum, pale yellow-brown with darker border, clothed in scattered recumbent hairs more dense at margins and with tuft between coxae IV. Labium, broad as long, without notch and with a few pale scattered hairs. Chelicerae, not geniculate, divergent, or projecting. Palps, truncated and somewhat tumid. Legs, same color as carapace, rather hairy with conspicuous trichobothria, femora with pair of feeble dorsal spines with a pair of apical ventral spines on femur III, apical ventral spines on posterior tibiae and metatarsi. Epigynum (fig. 3), quite distinctive, probably of the Group I type. This placing is supported by the structure of the male palp, which possesses a comparatively short embolous, free for only about a quarter turn.

DESCRIPTION OF MALE ALLOTYPE

Body length (excluding chelicerae and spinnerets), 2.55 mm.; carapace length, 1.2 mm.; carapace width, 0.98 mm.; sternum length, 0.9 mm.; sternum width, 0.65 mm.; diameter of AME, 0.08 mm.; eye group width, 0.32 mm.; eye group depth, 0.29 mm.

→

FIGS. 3–4. 3. *Prodidomus* **venkateswarai**, new species. Epigynum. 4. *Prodidomus* **papavanasanemensis**, new species. Epigynum. Scale line equals 0.1 mm.



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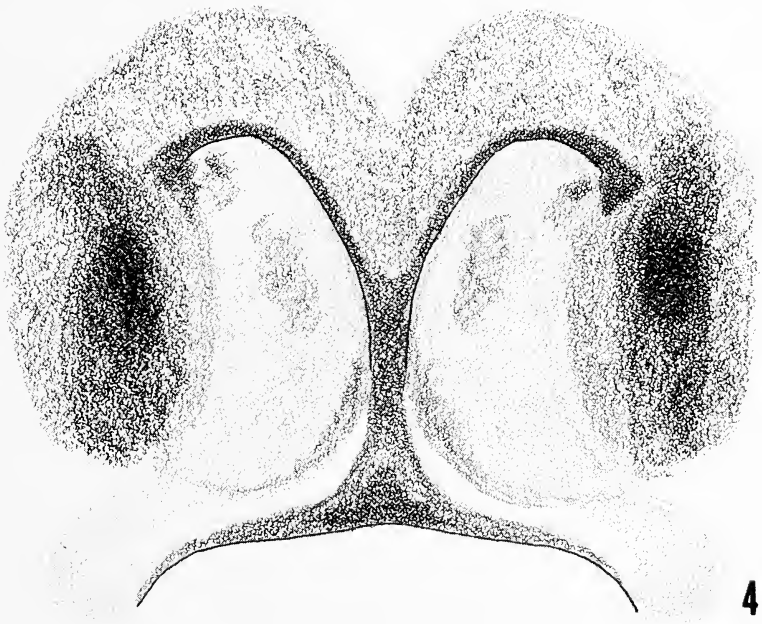

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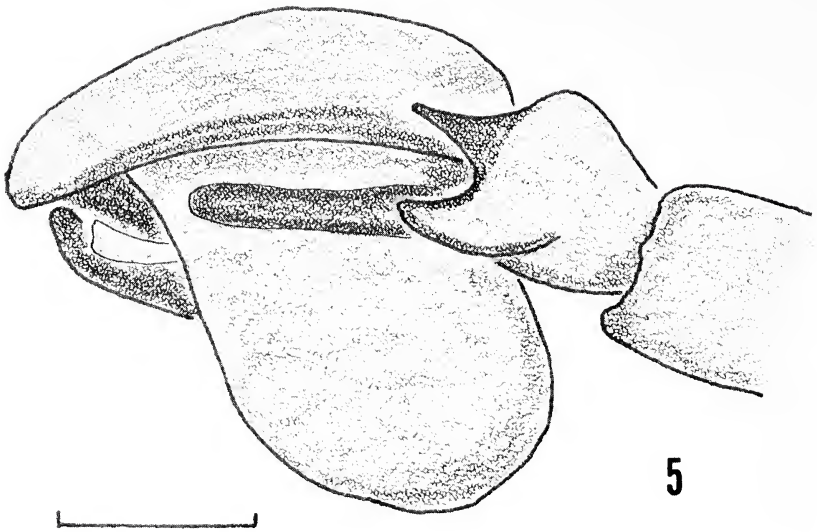

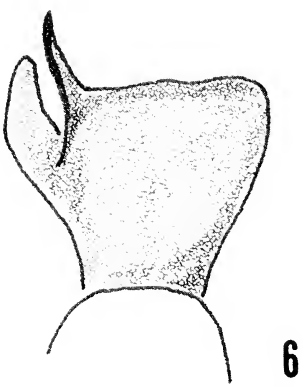

FIGS. 5–6. *Prodidomus* **venkateswarai**, new species. 5. Left male palp, lateral aspect. 6. Left male palpal tibia, dorsal aspect. Scale line equals 0.2 mm.

Carapace, pale yellow-brown with dark margins and faint reticulations, with pale and inconspicuous scattered recumbent hairs. AME separated by one-third of their diameter, PME separated by one-third of their minor diameter, other eyes contiguous. Clypeus, width one-half diameter of AME. Abdomen, pinkish with darker median stripe anteriorly, pale ventrally, covered in recumbent hairs. Sternum, pale with narrow dark border and faint sooty markings, some scattered marginal hairs and a tuft between coxae IV. Labium, broad as long, without indentation. Chelicerae, not geniculate,

projecting, or divergent. Palps, anomalous, the right one being small and apparently atrophied. The left-hand palp (figs. 5, 6) is large and presumed to be normal. Legs, similar to female.

MATERIAL

Holotype female, collector's field number 151663; India, Andrah Pradesh, near Tirupati, Tirumala; 2,400 ft., January 15, 1966 (J. A. L. Cooke); allotype male, same date and locality as holotype. Types deposited in the American Museum of Natural History.

ETYMOLOGY

This species is named for Sri Venkateswara, an incarnation of Krishna and principal deity of the Tirumala temple.

ECOLOGY

Under stones amongst litter in deep forested valley in the same area as *P.* **tirumalai** and *P.* **palkai**.

Prodidomus **papavanasanemensis**, new species

DIAGNOSIS

The form of the epigynum, together with the nondivergent chelicerae, unite this species with *P. birmanicus* Thorell, *P. bicolor* Denis and *P. nigellus* Simon, but its large size, coloration, and spination serve to distinguish it. The epigynum, although similar in form, is unlikely to be confused with any of these species.

DESCRIPTION OF HOLOTYPE

Body length (excluding chelicerae and spinnerets), 5.6 mm.; carapace length, 2.4 mm.; carapace width, 1.9 mm.; sternum length, 1.6 mm.; sternum width, 1.2 mm.; diameter of AME, 0.16 mm.; eye group width, 0.64 mm.; eye group depth, 0.47 mm.

Carapace, yellow-brown with darker border and paler posteriorly, with few faint markings and pale fine recumbent hairs (difficult to see) directed toward midline. AME separated by half their diameter, PME separated by half their major diameter, AME with tuft of hairs between and ringed in black, clearly separated from ALE, remaining eyes not ringed and almost contiguous. Clypeus, width half diameter of AME, fringed with forward-pointing hairs. Abdomen, slightly tinged with pink and without pattern, paler ventrally, uniformly clothed in fine recumbent hairs. Sternum, with narrow dark border and clothed in recumbent hairs, longer at margins and with tuft between coxae IV. Maxillae, same color as sternum but with paler tips, clothed in erect hairs. Labium, broad as long without notch and clothed in erect hairs. Chelicerae, not geniculate or divergent and only slightly projecting. Palps, slightly tumid and truncated. Legs, same color as carapace, femora with pair of fine spines and apical ventral spines on posterior tibiae and metatarsi. Epigynum (fig. 4), of Group II type with distinctive median septum bifurcating anteriorly.

MATERIAL

Holotype female, collector's number 181665; India, Andrah Pradesh, near Tirupati, Tirumala; 2,400 ft., January 18, 1966 (J. A. L. Cooke). Type deposited in the American Museum of Natural History.

ETYMOLOGY

The holotype was collected close by the holy waterfall at Papavanasanem near the temple community of Tirumala and the name refers to this locality.

ECOLOGY

Under stone lying on rock outcrop in open forest. As the stone was exposed to the full heat of the sun and had little soil beneath, the habitat of *P.* **papavanasanemensis** resembles the more typical desert conditions with which other members of the genus are associated rather than the moist habitat of *P.* **palkai**, *P.* **tirumalai**, and *P.* **venkateswarai** occurring in the same area.

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Baited McPhail Fruitfly Traps to Collect Euglossine Bees

Fred D. Bennett
Commonwealth Institute of Biological Control, Gordon Street, Curepe, Trinidad

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Abstract: Modified McPhail traps baited with essences were utilized to capture male euglossine bees in British Honduras. The performance of these traps was superior to that of Steiner traps during trials in British Honduras and demonstrated that many of the euglossine species occurring in the area could be collected with little expenditure of time and effort. The presence of female euglossines in McPhail traps baited with SIB7, a partially hydrolyzed protein used in Mexican fruitfly trapping programs, is also reported.

Males of euglossine bees are the sole pollinators of certain neotropical orchids, e.g., *Gongora*, *Catasetum*, *Coryanthes*. They are attracted to the essences or perfumes produced by the flowers of these orchids as well as to certain other plants which they collect, by means of special pads on the tarsi of the forelegs, and store in the pockets in the hind tibia (see Evoy and Jones, 1971). As the reasons for the collection of these esssences is not well understood and as the biology and the identity of many of the species is not known, any methods which facilitate the collection of representative series of adults are of interest.

While testing new compounds to obtain a satisfactory lure for the Mexican fruitfly *Anastrepha ludens* (Loew), Lopez (1963) reported the collection of large numbers of males of *Eulaema polychroma* (Mues.) (= *Eulaema tropica* Auct. non L.) in McPhail traps baited with a mixture of a-ionone and b-ionone. The use of essences to attract males of euglossine bees has since attracted widespread attention (Dodson et al., 1969), and enormous collections containing previously unknown species have been assembled from various parts of the neotropics. The usual methods of utilizing these compounds have been quite simple. A 5 × 5 cm. square of blotting paper saturated with a few drops of the appropriate compound is tacked to a convenient tree and the bees as they approach are collected with a net or, later, after they have alighted and become less wary, are collected by hand (Dodson et al., 1969). While very straightforward and rewarding, this method requires almost constant attendance during the hours when the bees are active. However, when I visited British Honduras in June 1969 to release parasites of the Mexican

Acknowledgments: Grateful acknowledgment is accorded to Prof. C. Dodson, Department of Biology, University of Miami, who provided the essences utilized in the experiments and to Dr. Keith Houston and Mr. A. Lewis, UWI Citrus Research Unit, British Honduras, who assisted with the trapping program.

fruitfly *A. ludens*, my investigations did not permit adequate time to follow these procedures and if bees were to be collected a method of trapping them had to be devised. Earlier attempts to construct a suitable trap for euglossine males had not been entirely satisfactory (H. Hills, pers. comm., 1968). However, in view of the work by Lopez (*loc. cit.*) and as McPhail traps utilized in the Mexican fruitfly control program were readily available, these were tried.

It was noted during the visit to British Honduras that euglossine females were occasionally present in fruitfly traps baited with a partially hydrolyzed protein, so data on the frequency of their appearance in the traps was recorded.

METHODS

A. *For trapping males.* Basically the McPhail trap (Fig. 1) consists of a glass dome 20 to 25 cm. in diameter and 12 to 15 cm. in height with a cork in the top and with an invaginated bottom which provides a ventral circular opening 12 to 16 cm. in diameter surrounded by a canal. In normal operation the canal is filled with a liquid bait in which the victims drown, e.g., to attract Mexican fruitfly the traps contain Staley's Insect Bait 7 (SIB7) which contains a partially hydrolyzed protein.

For the present purpose the traps were modified slightly; a 2-dram glass vial filled with the appropriate attractant and plugged with an extruding cotton wick was suspended wick downward within the dome of the trap (Fig. 1). After filling the canal with water containing a small amount of household detergent, the trap was suspended from the branch of a tree ca. 1.5 m. from the ground. Traps containing one of the following compounds, methyl salicylate, 1,8-cineole, b-ionone, eugenol, benzyl acetate, or methyl cinnamate were suspended in mango trees at the UWI Citrus Research Unit, Melinda, in the Stann Creek Valley, about 60 meters from a forested area. Although the traps were inspected daily and the bees removed, the attractants needed to be replenished only once or twice per week. Traps with these attractants were operated from June 30 to July 12, 1969, at Stann Creek.

During a second visit, a series of traps was operated for a further two-week period (October 28 to November 15, 1969). In addition to the attractants utilized earlier methyl benzoate, piperonal, 2-phenyl ethyl acetate, 2-phenyl ethyl alcohol, skatole, b-pinene, coumarin "stock," and "stock" plus ocimene were also tried. "Stock" consisted of 2.0 parts of a-pinene, .08 parts b-pinene, 1.6 parts myrcene, and 16.0 parts cineole. The formula "stock" plus ocimene was the same except for the addition of 15 parts of ocimene.

To compare the efficiency of the McPhail traps with the traditional method of placing a few drops of the compound on a 5 cm. square of blotting paper and netting the approaching adults, traps baited with a number of compounds

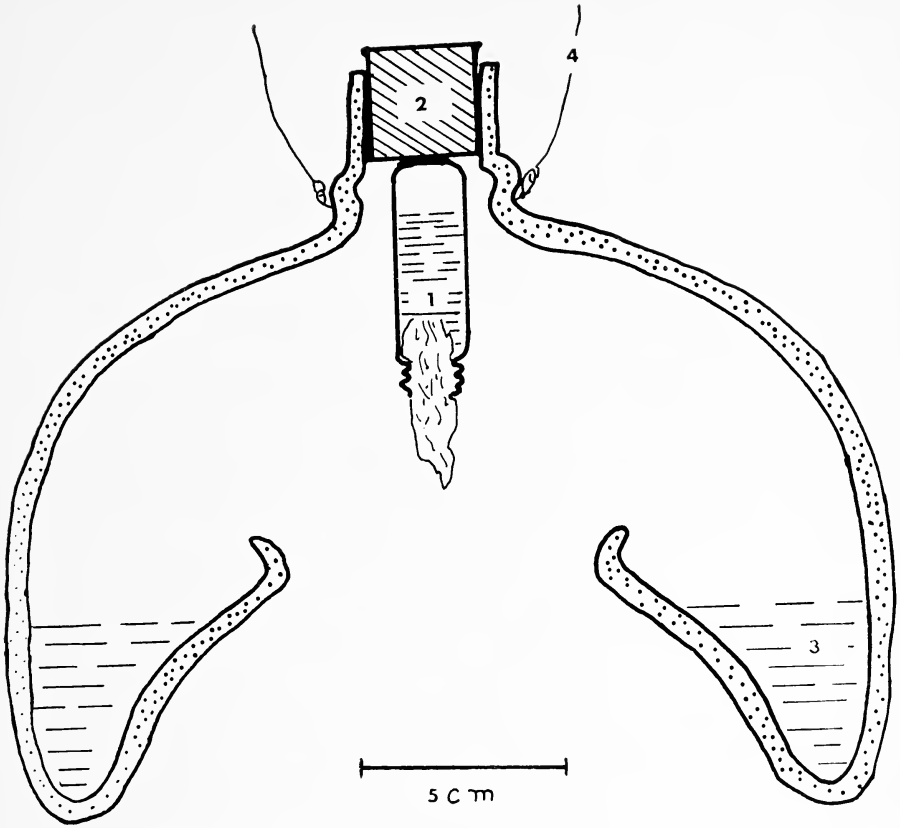

Fig. 1. McPhail Trap—Cross Section. Vial of attractant (1) with cotton wick glued or wired to rubber cork (2). Canal of trap (3) filled with water and detergent. Trap suspended by wire (4) from convenient tree.

were placed in one location and at another ca. 3 km. distance, squares of blotting paper kept moist with the same attractants were pinned to the sides of trees, and observed at frequent intervals from 8:00 A.M. to midday. Bees were netted as they were about to settle on the pads for comparison with those caught in the McPhail traps during the same period.

On a third visit to British Honduras (July 7 to 12, 1970), an experiment was set up to compare the effectiveness of the McPhail trap to the Steiner trap which is commonly used in programs of trapping Mediterranean fruitfly *Ceratitis capitata*. As the Steiner trap modified to hold a vial of essence (Fig. 2) is not designed to retain liquids, aldrin powder was dusted in the bottom of the trap to kill any bees that entered. Paired traps, i.e., one Steiner and one McPhail each baited with the same essence, were hung on

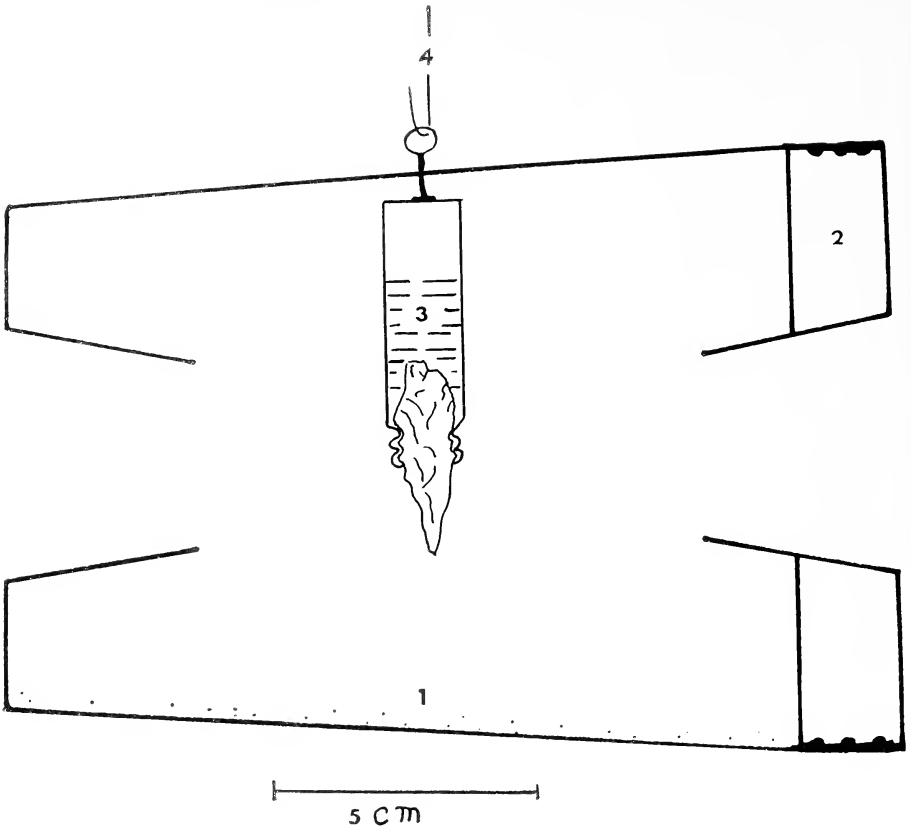

FIG. 2. Modified Steiner Trap—Cross Section. Poison sprinkled in bottom of trap (1). Removable end (2). Vial of attractant with cotton wick (3). Wire to suspend trap (4).

opposite sides of a large mango tree or on two adjacent citrus trees. The traps were interchanged every two days to offset the possibility that one site might have been more favorable than another. Dr. K. Houston kindly continued to record the trap contents until July 19, by which time most of the vials of essence were dry.

B. *For trapping females.* During the time of the visit the UWI Citrus Research Unit was operating a grid of 350 McPhail traps distributed through 7,000 acres of citrus groves. The traps baited with SIB7 are examined for fruitflies at weekly intervals. As four females of *Eulaema* spp. were collected during the first afternoon of my visit, Mr. A. Lewis, the technician who inspects the traps kindly consented to collect and save all bees found in the traps during the next fortnight. During the first week, specimens were saved without

Table 1. Euglossine males collected in McPhail traps, June 30 to July 12, 1969. Stann Creek, British Honduras

	1,8 cineole	methyl salicylate	eugenol	b-ionone	benzyl acetate	methyl cinnamate*	Total
Eulaema cingulata (Fab.)			2	76	3		81
Eulaema polychroma (Mocs)				20			20
Eulaema meriana (Oliv.)					1		1
Euplusia schmidtiana (Friese)	3						3
Euglossa imperialis Ckll.	3	1					4
Euglossa tridentata Moure	7					1	8
Euglossa ? variabilis Friese	3		3			13	19
Euglossa viridissima Friese	1						1
Euglossa heterosticta Moure	1						1
Euglossa cognata Moure	1	3					4
	19	4	5	96	4	14	142

* Benzyl acetate and methyl cinnamate used only from July 7 to 12.

reference to the traps from which they were obtained. During the second week, the trap numbers were recorded to determine whether catches were localized. On a later visit, October to November 1969, the contents of the traps were again examined. Specimens were identified with the aid of an unpublished key prepared by R. L. Dressler, and by comparison with named euglossines in Prof. C. Dodson's collection at the University of Miami, Coral Gables.

RESULTS

a) *Males in McPhail Traps*: During the first visit, 142 euglossine males representing 3 genera and 10 species were captured in the McPhail traps. The numbers of each species caught at the various compounds are listed in Table 1.

Of the fragrances exposed during the second visit, no euglossines were attracted to methyl salicylate, benzyl acetate, or eugenol, all compounds which had attracted species in the first experiment. Nor were bees caught in the traps baited with methyl benzoate, piperonal, b-pinene or coumarin. Two other compounds, 2-phenyl ethyl acetate and 2-phenyl ethyl alcohol, each attracted one male of *Eulaema cingulata*. The remaining traps caught 147 euglossine males (Table 2). In addition four females of *E. cingulata* were also taken, three in the trap baited with "stock" and one in the trap baited with "stock" plus ocimene.

b) *Comparison of McPhail Trap to Netting*: The results of the experiment to compare the numbers caught in McPhail traps with the number caught by netting at pads were not very conclusive. Only 11 male euglossines were captured in the McPhail traps and 14 with the net.

TABLE 2. Euglossine bees collected in McPhail traps, October 28 to November 10, 1969. Stann Creek, British Honduras

	cineole	dilute b-ionone	methyl cinnamate	skatole	"stock"	"stock" plus ocimene	Total
Eulaema cingulata (Fab.)		11		17			28
Eulaema polychroma (Mocs)		27					27
Euglossa imperialis (Ckll.)	1						1
Euglossa allosticta Moure				8			8
Euglossa mixta Friese				2	1		3
Euglossa purpurea Friese				19			19
Euglossa tridentata Moure	9				11	2	22
Euglossa ? *hemichlora* Ckll.						1	1
Euglossa deceptrix Moure			1				1
Euglossa ? *variabilis* Friese	1				7		8
Euglossa heterosticta Moure	6		4		9	3	22
Euglossa sp. indet.	1		2	1	2		6
Euglossa ? *gorgonensis* Cheeseman				1			1
	18	38	7	48	30	6	147

c) *Comparison of McPhail and Steiner Traps*: The results of the experiment comparing the two types of traps indicate that the McPhail trap is considerably more efficient than the Steiner trap. The specimens from the traps were determined only to genus; of the euglossines, 100 (92.6%) were caught in the McPhail traps and eight (7.4%) were taken in the Steiner traps.

d) *Other bees Captured in McPhail Traps*: In addition to male euglossines, three females of *E. cingulata* were taken in a trap baited with "stock" and one in a trap baited with "stock" plus ocimene. Non-euglossine bees were also occasionally attracted. On July 10, 1969, about 20 specimens of *Trigona* sp. entered the trap baited with b-ionone and two specimens of a second species of *Trigona* were drowned in the trap baited with methyl salicylate. Again, on November 1 *Trigona* entered the trap baited with b-ionone, over 30 individuals drowning in the water. On July 12, a female of *Ptiloglossa* sp. was captured in the trap baited with benzyl acetate. The same species was noted hovering near filter paper saturated with this compound on a different day. In July one worker of the honey bee, *Apis mellifera* (L.) drowned in the trap baited with eugenol.

e) *Capture of Females in Traps Baited with SIB7*: Females of three species of *Eulaema* and one species of *Euglossa* were present in the traps baited with SIB7.

In 1969 during a two-week period in June to July, 41 females of *Eulaema cingulata*, 10 of *E. polychroma*, one of *E. meriana*, and two of *Euglossa* sp. were captured. During a comparable period in October to November of the same year, 33 *E. cingulata* and two *E. polychroma* were taken.

DISCUSSION

There is no doubt that the McPhail trap baited with attractants is a useful apparatus for collecting euglossine males. While in a single experiment more specimens were obtained by collecting with a net at moistened pads than in the traps, the time involved was much greater and it is likely that over an extended period all of the species attracted to the pads would be taken in the traps. Compared with catches in many parts of Central America and northern South America, the daily catches either from the traps or by netting are low both in the number of species taken and the total number of adults, suggesting that the area is not ideal for collecting euglossines. They do, however, compare favorably with those obtained by Dodson et al. (1969) for nearby Guatemala where 68 specimens representing six species were collected in six days, i.e., a daily average of 11. During the three visits to British Honduras, 15 or more species of euglossines and including all of the species taken with a net at baited pads were collected in the McPhail trap.

The catches at the Steiner trap were disappointingly small and there are a number of reasons which may account for this. The entrance holes to the traps are considerably smaller, less than 4 cm. in diameter, and while the horizontal opening permits bees to alight and crawl in, the larger species can enter less freely than into the McPhail trap. Furthermore the killing agent differed, i.e., aldrin powder in the Steiner trap versus detergent and water in the McPhail trap. While there was apparently no repellent effect from the aldrin, adults did not die very rapidly and on two occasions *Euglossa* adults were observed to leave the trap after visiting the bait.

An important advantage of the McPhail traps is that they are in place throughout the entire period that euglossine males are active. Whereas it is generally accepted that the peak period of activity around baits, orchids, etc., of most species is in the morning, a smaller peak often occurs during the late afternoon. Sporadic visits may also take place during the balance of the afternoon and during this period the bees are frequently very wary and retreat if disturbed. Hence while the patroling of pads to detect the sporadic visits of bees is time consuming and may tend to frighten the bees away, the traps remain attractive and capture bees regardless of the hour they visit the essences. If data on the time that the various species are attracted are required, the traps can be inspected at hourly intervals.

The use of McPhail traps may also be preferable when comparing the relative attractiveness of various fragrances and combinations of fragrances. As stated by Dodson et al. (1969) the strong attraction of euglossine bees to specific fragrances produced by the flowers provides the necessary reproductive isolation to maintain the integrity of interfertile species of orchids. Whereas many bees are attracted to the general locality by one essence, e.g., over

70% of the euglossine species collected at fragrances were collected at 1,8-cineole yet the addition of one or two other compounds greatly reduced the number of species visiting the mixture (Dodson et al., 1969). Bees attracted from great distances by one component might approach to within a few centimeters pads containing a combination of fragrances but once in the vicinity may be repelled from actually collecting by the presence of a second less volatile component. Whereas these species might be collected by means of a net as they approached but did not settle on the impregnated pads, they might be less likely to enter the traps.

Only one male of *Eulaema cingulata* was collected at each of the two compounds phenyl ethyl acetate and phenyl ethyl alcohol. The two males were obtained on the same day, whereas on previous and on succeeding days all other males of this species were collected at skatole and/or b-ionone. The trap containing phenyl ethyl alcohol was under observation as the bee approached and entered. This trap was about 4 meters downwind from the one containing skatole and as the odor of skatole was very evident at the point of observation another three meters downwind and as the bee hovered beneath the first trap for more than one minute it could hardly have failed to detect the aroma from the skatole trap. The two males entering traps containing phenyl ethyl compounds on the same day, whereas males of this species visited the other traps on all other occasions, suggests that the requirements must vary from time to time. Dodson et al. (1969) reported that males of *E. cingulata* are attracted to at least nine compounds. Furthermore in Trinidad males of *E. cingulata* have been observed to visit in sequence three pads, each moistened with a different essence (author's unpubl. data).

McPhail traps baited with essences, if run throughout the year at the same location, should provide reliable quantitative and qualitative data on the seasonal fluctuations of populations of male euglossines, and might also indicate any seasonal shift in preference for one compound over another.

Turning to the attraction of females of *Eulaema* spp. to McPhail traps baited with SIB7, the factor triggering this response has not been ascertained. The following are possible stimuli: (a) searching for materials to construct or provision cells; (b) searching for food for their own use; (c) searching for a suitable nesting site; (d) responding to a sex attractant. The first suggestion seems the most probable. As in addition to *Anastrepha ludens* and *Eulaema* spp., the traps frequently contain several thousand adults of other insects, mainly Diptera belonging to the families Calliphoridae and Muscidae, and as the traps are emptied only once a week it is possible that odors emitted by the decomposing carcasses of these insects suggest the presence of suitable materials for cell construction. Females of *E. cingulata* are known to collect a variety of substances including human feces to construct their cells (Dodson and Frymire, 1961).

Dodson et al. (1969) when collecting male euglossines mentioned that myrcene was the only compound to which females were also attracted. During the current investigations females of *E. cingulata* were taken in traps baited with "stock" and with "stock" plus ocimene, both containing myrcene. Females collect resinous materials for lining their cells and it is surmised that the odor produced by myrcene or another component of "stock" suggested the presence of resinous materials and attracted the females. Two of the trapped females already had particles of a white resinous material on the scopae of the hind legs. Hence the same principle, i.e., the emission of odors suggesting the presence of materials suitable for cell construction, may be involved when *Eulaema* females visit traps baited with SIB7.

The wing margins of several (9 of 23 examined in November) of the *E. cingulata* females were somewhat frayed and the mandibles worn, suggesting that these individuals had been active for an extended period, whereas the wings and mandibles of the remainder being intact indicated that bees of varying ages visited the traps. Hence it seems unlikely that a sex attractant or a search for a suitable nesting site is the motive for entering the traps.

Whether the occasional *Euglossa* female enters a trap baited with SIB7 for the same reason cannot be readily ascertained. As they use predominantly resinous materials for cell construction, they may have been attracted for an entirely different reason.

Finally it would be interesting to know but difficult to determine in the absence of population data before the fruitfly trapping program commenced, whether the weekly removal of 15 or more females drastically affects the population of *E. cingulata* in the Stann Creek Valley.

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A New Species of *Cryptocellus* (Arachnida: Ricinulei) from Cuba

J. A. L. COOKE
AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK 10024

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Abstract: Both sexes of the epigeal ricinuleid *Cryptocellus* **paradoxus**, new species, from Cuba are described. This is the first record of an island ricinuleid.

INTRODUCTION

For many years the order Ricinulei has been regarded as one of the most obscure groups of arthropods. Recently several large ricinuleid populations have been found in Mexican caves and this has resulted in substantial advances in our understanding of their ecology (Mitchell, 1970), morphology (Pittard and Mitchell, 1972), and behavior (Cooke, 1971). In addition three new Mexican cave species have been described (Gertsch, 1970). The description of *Cryptocellus pelaezi* by Coronado (1970) and the recognition by Beck and Schubart (1968) that *C. simonis* Hansen and Sørensen is only the male of *C. foedus* Westwood bring the number of published species of *Cryptocellus* to 20, and at least four additional epigeal species from Central America have been recognized (Cooke, in preparation).

Hitherto all known ricinuleids have come from continental land masses—*Cryptostemma* in West Africa and *Cryptocellus* in the tropical Americas. Hence the discovery of an isolated island species, *Cryptocellus* **paradoxus** sp. n. in Cuba, is an event of considerable interest. As can be seen in the accompanying description, *C.* **paradoxus** is distinctive in several respects, but the most curious feature is the structure of the sperm-transfer organs on leg III of the male. Whereas in all other known species the tarsal process (Cooke, 1967; Pittard and Mitchell, 1972) is a long, bifurcated structure lying within the protective sweep of the lamina cyathiformis, in *C.* **paradoxus** it is a small trowel-like stump. It may be that in the unique male holotype the tarsal process has been damaged and that what remains is only the basal portion. However, as both left and right sides are identical it seems highly improbable that such an injury could occur accidentally. Alternatively, loss of the distal parts may have occurred during copulation, for it is now known (Cooke, 1971) that the tarsal processes are inserted into the female simultaneously. However, there is no evidence of physical damage on either the left or right tarsal process of the holotype and neither is there any trace of an erstwhile junction. The form of the first tarsomere also lends weight to the idea that the

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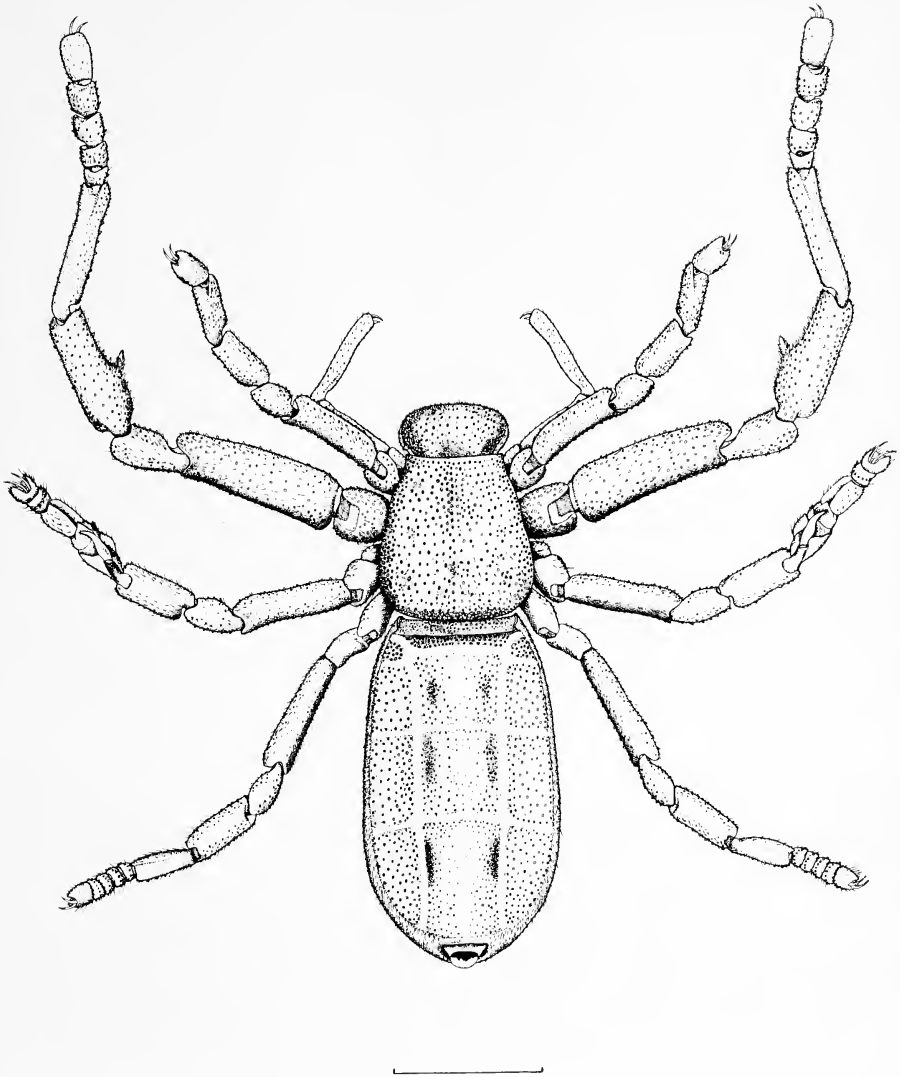
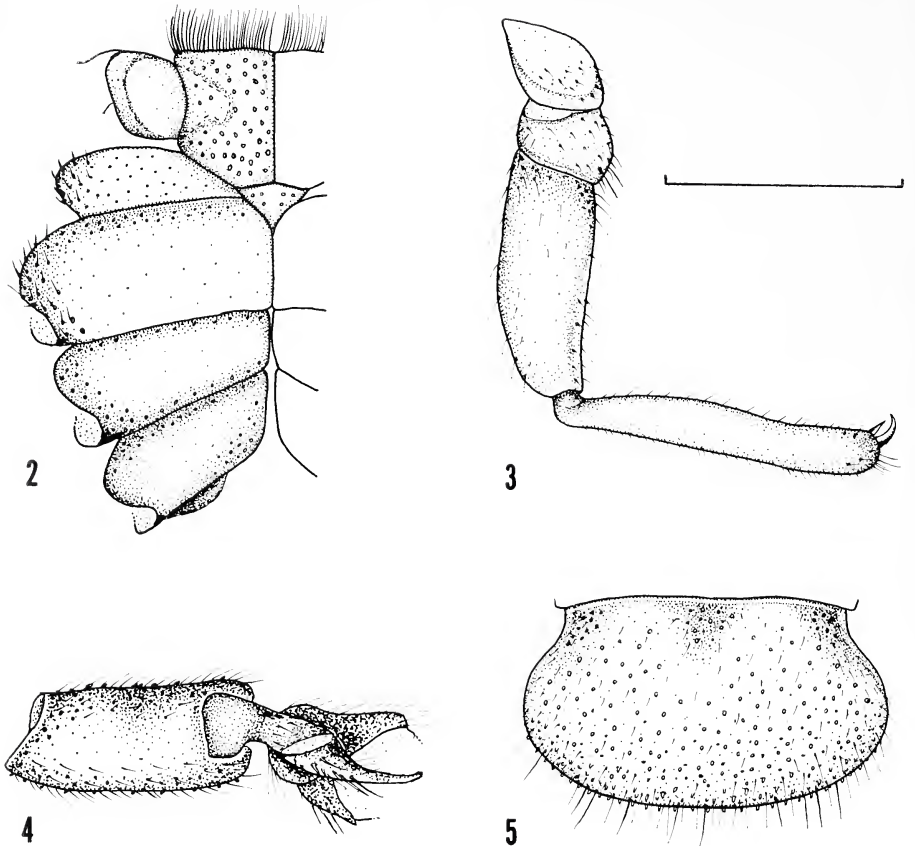


Fig. 1. *Cryptocellus* **paradoxus**, new species. Male holotype. Scale line equals 1.0 mm.

tarsal process is naturally atrophied in this species. In other ricinuleids the lamina cyathiformis of tarsomere 2 apparently acts as a shield to protect the long, delicate tarsal process and its accessory member, while tarsomere 1 is small and simple. In *C.* **paradoxus** tarsomere 1 is similarly drawn up into a spoonlike structure, though smaller than the lamina cyathiformis, and neatly accommodates the squat tarsal process with its delicate, leaflike tip. A possible interpretation is that the tarsal process has become secondarily simplified



FIGS. 2 to 5. *Cryptocellus* **paradoxus**, new species. Male holotype. 2. Sternal region. 3. Left pedipalp. 4. Left leg III, dorsal view of tibia and metatarsal process. 5. Cucullus. Scale line equals 0.5 mm.

and reduced so that it is no longer protected adequately by the lamina cyathiformis and in consequence there has been pressure for the enlargement of tarsomere 1 to take over the role of the redundant lamina. Until further material becomes available to provide some knowledge of the mechanism of sperm transfer in this species, no definite conclusion can be reached on whether the tarsal process of the holotype is normal or not.

Cryptocellus **paradoxus**, new species

DIAGNOSIS

Medium-sized species with distinctively large second pair of legs and unnotched post-abdomen. The females may be distinguished from *C. relictus* Chamberlin and Ivie, *C. spinotibialis* Goodnight and Goodnight, and *C. mitchelli* Gertsch on the grounds of size,

cheliceral dentition, and shape of the cucullus. Males are readily recognized by the large spur on tibia II and by the form of the copulatory apparatus on leg III, particularly the enlarged first tarsomere.

DESCRIPTION OF HOLOTYPE

Body length, 3.32 mm.; carapace length, 1.10 mm.; carapace width, 1.04 mm.; abdomen length, 2.00 mm.; abdomen width, 1.32 mm.; cucullus length, 0.46 mm.; cucullus width, 0.72 mm.; pedipalp femur length, 0.54 mm.; pedipalp tibia length, 0.75 mm.

Carapace (fig. 1), longer than wide, dilated posteriorly and with slight median depression; color uniformly reddish brown; surface covered in small, well-spaced tuberculate granules that under some lighting conditions appear to possess a minute white reflective tip; uniformly clothed in short, fine translucent hairs. Cucullus (fig. 5), wider than long, same color as carapace and similarly covered in tuberculate granules and fine translucent hairs. Chelicerae with six teeth of subequal size on both fingers, those on the fixed finger increasing slightly in size distally. Abdomen (fig. 1), proportionately quite long with conspicuous, well-spaced tergal plates; same color as carapace and bearing similar granules and hairs; postabdominal turret with smooth unindented margin; penis similar to that of *C. pelaezi* Coronado. Pedipalps (fig. 3), small, pale yellow-brown, devoid of granules on the distal segments but with scattered pale, fine hairs; claws smooth. Legs same color as carapace but legs II rather darker; covered in fine, pale hairs and scattered granules, particularly on anterior pairs; tibia II (fig. 1) with large spur and numerous tubercles ventrally; tarsomeres of leg II increasing in size distally, fifth tarsomere 0.36 mm. in length, equal to the combined lengths of second and third tarsomeres. Copulatory apparatus (figs. 4, 6, 7) on leg III distinctive, somewhat atypical of the order; first tarsomere strongly developed and drawn up posteriorly like lamina cyathiformis of second tarsomere but smaller; tarsal process short, club-shaped and undivided.

	Femur	Patella	Tibia	Metatarsus	Tarsomere(s)
I	0.58	0.34	0.40	0.60	0.28
II	1.06	0.52	0.72	0.90	1.04
III	0.72	0.36	0.36	0.52	0.75
IV	0.73	0.34	0.34	0.49	0.45

	I	II	III	IV
Femur diameter	0.18	0.34	0.18	0.14

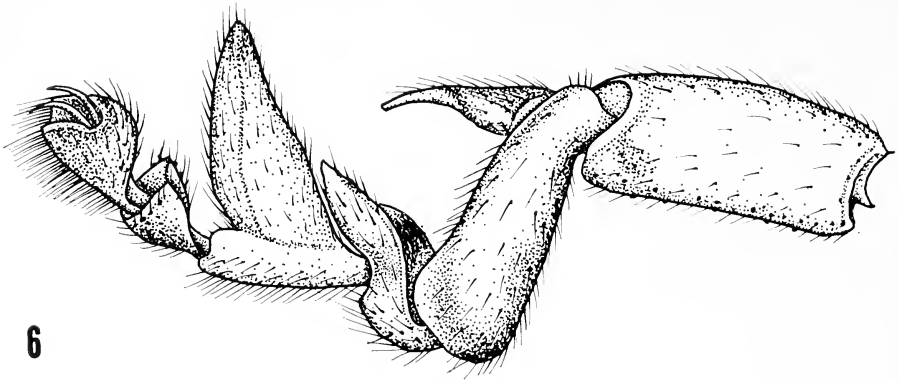
N.B. Left leg I of holotype significantly shorter than right and presumed to be incompletely regenerated following injury.

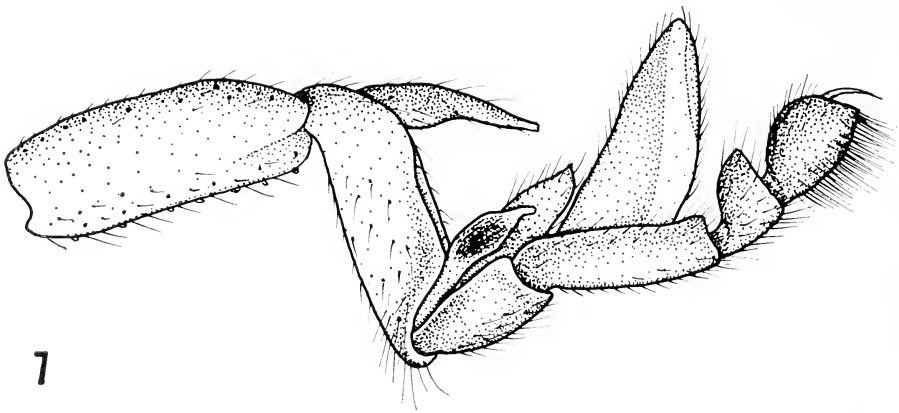
DESCRIPTION OF FEMALE ALLOTYPE

Body length, 3.94 mm.; carapace length, 1.34 mm.; carapace width, 1.24 mm.; abdomen length, 2.60 mm.; abdomen width, 1.60 mm.; cucullus length, 0.55 mm.; cucullus width, 0.88 mm.; pedipalp femur length, 0.73 mm.; pedipalp tibia length, 1.02 mm. General appearance very similar to male holotype with following differences: anterior edge of cucullus slightly more indented; pedipalps substantially larger, tibia proportionately more slender; tibia II without spur but with well-developed tubercles ventrally.

	Femur	Patella	Tibia	Metatarsus	Tarsomere(s)
I	0.63	0.42	0.42	0.70	0.30
II	1.15	0.58	1.00	1.00	1.20
III	0.80	0.40	0.45	0.60	0.46
IV	0.84	0.40	0.50	0.60	0.57

	I	II	III	IV
Femur diameter	0.23	0.33	0.22	0.18





FIGS. 6 and 7. *Cryptocellus* **paradoxus**, new species. Left leg III of male holotype. 6. Posterior view. 7. Anterior view. Scale line equals 0.5 mm.

DESCRIPTION OF FEMALE PARATYPES

Both paratypes fit description of female allotype closely but one specimen larger, thus: carapace length, 1.45 mm.; carapace width, 1.32 mm.; abdomen length, 3.2 mm.; abdomen width, 1.74 mm.; tibia II length, 1.50 mm.; tibia II diameter, 0.45 mm.

MATERIAL

Holotype male and allotype female (deposited in the Instituto de Zoologia, Academia de Ciencias de Cuba, Havana); two paratype females (deposited in the American Museum

of Natural History). Cuba: Oriente Province, Puerto Boniato, Santiago de Cuba, 500 meters, November 6, 1971 (L. F. Armas).

ETYMOLOGY

The specific name refers to the anomalous condition of the tarsal process of the male copulatory apparatus.

HABITAT

In little furrows under stones.

Literature Cited

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Dermatophagoides farinae: The Digestive System[1]

ARNOLD R. BRODY,[2] JOHN C. MCGRATH, AND G. W. WHARTON
ACAROLOGY LABORATORY, OHIO STATE UNIVERSITY,[3]
484 WEST 12TH AVENUE, COLUMBUS, OHIO 43210

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Abstract: The digestive system of the house-dust mite was studied by means of light microscopy, and transmission and scanning electron microscopy. The system consists of: 1) a prebuccal cavity which is surrounded by mouthparts comprising a gnathosoma, 2) a cuticle-lined foregut which consists of a muscular pharynx and a thin-walled esophagus, 3) a microvillous midgut which is divided into a large anterior portion with two caeca and a bulbous posterior section, and 4) a cuticle-lined hindgut consisting of a broad anterior portion and a narrow posterior section. The relationships of the mouthparts, the morphology of the systematic components, and the varying cell types are demonstrated. Discussed are possible digestive processes including formation of a peritrophic membrane and the production of salivary secretions which originate in the idiosoma and are channeled anteriorly to be utilized in the prebuccal cavity. An attempt is made to homologize the diverse nomenclature previously used for naming the gut regions of the Acari.

INTRODUCTION

The arthropod digestive system is remarkably constant in terrestrial forms (Barrington, 1967). It consists of a foregut, midgut, and hindgut, and each section may be further subdivided. The foregut is cuticle-lined while the midgut lacks a cuticular lining. The hindgut is usually lined with a cuticle along its entire length and always terminates with a cuticular lined section. Malpighian tubules, if present, enter the gut at the junction of the mid- and hindguts.

Insects have been extensively studied, and portions of the gut of several insects have been observed with the electron microscope. Among these studies are a book by Smith (1968) and articles by Peters (1969) and Richards and Richards (1971).

Typical arachnid digestion has been described (Mitchell, 1970), and digestion in a phalangid has been studied (Phillipson, 1961).

The anatomy of the digestive system, in whole or in part, of different groups of mites has been studied at the level of resolution of the light microscope

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[2] Present address: Department of Pathology, Medical Alumni Building, University of Vermont, Burlington, Vermont 05401.

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(Michael, 1901; Reuter, 1909; Bader, 1938; Vitzthum, 1940; Blauvelt, 1945; Hughes, 1954; Perron, 1954; Johnston, 1965; Prasse, 1967; Rohde and Oemick, 1967; Kuo and Nesbitt, 1970). Fine structure studies on the digestive tracts of mites have been reported (Wright and Newell, 1964; and Whitmoyer *et al.*, 1972).

It is the purpose of this study to describe the digestive system of *Dermatophagoides farinae* Hughes, a mite which has been associated with the allergen in house dust (Mitchell *et al.*, 1969). The formation of food balls and the fine structure of the peritrophic membrane of *D. farinae* have been reported by Wharton and Brody (in press).

MATERIALS AND METHODS

Mites cultured by the Acarology Laboratory were used. *D. farinae* was kept in small jars at constant 75% relative humidity at room temperature by means of desiccators containing a saturated solution of sodium chloride (Larson *et al.*, 1969). Most of the mites studied here were cannibalistic (Portions of the cuticle of ingested mites were almost invariably seen in the mid- and hindgut). The mites were removed from the tops of cultures where other mites were the only source of food.

Mites were removed from the culture jars and studied in several ways. 1) Living mites were studied under the dissecting microscope to observe gross movements of feeding behavior and by scanning electron microscopy (SEM) to study surface details. Living mites were placed on glass slides in two drops of Crown® immersion oil, covered with a cover slip, and observed by phase contrast and bright-field microscopy. 2) Whole mounts were cleared in Nesbitt's solution, mounted on glass slides in Hoyer's mounting medium, and observed by phase contrast microscopy. All the mouth parts and sclerotized portions of the digestive tract can be observed in whole mounts. 3) Thick sections (1 to 3 microns) of plastic embedded mites were studied by phase contrast and bright field microscopy. Sagittal and cross sections were cut through whole mites (which had been prepared for sectioning according to procedures described below) and stained for 30 sec with Azure B solution. 4) Thin sections (350 to 900 Å) were studied by means of transmission electron microscopy (TEM). In preparing specimens for TEM, living mites were fixed in 12.5% glutaraldehyde at room temperature and then postfixed in 1% osmium tetroxide at pH 7.4. Primary aldehyde fixation was from 5 hr to overnight, followed by postfixation in 0.1M cacodylate buffered osmium for 5 to 8 hr; these extended fixation periods gave better results. After fixation and before embedding, the mites were dehydrated in a graded series of ethyl alcohols (50, 70, 95, 100%). The mites were left for at least 10 min in the 50% to 95% range, and 20 to 30 min in the absolute alcohol. Propylene oxide was the most satisfactory transitional solvent. A mixed resin (catalyzed with DMP-30) of

Epon 812 and Araldite 502 was used in the following proportions (propylene oxide to resin): 3:1 for 1 hr, 2:2 for 1 hr, 1:3 overnight, and then 24 hr in 100% fresh resin before final embedment in fresh plastic in an oven at 60°C for 2 to 3 days. Glass knives were used to cut cross sections on a Porter-Blum MT-2 ultramicrotome. Sections were picked up on 100- or 200-mesh, parlodion-coated copper grids and stained with uranyl acetate and lead citrate. Thin sections were examined on an RCA transmission electron microscope model EMU-3G.

Whole mites were examined on a Cambridge scanning electron microscope, model Mark 2a. Live, uncoated mites, or mites treated with Gylcerol-KCL (Brody and Wharton, 1971) were stuck to specimen stages with carbon paint. Live specimens were mounted one day previous to observation to assure proper orientation and were kept alive by covering the specimen stage with a vial containing a small piece of moist cotton.

RESULTS

The digestive system of the house-dust mite (Fig. 1) begins anteriorly with a prebuccal cavity which is surrounded by mouthparts comprising a gnathosoma (Fig. 2). The cuticle-lined foregut follows the prebuccal space and consists of a muscular pharynx and thin walled esophagus (Fig. 1). The next section of the system is the midgut which is lined with microvillous epithelium and is divided into two sections, a large anterior portion with two caeca and a bulbous posterior section (Fig. 1). The hindgut is lined with cuticle and has a broad anterior portion and a narrow posterior section portion which leads to the anal

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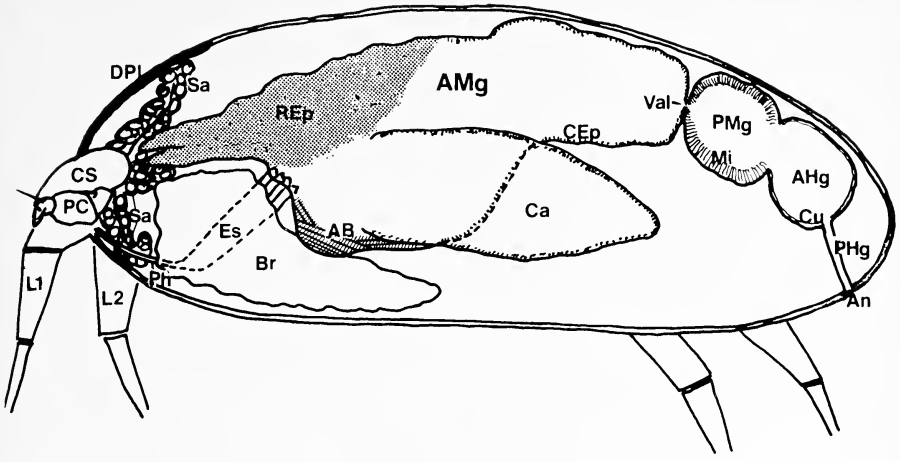
FIGURE KEY

A = apophysis; AB = active bands; AC = attached cell; AHg = anterior hindgut; AMg = anterior midgut; An = anus; AP = anal plate; B = buccal space; BM = basement membrane; BP = basal podomere; Br = brain; C = channel; Ca = caecum; CAB = cell of active bands; CEp = cuboidal epithelium; CF = cuticular fold; CM = cell membrane; CMu = circular muscles; CnMu = constrictor muscle; CS = cheliceral shaft; Cu = cuticle; DM = dilator muscle; DP = distal podomere; DPl = dorsal plate; E = epistome; Egg = egg; ECu = esophageal cuticle; Ep = epithelium; Epc = epicuticle; ER = endoplasmic reticulum; Es = esophagus; F = longitudinal fold; FB = food ball; FeB = fecal ball; FC = free cell; FD = fixed digit; H = hypostome; Ha = haemocoel; HP = hypostomal process; IC = ingested cuticle; L = labrum; L_1,L_2 = leg one, leg two; LR = lateral reflection; Ly = lysosome; M = microorganisms; MD = movable digit; Mi = microvilli; Mit = mitochondria; MR = median ridge; Mu = muscle; Muc = mucous-like lining; N = nucleus; PC = palp coxa; PCa = pore canal; Ph = pharynx; PHg = posterior hindgut; PM = peritrophic membrane; PMg = posterior midgut; R = cuticular ridge; Re = reproductive system; REp = reduced epithelium; S = solenidion; Sa = salivary gland; SCu = sloughed cuticle; Se = seta; SG = supracoxal gland; Sh = sheath; SL = separating layer; T = trough; Te = tendon; V = venter; Va = vacuole; Val = valve.



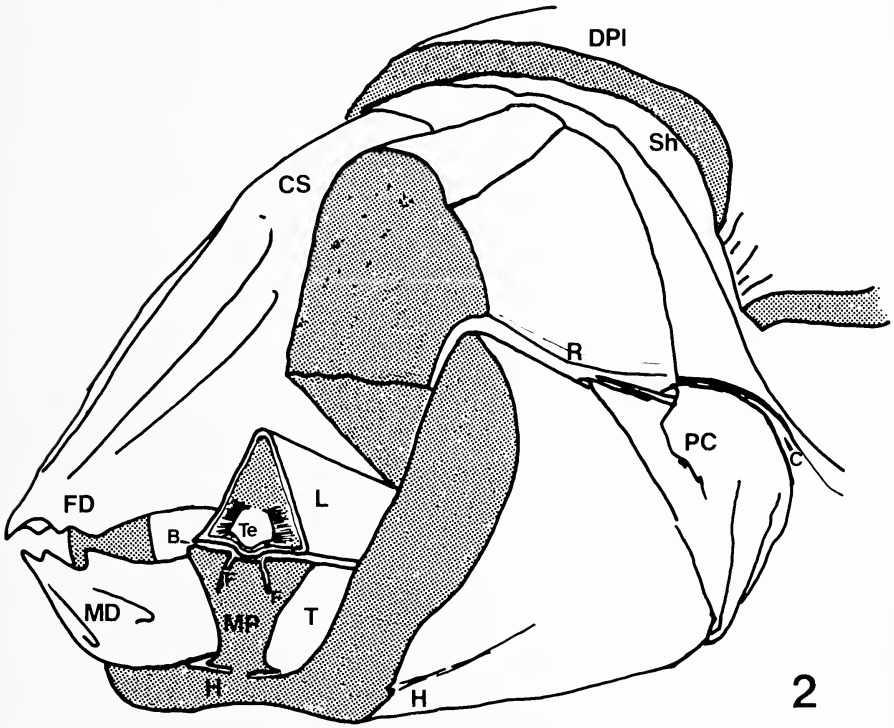
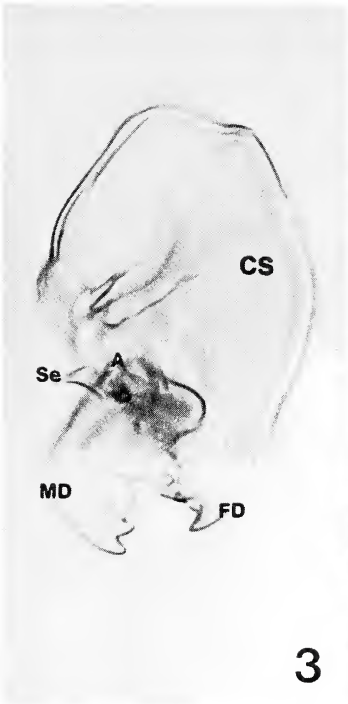


FIG. 1. Diagram representing a sagittal section through an adult female house-dust mite demonstrating the gross components of the digestive system. × 220.

FIG. 2. Diagram of a cross section of the gnathosoma revealing the prebuccal cavity and surrounding mouthparts. An intact chelicera remains in its relative position. × 2,000.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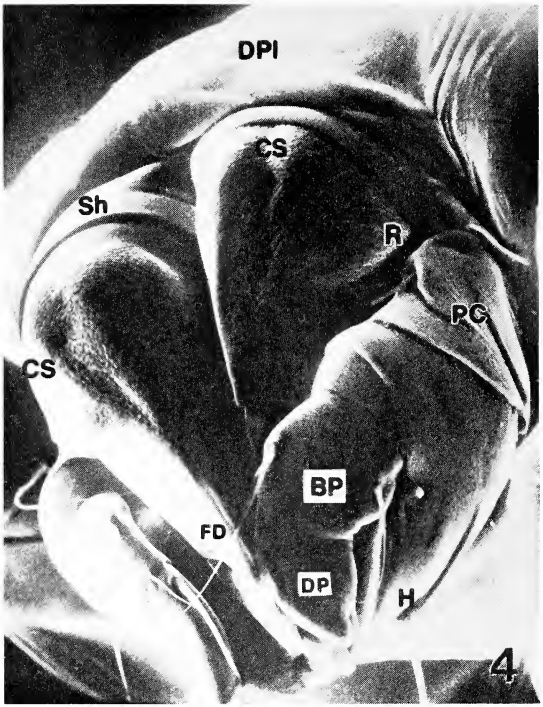
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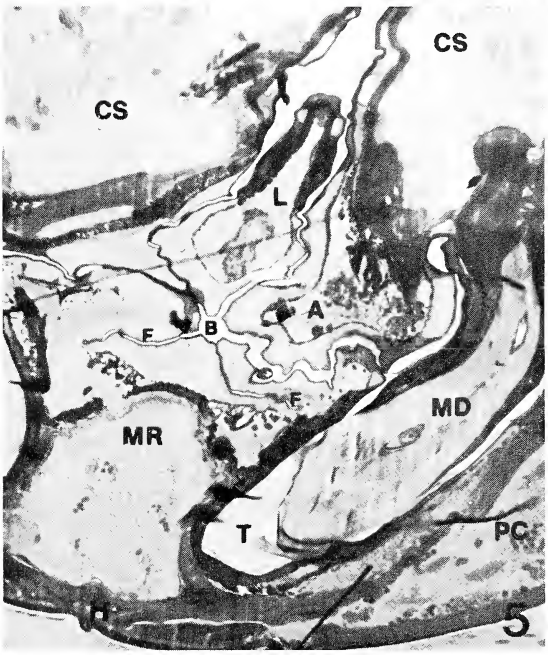
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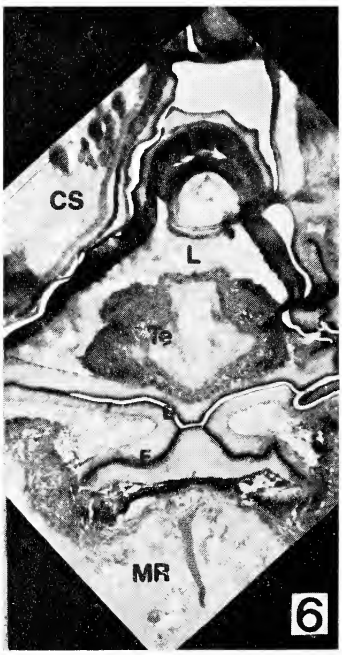
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opening (Fig. 1). Salivary glands are found associated with the digestive system (Fig. 1).

The gnathosoma is the anterior functional unit of the digestive system. It is articulated at the perignathosomal[4] furrow with the rest of the body known as the idiosoma (Fig. 1). The gnathosoma of *D. farinae* is approximately one-fifth the length of the idiosoma and is composed of two dorsal chelicerae, an epistome that supports the medial-anteriorly projected labrum, a ventral hypostome, and two lateral pedipalps (Fig. 2). Anteriorly these gnathosomal components surround the prebuccal space and posteriorly they surround the anterior one-fourth of the pharynx.

Each heavily sclerotized chelicera is oval in cross section and tapers anteriorly in width (from 35 microns posteriorly to 10 microns anteriorly) and height (from 40 microns posteriorly to 30 microns anteriorly). It consists of two segments (Fig. 3). The basal segment has a proximal shaft that is a hollow, oblate, truncated cone to which is attached a distal fixed digit. The movable digit is the second segment and it articulates with the cheliceral shaft proximal to the fixed digit so that the digits are in opposition. The natural position of the chelicerae is such that the dorsal aspects of the shafts are actually the anterior face of the gnathosoma, and the movable digit is posterior to the fixed digit (Fig. 4). On the shaft are two medial apophyses; one is rather small, blunt and centrally located on the shaft, while the other is just posterior to the point of articulation of the movable digit and has a heavy base which tapers to a narrow tip directed anteromedially. The single spike-like seta on the chelicera is slightly posterior and ventral to the larger apophysis and is also directed anteromedially (Fig. 3). A heavy dorsolateral cuticular ridge runs along one-third of the length of the cheliceral shaft (Figs. 2 and 4). The chelicerae are provided with intrinsic and extrinsic musculature as described for *Caloglyphus berlesei* by Johnston (1965). The extrinsic musculature includes powerful

[4] This furrow is most frequently designated circumcapitular. It is recommended that "circumcapitular" be replaced for the same reason that "capitulum" has been retired.

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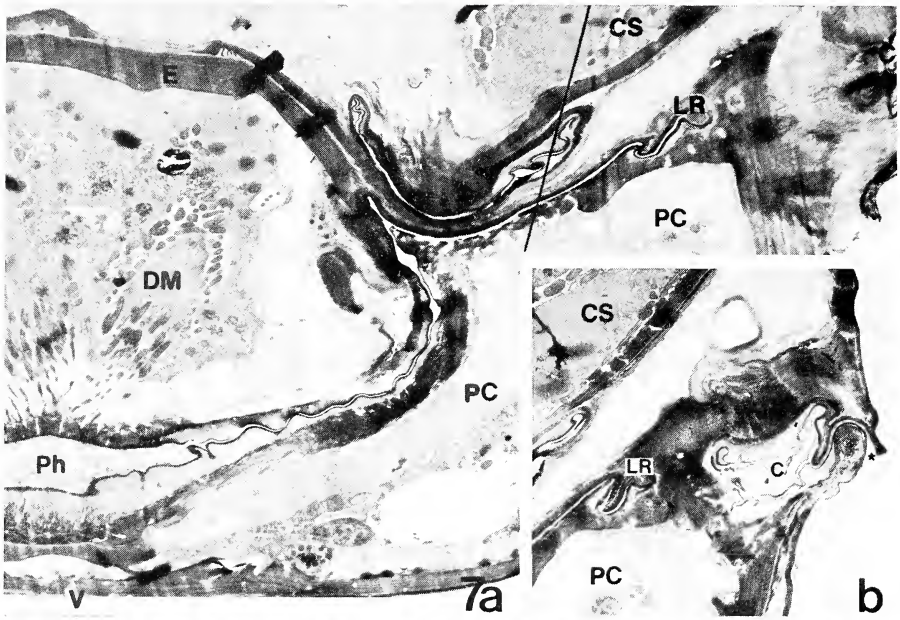
Fig. 3. Photomicrographs showing a medial view of an excised chelicera. × 1,000.

Fig. 4. Scanning electron micrograph (SEM) of an anterior view of the gnathosoma. Note that the right chelicera is extended while the left one is retracted. × 1,000.

Fig. 5. Transmission electron micrograph (TEM) of a cross section through the gnathosoma. The movable digit (MD) of the retracted chelicera is accommodated by a trough (T) formed from the median ridge (MR) of the hypostome (H) and the palpal coxa (PC). × 2,000.

Fig. 6 TEM of cross section through labrum (L) as it covers the prebuccal space (B). The presence of longitudinal folds (F) is a constant on the dorsal surface of the hypostomal median ridge (MR). × 2,000.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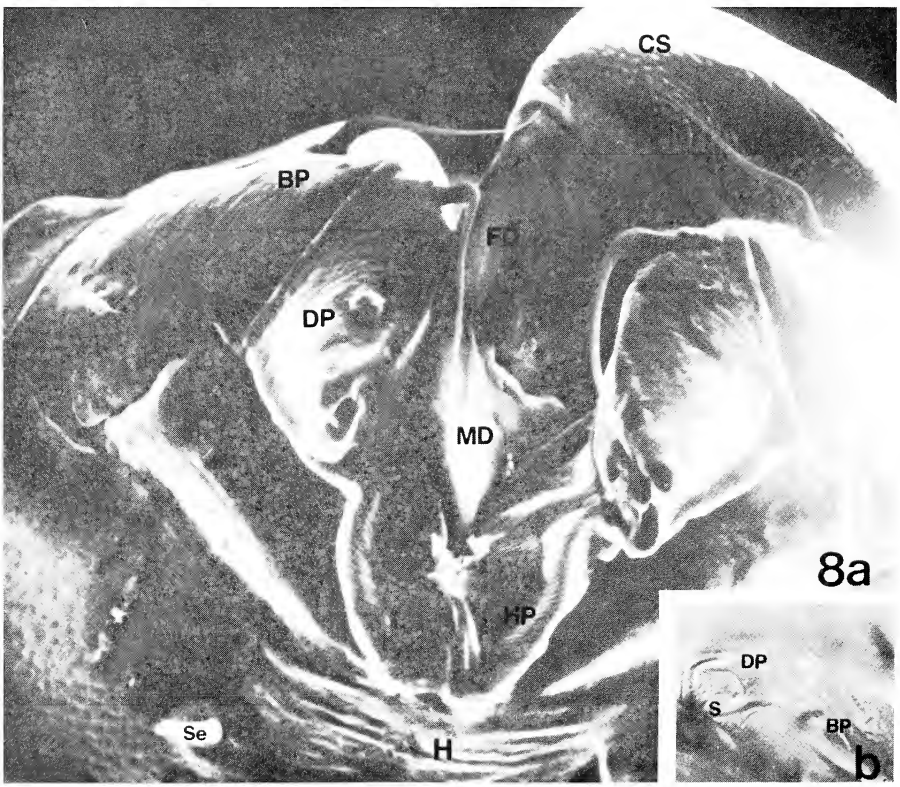
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retractor muscles which insert on the ventral surface of the shaft and originate on the ventral surface of the idiosomal dorsal plate. The levator and depressor muscles provide intrinsic opening and closing action to the movable digit. The chelicerae articulate with the idiosoma by a complex synarthrodial membrane known as the cheliceral sheath. The sheath is attached to the cheliceral shaft (which is about 70 microns long) about 33 microns from its posterior margin (Figs. 2 and 4). The sheath extends forward for a short distance and then doubles back on itself. Dorsally and laterally the sheaths are continuous with the synarthrodial cuticle of the perignathosomal suture. The sheaths accommodate increased mobility of the chelicerae and permit independent movement of each chelicera by virtue of the fact that the sheaths are independent of each other. At the ventral surfaces of the cheliceral shafts, the sheaths are reduced to a simple synarthrodial membrane. The ventral articulation of each chelicera appears to be hinge-like so that a sheath is required only for that portion distal to the hinge. The ventral surfaces of the cheliceral shafts cover the dorsal-lateral aspects of the prebuccal space (Figs. 2 and 5). The larger medial apophyses form a portion of the prebuccal roof (Fig. 5), and the heavy dorsolateral cuticular ridges on the cheliceral shafts close off the lateral, most posterior reflections of the prebuccal cavity by fitting snugly onto the dorsal rims of the palpal coxae (Figs. 2 and 4).

The labrum is a long tongue-like structure which lies between the ventromedial aspects of the chelicerae and extends anteriorly from the epistome approximately 27 microns (Figs. 2 and 5). The labrum is widest posteriorly and within its haemocoel is the labral retractor muscles and its long tubular tendon (Fig. 6). The labrum is also bulbous posteriorly and anteriorly tapers to a rather narrow tip (4 microns across). Anteriorly the labrum is roughly triangular in cross section (Fig. 6), and in its position between the chelicerae the broad ventral base serves to cover the medial-dorsal aspect of the prebuccal space (Figs. 2, 5, and 6). Posteriorly the ventral surface of the labrum fuses with the dorsal

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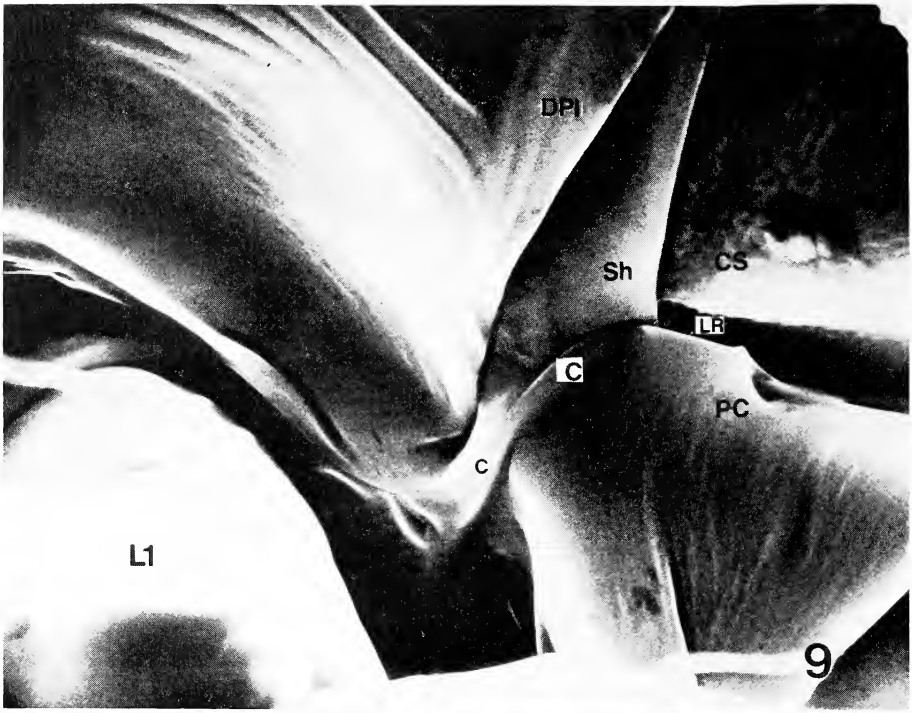
Fig. 7*a*. TEM of a cross section through the anterior pharyngeal region. At this level, lateral reflections (LR) of the alimentary canal have lost their communications with the external channel (C). The dilator muscles (DM) originate on the ventral surface of the epistome (E). × 2,000.

b. TEM of the lateral channel (C) at a more anterior level than in 7*a*. The lateral reflection (LR) is closer to the channel and still more anteriorly will form a continuous passage over the dorsal rim of the palpal coxa (PC). The external communication (*) of the channel is demonstrated. × 2,000.

Fig. 8*a*. SEM of an anteroventral view of the gnathosoma. The tips of the distal podomere (DP) are covered by hyaline cuticle; thus the three apical setae may not be observed by SEM. × 2,500.

b. Photomicrographs of the palpal podomeres. The tip of the distal podomere (DP) has three small setae, one is a solenidion (S) which is in a pit. × 800.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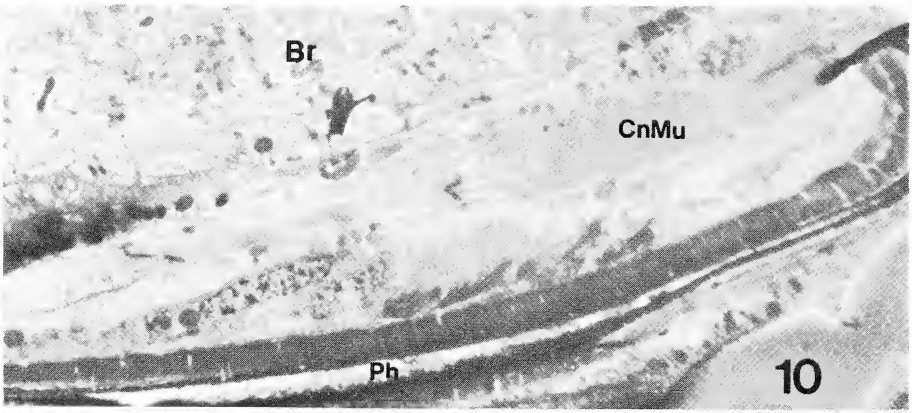
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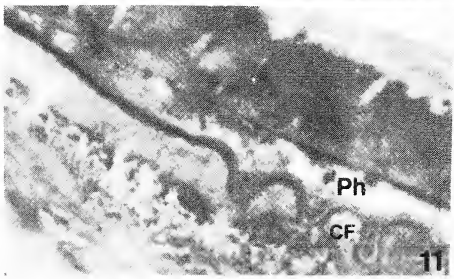
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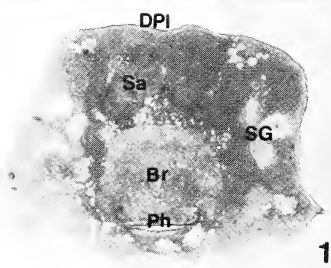
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wall of the pharynx while the dorsal surface of the labrum is continuous with the epistome. The epistome is a heavy apodeme which ventrally bears the origins of the pharyngeal dilator muscles (Fig. 5). It extends posteriorly approximately 30 microns and at its posterior limit, the labral retractor muscle has its origin. This internal sclerite forms the roof of the hypognathosoma.[5]

The hypostome forms the ventral face of the gnathosoma and lies between a pair of appendages, the pedipalps, whose large coxae form the posterior latero-ventral walls of the gnathosoma (Figs. 2 and 4). The hypostome consists of two portions, a median ridge and lateral elements which articulate with the ventromedial aspects of the palps (Fig. 2). A medial-ventral process of the hypostome that is independent of the palps extends anteriorly (22 microns) to a tip which is directed ventrally (Fig. 8*a*). On the dorsal surface of this tip are the most anterior extensions of two deep troughs (Fig. 8*a*) which run longitudinally between the median ridge of the hypostome and the palps (Fig. 2). The posterior limits of the troughs are just anterior to the level of the pharynx, and the troughs accommodate the movable digits of the chelicerae (Figs. 2 and 5). The lateral surface of the hypognathosoma is formed by the pedipalps (Figs. 2 and 4). The ventral hypognathosomal surface is heavily sclerotized and has one pair of anteriorly placed setae approximately 13 microns lateral to the midline. The dorsal surface of the median hypostomal ridge is regularly observed with two longitudinal folds and forms the floor of the prebuccal cavity (Figs. 5 and 6).

Each pedipalp consists of a large coxal segment which is fused insensibly both medially and ventrally to the hypostome, and two small podomeres (Fig. 4). The two podomeres of the palps are about 25 microns long and are oval in cross section. The basal podomere has two seta (one dorsal, one ventro-lateral) and is somewhat longer than the distal podomere (Figs. 4 and 8*a*). The distal podomere curves ventromedially and has one dorsal seta (Figs. 4

[5] A substitute word for subcapitulum of authors.

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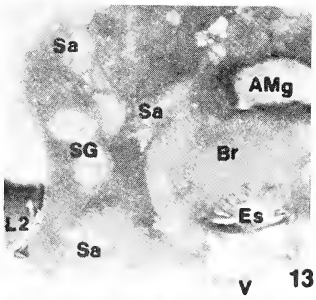
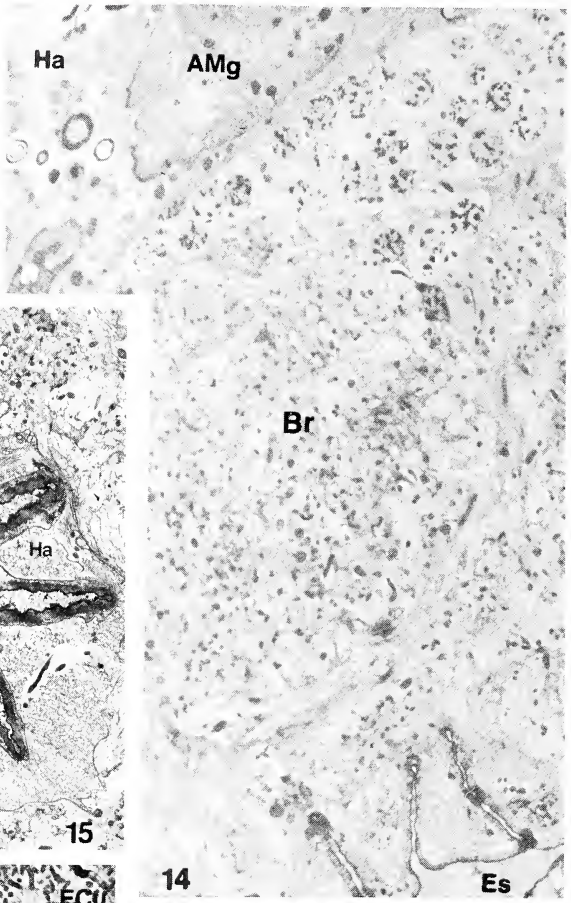
Fig. 9. SEM of a lateral view of the right side of the house-dust mite which demonstrates the course of the external channel (C) and where it communicates with the lateral reflection (LR) of the prebuccal cavity over the palpal coxa (PC). × 2,500.

Fig. 10. TEM of a cross section through the posterior pharynx (Ph) where the cuticle is rather thin and constrictor muscles (CnMu) are found. × 10,000.

Fig. 11. TEM of a cross section through the central phraynx (Ph) where the floor is ribbed by longitudinal cuticular folds (CF). × 10,000.

Fig. 12. Photomicrograph of a cross section through the region of the posterior pharynx (Ph) which underlies the brain (Br) at this level. A portoin of the dorsal salivary mass (Sa) is seen on the right side while several cells of the supracoxal gland (SG) are obvious on the left side of the mite. × 250.


Sa
AMg
Sa
SG
Br
L2
Es
Sa
V
13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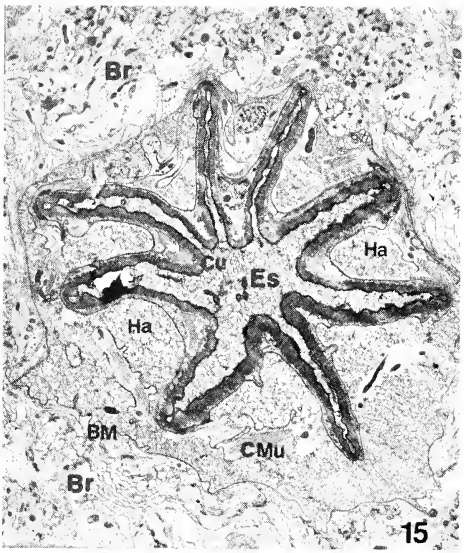
14
Es


Br
Cu
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CMu
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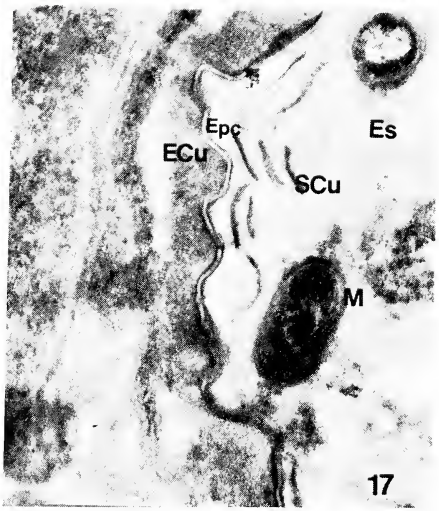
15


ECu
IC
AMg
M
Es
Br
Fc
16


Es
Epc
ECu
SCu
M
17

and 8*a*). On the tip of the distal podomere are three rod-like setae which appear to be a single solenidian and two eupathidia (Fig. 8*b*); the solenidion (largest of the three) is ventral and is found in a pit, the smallest seta is dorsal, and all are covered by a hood of hyaline cuticle. The palps limit the most lateral aspects of the prebuccal cavity (Fig. 4). At the level where the hypognathosoma articulates with the idiosoma, a channel partially closed from the outside by a cuticular flap crosses over the dorsal margin of the palp (Fig. 9) and delivers glandular secretions into the prebuccal cavity.

The prebuccal cavity is not a permanently sealed compartment. It has a number of external connections. Not only is the cavity open between the labrum and hypostome but there are also dorsal openings between the chelicerae and lateral openings across the aforementioned troughs and over the dorsal rim of each palp (Fig. 2). The end of the prebuccal cavity and the beginning of the pharynx is at the level where the lateral reflections of the prebuccal space no longer have an external communication (Fig. 7*a*).

Two masses of glandular tissue located anterodorsally and one anteroventral mass can be seen within the idiosoma (Fig. 1). From the glandular masses, ducts run laterally and anteriorly to communicate with the channels that cross the palps and enter the prebuccal space (Fig. 7*b*). When the mite is standing in the usual position, the channel is located between the coxa of leg I and the gnathosoma and is difficult to observe (Fig. 9). Salivary secretions produced in the idiosoma are thus delivered to the prebuccal cavity. The salivary glands are intimately associated with the large supracoxal glands which open dorsal to coxa I (Fig. 13). In living mites mounted in mineral oil, the salivary glands appear to be made up of grapelike clusters.

The alimentary canal of *D. farinae* is separated into three main sections, each

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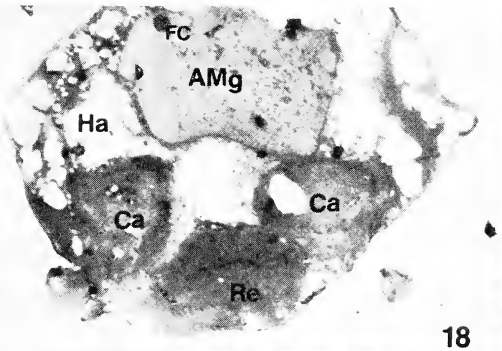
Fig. 13. Photomicrograph of a section at the level where the pharynx merges with the esophagus (Es) and the latter is becoming plicated. The anterior midgut (AMg) is now seen dorsal to the brain (Br) and elements of the salivary glands (Sa) are shown relative to cells of the supra coxal gland (SG). × 450.

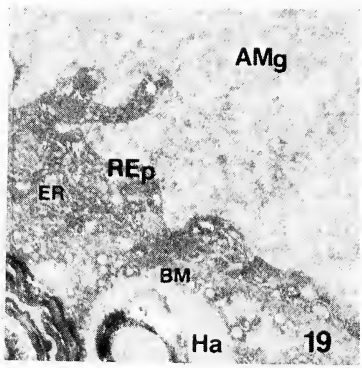
Fig. 14. TEM of the anterior esophagus (Es) as it lies ventral to the brain (Br). Dorsal plications are obvious. × 4,000.

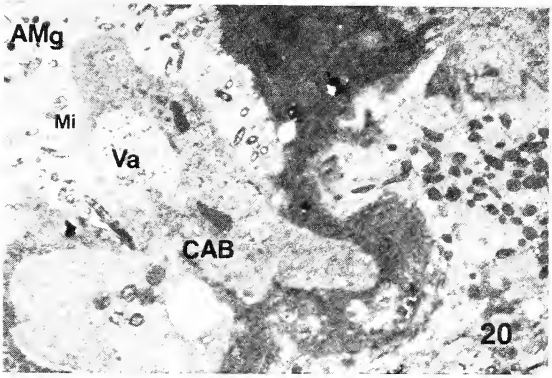
Fig. 15. TEM of a cross section through the central level of the esophagus (Es) as it passes through the midst of the brain (Br). Circular muscles (CMu) extend between the plicae. × 5,000.

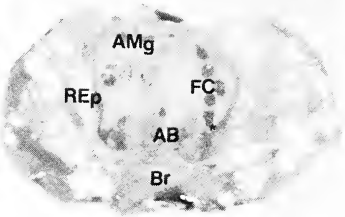
Fig. 16. TEM of a section through the esophagus (Es) at the level where it protrudes into the anterior midgut (AMg) dorsal to the brain (Br). Flaps of esophageal cuticle (ECu) form a valve to prevent reverse peristalsis. Numerous unidentified microorganisms (M) are found in the gut of the house-dust mite. × 5,000.

Fig. 17. TEM of esophageal cuticle (ECu) which has a distinct epicuticle (Epc) and sloughed material (SCu) which may have originated from the cuticle. × 25,000.


FC
AMg
Ha
Ca
Ca
Re
18


AMg
REp
ER
BM
Ha
19


AMg
Mi
Va
CAB
20


AMg
REp
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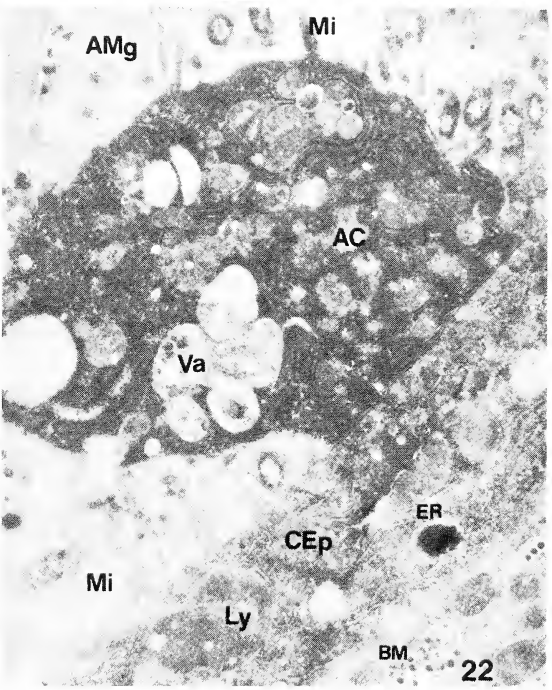
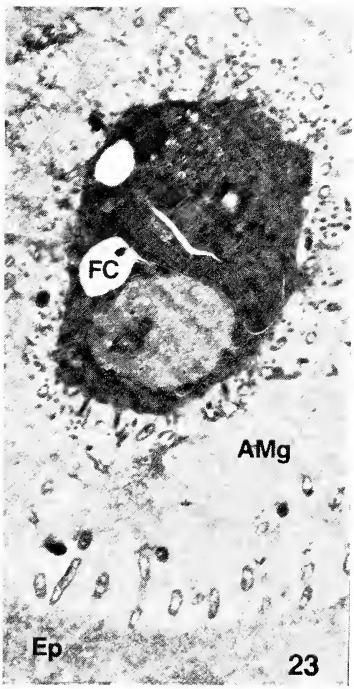
Br
21


AMg
Mi
AC
Va
ER
CEp
Mi
Ly
BM
22


FC
AMg
Ep
23

of which can be subdivided at least once on morphological criteria. The three major regions are the foregut, midgut, and hindgut.

The foregut begins with the pharynx at the mouth or entrance to the alimentary canal. The pharynx, a muscular pump, is lined anteriorly with fibrous cuticle approximately 1 micron thick (Fig. 7*a*). The cuticle of the anterior portion of the pharynx has many pore canals. The pharynx is flattened and its lateral aspects curve dorsally (Fig. 12). Muscles are associated with the dorsal pharyngeal wall; five bands of dilator muscles originate on the ventral surface of the epistome and insert on the dorsal wall of the pharynx (Fig. 7*a*). Several bands of constrictor muscles originate medially on the dorsally curved lateral aspects of the pharynx and run transversely to the opposite medial side (Fig. 10). The most anterior constrictor muscle is found between the third and fourth dilator muscles, and the second constrictor is found between the fourth and fifth dilator. The remaining constrictor muscles are posterior to the dilators. The middle third of the pharyngeal floor is ribbed by longitudinal cuticular folds (Fig. 11), and posteriorly the cuticular pharyngeal lining becomes more heavily sclerotized and progressively thinner (to 0.75 micron). At the juncture of the pharynx and esophagus, the alimentary canal becomes highly plicated (Fig. 13).

The esophagus arises from the pharynx in the region of the brain. The dorsal wall of the pharynx comes in contact with the basement membrane of the brain as the ventral wall of the pharynx separates from the midventral wall of the idiosoma (Fig. 13). The dorsal wall of the alimentary canal becomes plicated as it is surrounded by nervous tissue (Fig. 14). These plications form grooves

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Fig. 18. Photomicrograph of a cross section through the anterior midgut (AMg) at a level where free portions of the caeca (Ca) can be observed. × 400.

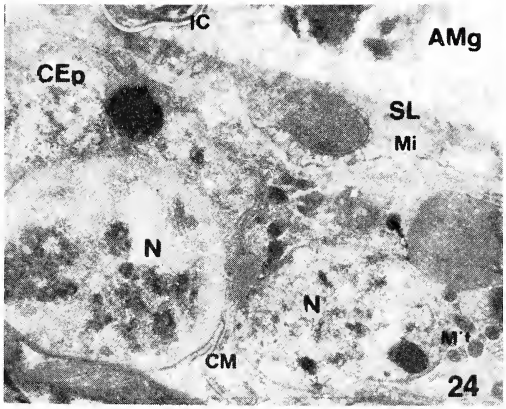
Fig. 19. TEM of the reduced epithelium (REp) which lines the dorsal-anterior region of the anterior midgut (AMg). These cells are reduced in apical-basal dimension. All gut epithelial cells are separated from the haemocoel (Ha) by a basement membrane (BM). × 12,000.

Fig. 20. TEM of a cell of the active bands (CAB) which line a portion of the ventral anterior midgut (AMg). Many cells of this type are found protruding into the gut lumen. × 2,500.

Fig. 21. Photomicrograph of a cross section which demonstrates the position of the active bands (AB) on the venter of the anterior midgut (AMg). Free cells (FC) in the gut lumen have originated from these bands, and one cell (*) was apparently fixed while in the process of becoming free. The remainder of the gut lining at this level is composed of reduced epithelium (REp). × 200.

Fig. 22. TEM of an attached cell (AC) about to become free in the gut lumen (AMg) but still adhering to the cuboidal epithelium (CEp) from which it originated. This cell appears to have undergone some degree of degeneration. × 8,000.

Fig. 23. TEM of a degenerating cell (FC) free in the lumen of the anterior midgut (AMg). × 4,000.


IC
AMg
CEp
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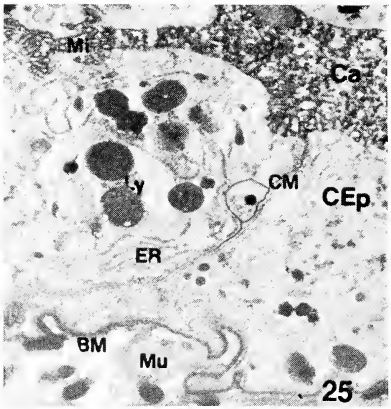
Mi
N
N
Mi
CM
24


Mi
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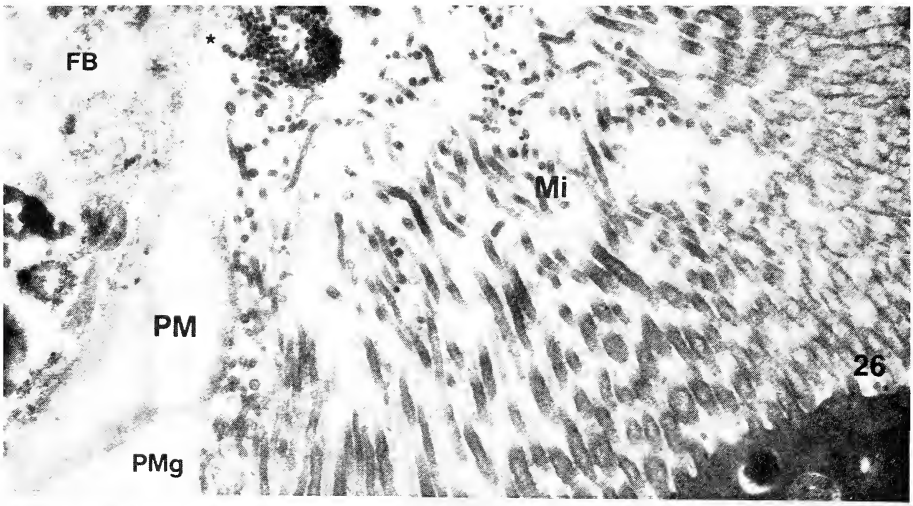
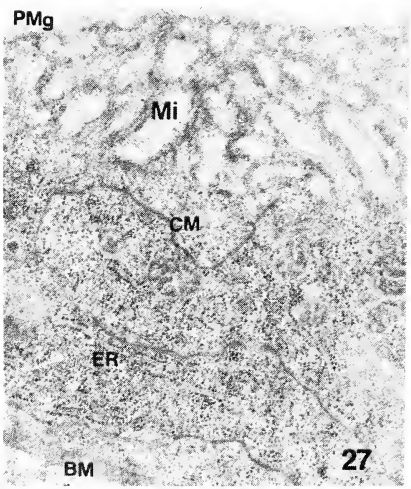
25


FB
*
Mi
PM
26
PMg


PMg
Mi
CM
ER
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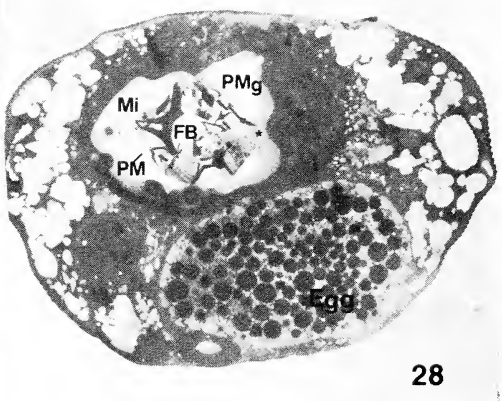
27


PMg
Mi
FB
*
PM
Egg
28

that become a part of the haemocoel (Fig. 15) so that a tubular extension of the haemocoel penetrates the brain from the level of the pharynx along the esophagus to the midgut. The nervous tissue is separated from this extension of the haemocoel by a well-defined basement membrane (Fig. 15). The plicated form of the alimentary canal as it is surrounded by the brain prevents the cerebral basement membrane from conforming to the outline of the gut epithelium (Fig. 15). As a result, the interface between brain and gut is filled with blood and connective tissue (Fig. 15). The entire esophagus passes in a dorsal direction through the midst of the brain (Fig. 15). The plications of the esophagus give it the appearance in cross section of an eight-pointed star. The central portion of the esophageal lumen is about 2.5 microns in diameter when collapsed. Each ray is about 0.25 micron wide at its tip and 0.8 micron wide at its base, and when expanded each ray would add approximately 10 microns to the total diameter of the esophagus. Thus the esophagus could accommodate particles over 20 microns in diameter. The lumen is lined by cuticle that is of almost uniform thickness (0.5 micron). Next to the lumen is a well-defined epicuticle that is 0.07 micron thick. Beneath the epicuticle, the rest of the cuticle seems to consist of exocuticle through which pore canals pass from the epithelial cells to the epicuticle. The pore canals are spaced 0.1 micron from each other and are about 0.42 micron in length. They appear to be unbranched and slightly larger in diameter at their interface with the epithelial cells. Constrictor muscles, limited from the connective tissue by basement membranes, are located between the plicae (Fig. 15) at one or more levels. In some specimens, portions of the epicuticular lining of the foregut have sloughed off in a laminar fashion (Fig. 17). The esophagus ultimately emerges dorsal to the brain and communicates with the midgut (Fig. 16).

The midgut of *D. farinae* is divided into an anterior and posterior region by a constriction (Fig. 1). The anterior region is approximately twice the size of the posterior section and is about 250 microns long. Extending posteriorly from

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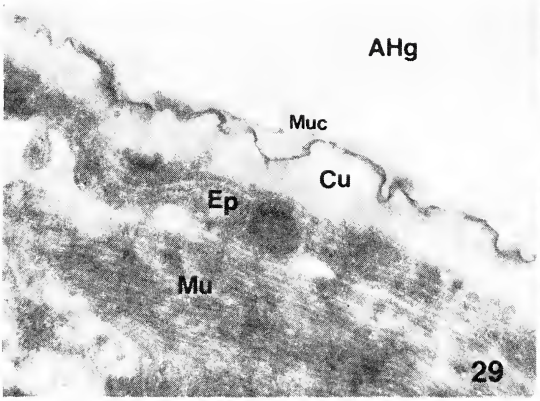
Fig. 24. TEM through the cuboidal epithelium (CEp) of the anterior midgut (AMg). The separating layer (SL) lies between gut contents and the epithelium. × 8,000.

Fig. 25. TEM of several cells which line the caecal lumen (Ca). Short microvilli (Mi) are numerous as are membrane-bound spheres interpreted to be lysosomes. × 6,000.

Fig. 26. TEM through the posterior midgut (PMg) at an anterior level where the long microvilli (Mi) are still partially adhering to the peritrophic membrane (PM). At the point of contact (*) the PM is relatively thin. × 12,000.

Fig. 27. TEM through the dense microvilli (Mi) of the posterior midgut (PMg). Rough endoplasmic reticulum (ER) is a characteristic of this epithelium. × 24,500.

Fig. 28. Photomicrograph of a cross section at the level of the posterior midgut (PMg). A peritrophic membrane (PM) surrounds a food ball (FB), and microvilli (Mi) which form the brush border contact the PM at its thinnest point (*) as in Fig. 26. × 450.


AHg
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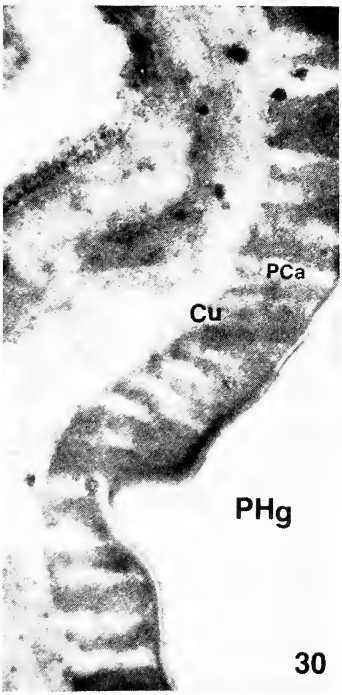
Mu
29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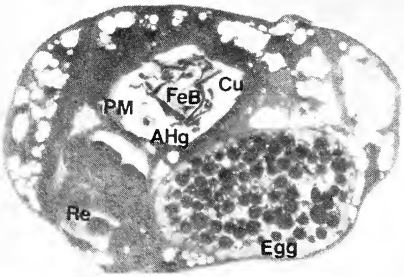
PHg
30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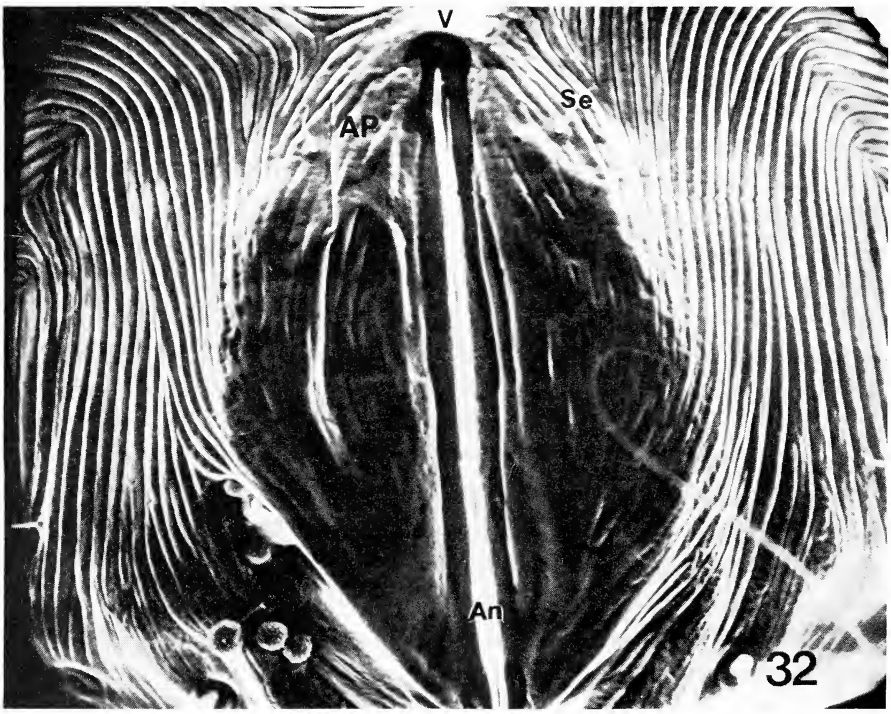
Re
Egg
31


V
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32

the ventrolateral aspects of the anterior midgut are two diverticulae (caeca) which are about 150 microns long (Figs. 1 and 18). The midgut epithelium displays an interesting variety of cell types. The dorsal, most anterior, midgut epithelial cells are reduced in apical-basal dimension (Fig. 19). There are few microvilli, and common organelles such as mitochondria and nuclei are seldom observed. However, ventrally in this anterior region of the midgut are two rows of apparently active cells. Beginning at the point where the esophagus enters the midgut, the rows of active cells are evident all the way up to the constriction between the anterior and posterior midgut (Fig. 1). The cells of this region are characterized by a single nucleus, numerous short microvilli, rough endoplasmic reticulum, and large vacuoles (Fig. 20). It appears as though cells which are floating freely in the gut lumen have originated from ventral cell rows (Fig. 21). Some were apparently fixed while in the process of doing so (Figs. 21 and 22). The free cells in the gut lumen are generally round or elliptical in outline with many short microvilli, large vacuoles (both filled and empty), condensed endoplasmic reticulum, and remnants of other organelles which are difficult to positively identify (Fig. 23). Those cells which were fixed while in the process of becoming free from the midgut epithelium are typically narrow at their attached basal portion (Fig. 22) and rounded apically. The cytoplasm of these cells is in a state of degeneration which appears intermediate between that of the ventral row cells and that of the free cells in the gut lumen (Figs. 22 and 23).

More posteriorly, but still within the anterior region of the midgut, the dorsal and lateral epithelium is made up of cuboidal cells with short microvilli as well as a single nucleus, a few lysosomes, multivesicular bodies, mitochondria, and an extensive, rough endoplasmic reticulum (Fig. 24). Closely associated with the short microvilli of the cuboidal cells is a band of material which separates the contents of the gut from the epithelial cells (Fig. 24). Several of these cuboidal cells comprise active sites which appear to be located randomly along the epithelial lining of the anterior midgut. Many of the degenerating cells found free in the gut lumen are from these active sites (Fig. 23).

The cytoplasm of the cuboidal cells is also typical of the cells which line the

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Fig. 29. TEM through the cuticle (Cu) and thin underlying epithelium (Ep) of the anterior hindgut (AHg). A mucous-like lining (Muc) covers the cuticle. × 12,000.

Fig. 30. TEM through the cuticle (Cu) of the posterior hindgut (PHg). Numerous pore canals (PCa) are present. × 15,000.

Fig. 31. Photomicrograph of a cross section at the level of the cuticle-lined (Cu) anterior hindgut (AHg). A fecal ball (FeB) surrounded by a peritrophic membrane (PM) is seen in the gut lumen. × 300.

Fig. 32. SEM of a posteroventral view of the anal plates (AP) of the house-dust mite. Each plate has a single seta (Se). × 1,000.

caeca (Fig. 25). The cells of the caeca, however, have numerous electron-dense inclusions which are interpreted to be lysosomes (Fig. 25). The lumen of each caecum is quite constricted and appears occluded by flocculent materials as well as great numbers of microvilli. The caeca are limited from the haemocoel by a heavy basement membrane which appears to provide an attachment for circular muscles (Fig. 25).

The anterior and posterior sections of the midgut are separated by a constricted region (Fig. 1) which acts as a valve in allowing food to pass into the posterior section. In mites mounted in mineral oil, the valve is observed to expand and contract during the passage of food. At its narrowest point, the diameter of the valve has been measured at 20 microns compared with a diameter of 100 microns for the anterior midgut and 85 microns for the posterior midgut. The lumen of the valve is practically obscured by long microvilli (Fig. 1), and all food material must pass through this region in the process of being included in a food ball.

The posterior region of the midgut has long microvilli (up to 3.5 microns). An obvious peritrophic membrane surrounding individual food balls is noted in this region (Figs. 26 and 28). Where the food is adpressed to the long microvilli of the posterior midgut, the peritrophic membrane is at its thinnest (Fig. 26). By the time the food has moved posterior to the valve and is free of the microvilli, the thicker peritrophic membrane has completely encased the food to form a food ball (Fig. 28). As well as long microvilli, the posterior midgut cells have an extensive, rough endoplasmic reticulum (Fig. 27), and other organelles typical of an actively secreting cytoplasm are observed.

The posterior midgut and the anterior hindgut are separated by a slight narrowing of the alimentary canal between the two regions (Fig. 1). No muscles have been found associated with this constriction, and the regular contractions noted in the more anterior valve were not observed here. Contractions which move food balls from the midgut to the hindgut are initiated in the posterior midgut and proceed less vigorously since no valve is involved.

The anterior and posterior regions of the hindgut are lined with cuticle (Fig. 1). Longitudinal folds in this cuticle run the entire length of the anterior hindgut and in cross section appear as indentations in the cuticle (Fig. 29). The cuticle of the anterior region (1.0 micron thick) may be covered by a substance which has the appearance of a mucous-like lining (Fig. 29). Although it is impossible to determine the exact composition of this material after utilizing basic TEM techniques, it has been noted that the material is electron-dense, homogeneous, and if present fills the many indentations of the hindgut cuticle (Fig. 29). Endoplasmic reticulum is often found in the hypodermis which underlies the hindgut cuticle (Fig. 29). What appear to be contractile cells have also been

seen (Fig. 29). Peritrophic-membrane-wrapped fecal material is observed in the hindgut (Fig. 31). This fecal material often contains the cuticle of ingested portions of mites. No valve was observed between the anterior and posterior hindgut; these cuticle-lined sections merely merge where the lumen narrows and the pore canals of the posterior hindgut become obvious.

The cuticle of the posterior hindgut generally has many pore canals (Fig. 30). The cuticle surrounds a narrow lumen only about 2.5 microns in diameter. The posterior region of the hindgut terminates at a pair of anal plates which together form an oval about the slit-like anus on the posteroventral aspect of the mite. Each plate has a single, anteriorly placed seta (Fig. 32).

DISCUSSION

Common to all orders of Acari is a gut divided into six more or less well-defined regions. Reuter (1909) has described four types of Acarine digestive systems, while Vitzthum (1940) considers three types, calling the gut of the Tetrapodili a special case (see Whitmoyer *et al.*, 1972, for a recent example). Mitchell and Nadchatram (1968) have also described a specialized gut in the chigger mites. However, all authors seem to agree on the use of the term pharynx for the muscular, cuticle-lined pump which anteriorly begins the alimentary canal, and the term esophagus for the cuticle-lined tube which leads posteriorly from the pharynx through the brain to the midgut. The remaining four gut regions of the Acari show great variation in form and nomenclature (Table 1).

The esophagus is followed by a sac-like, epithelial-lined structure commonly labeled a stomach or ventriculus which may have two or more diverticulae (caeca). The next section of the gut is a second epithelial-lined region which has considerable morphological variety and a matching lack of uniformity in nomenclature, e.g., colon, intestine, hindgut, posterior midgut. If present, excretory tubules are located posterior to this latter region and anterior to the next region. The two posterior sections of the gut may be lined wholly or in part by cuticle and have been named hindgut, rectum, post-colon, and anus in varying combinations.

A great deal of variety also exists in the literature concerning the naming of the gut regions of acarid mites. There are three main sections of the gut to be considered, the foregut, midgut, and hindgut. In most cases, however, investigators of acarid mites have avoided the use of fore-, mid-, and hindgut. The digestive systems of several free-living relatives of *D. farinae* have been described, and the gut regions demonstrated are strikingly similar in each case. The foregut is regularly described as consisting of an anterior pharynx followed by the esophagus. The remaining gut is then divided into three or four sections (Table 1).

Table 1. The nomenclature as proposed by authors for divisions of the digestive systems of several mites (with special reference to the Acaridei). The homologies of the gut regions may be identified in the corresponding vertical columns. The first three authors do not use the fore-, mid-, and hindgut designations; the final three authors do so categorize the gut regions.

Vitzthum (1940) Acaridei	pharynx	esophagus	midgut	intestine	colon	rectum	anus
Michael (1901) *Glycyphagus platygaster*	pharynx	esophagus	ventriculus	colon	rectum		anus
Kuo & Nesbitt (1970) *Caloglyphus mycophagus*	pharynx	esophagus	stomach	colon	rectum		anus
	foregut		*midgut*		*hindgut*		
Brody, McGrath, and Wharton *Dermatophagoides farinae*	pharynx	esophagus	anterior midgut	posterior midgut	anterior hindgut	posterior hindgut	anus
Prasse (1967) *Caloglyphus berlesei*	pharynx	esophagus	ventriculus	colon	post-colon	rectum	anus
Evans, Sheals, and Macfarlane (1961) all mites	pharynx	esophagus	stomach or ventriculus	intestine		rectum	anus

Homologies of the gut regions have been considered by a number of investigators. All authors agree on the terms pharynx and esophagus (Table 1). Michael (1901) studied a number of acarid mites and has had a significant influence on the anatomical nomenclature. For *Glycyphagus platygaster* (syn. *Labidophorus talpae* Kramer, 1877), he divided the gut into three sections, a ventriculus, colon, and rectum (Table 1). Several investigators have followed this pattern, and subsequent difficulties in naming the gut regions have arisen because of the anatomical variation in the acarid mites. Furthermore, the use of fore-, mid-, and hindgut categories are used by some authors and ignored by others (Table 1). Two morphological criteria may be recognized for naming the gut regions posterior to the foregut, the presence or absence of a cuticular lining and the location of Malpighian tubules. If present, the Malpighian tubules enter the gut at the juncture of the mid- and hindguts. Prasse (1967) found that the chamber posterior to the colon of *Caloglyphus* had a lining of cells characterized by a striated border. Because of this he referred to this posterior region as the post-colon and included it as a portion of the midgut (Table 1). Using the criterion based on presence or absence of cuticle this is an appropriate decision, but it places the Malpighian tubules between two sections of the midgut. Malpighian tubules are reported in a number of acarid mites, but Michael (1901) and Vitzthum (1940) have indicated several species with no apparent excretory tubules. *D. farinae* fits into the latter category; no Malpighian tubules have been observed.

The division of the gut into the three primary regions (of foregut, midgut, and hindgut), using the criterion of presence or absence of cuticle, is followed in this study of *D. farinae*. The gut of *D. farinae* has a cuticular lining on both posterior regions and so both are designated as hindgut. The anterior region of the hindgut is homologous to the post-colon of *Caloglyphus* (Prasse, 1967) but differs from it by having a cuticular rather than an epithelial lining. Certainly the terminology for homologous regions should be uniform. In many acarid mites, the presence of Malpighian tubules can be used to delimit the division between mid- and hindgut. The fact that the use of this criterion for the acarid mites leads to the same divisions as the cuticular criterion does in pyroglyphid mites suggests that it should be used, and that the post-colon should be recognized as the anterior region of the hindgut.

A developmental definition of fore-, mid-, and hindgut, equating them as derivatives of stomodaeum, endoderm, and proctodaeum, respectively, has been used in the past without extensive confirmatory developmental studies. The embryology of gut formation in insects has been discussed by Sharov (1966). He reports the formation of microvillate epithelium from the stomodaeum and proctodaeum, thus claiming the ectodermal origin of the entire alimentary canal at least in some cases. Certainly his findings suggest that a developmental definition of the fore-, mid-, and hindgut regions is at best questionable.

It seems that many authors (e.g., Evans, Sheals, and Macfarlane) followed Michael's implication that everything behind the ventriculus was hindgut. Certainly Michael's use of the term colon could be interpreted in this manner. This confusion has persisted, but it is hoped that it will be dispelled in time. In the acari, the midgut is usually divided into two regions. Up to now at any rate, the entrance of the Malpighian tubules into the gut seems to be a certain landmark for differentiating between mid- and hindgut in those forms that have tubules. Using this criterion, no acarine is known to have more than one transverse division of its midgut.

In *D. farinae*, ingestion begins with mouthparts specifically designed for manipulating solid particles. The large dentate chelicerae, with the medial apophyses fitting snugly over the prebuccal space (Fig. 5), tear off and pick up pieces of food that are placed in the buccal region. The chelicerae move in an anterior-posterior direction in such a manner that when one chelicera is extended forward the other is pulled back. The food material which has been placed in the buccal space by the chelicera that is moving forward is now pushed posteriorly by the retracting food-laden chelicerae of the opposite side. In this manner the prebuccal space of a feeding mite is filled with food. The prebuccal cavity must then be sealed from the outside so that the pharyngeal pump can suck the food material back, presumably in a bath of digestive juice secreted by the salivary glands. The prebuccal region may be sealed anteriorly by the labrum, dorsally by the labrum and chelicerae, and laterally by the cuticular ridges on the chelicerae which can be adpressed to the dorsal margins of the palps. The prebuccal cavity and pharynx are capable of great distension, allowing appendages (of other mites) with a diameter up to 20 microns to be ingested. The cuticle-lined, distensible foregut (Fig. 15) can accommodate large pieces of food passing into the midgut for digestion. The pharyngeal dilators and constrictors are antagonistic muscles (Johnston, 1965), and their alternate contractions result in the pumping action of the pharynx. On the other hand, only circular muscles, which are interpreted to be constrictors, have been found associated with the esophagus (Fig. 15). This suggests a peristaltic action for the latter. The pharyngeal pump, closed as described above, forces material back into the esophagus which is plicated when empty. The constrictor muscles, upon distension of the esophagus, may then act in sequence to move the food along the tract and into the midgut.

Studies concerning the digestive functions of several arachnids have indicated that the midgut epithelium carries out post-oral food processing and absorption by intracellular digestion (Bader, 1938; Phillipson, 1961; Wright and Newell, 1964; Mitchell, 1970). This study offers evidence of extracellular as well as intracellular digestive processes within *D. farinae*. The intracellular process requires an engulfing of food material by the individual midgut cells. Intracellular digestion takes place in cells that are at some time sloughed off into the

gut lumen and are eventually decomposed. The midgut may actually be filled with free-floating gut cells (Phillipson, 1961; Wright and Newell, 1964).

The house-dust mite ingests fluids, but it also takes in relatively large, solid particles. In its most common habitat, the human abode, *D. farinae* is reported to live on sloughed epidermal cells (Larson *et al.*, 1969). In culture, yeast is provided as food, but in the absence of other food, cannibalism is common among house-dust mites. Consequently, one may assume that *D. farinae* has evolved a method of ingesting large pieces of keratinized (dander) or sclerotized (cuticle) material. In the anterior midgut and possibly the caeca, these ingested particles are suspended in a flocculent mass of food (Fig. 24) which apparently undergoes intracellular digestion. This assumption is based on the presence of numerous degenerating cells which have been sloughed off into the gut lumen (Figs. 21 and 23) or are in the process of pinching off and degenerating before being lost from the epithelial lining (Fig. 22). These cells, both attached and free, have clear cytoplasmic regions which may be food vacuoles (Fig. 20). An extensive supply of rough endoplasmic reticulum, plus food vacuoles, may indicate an intracellular digestive process in the anterior midgut. On the other hand, food vacuoles have not been observed in the caecal cells, nor has particulate material been seen in the caecal lumen. This may suggest an extracellular digestive process. Furthermore, the presence of circular muscles (Fig. 25) surrounding the caeca may indicate that enzymes produced there are squeezed anteriorly to be made available for extracellular digestive processes in the midgut.

However, the digestive process may not be completed in the anterior midgut. It appears impractical for a midgut cell to engulf pieces of material as large and ragged as those seen in the gut lumen. Therefore it is suggested that some degree of extracellular digestion may occur in the posterior midgut of *D. farinae*. Prasse (1967) and Akimov (1971) have reported digestive processes in the post-colon of *Caloglyphus* and *Rhizoglyphus* respectively.

Prior to further consideration of extracellular digestion, it is necessary to point out that the function of the dorsal anterior midgut cells, other than their role of maintaining continuity of the digestive tract, is not clear. This area in insects is described as a site of peritrophic membrane production (Peters, 1969; Richards and Richards, 1971), but there is nothing in this study of *D. farinae* to indicate a similar function for this region. The ventral bands as well as all the posterior cells of the anterior midgut have cytoplasm which appears to be active (Figs. 20 and 24).

Considering the pieces of cuticle which are commonly found in the midgut, some form of protection for the midgut epithelium is appropriate. Consequently, there is the peritrophic membrane (PM) which envelops the food material as it is pushed through the valve between the anterior and posterior midgut (Wharton and Brody, 1972). It is difficult to determine the precise origin of the PM, but its components may be produced in different regions of the gut as

has been proposed for some insects (Smith, 1968). In *D. farinae*, situated between the microvilli and the contents of the anterior midgut lumen, is a band of electron-dense material (up to 4.5 microns thick) that may contribute to the formation of the peritrophic membrane in the posterior midgut (Fig. 24). There is also the peculiar laminated material which has sloughed off in the foregut (Fig. 17), which may be another component of the PM. It does seem clear, however, that the PM takes its final form at the juncture of the anterior and posterior midgut and is there consolidated into a sheet completely surrounding a food ball (Fig. 28). The PM remains evident around the feces in the hindgut as well (Wharton and Brody, 1972) and is ultimately excreted in a fecal pellet composed of 3 to 5 processed food balls.

The presence of a peritrophic membrane in the posterior midgut of *D. farinae* precludes any further intracellular digestion of particulate material from taking place. Furthermore, the posterior midgut epithelium has cells with extremely long, often densely packed microvilli (Figs. 26 and 27), and this may be the region of most active nutrient absorption as the greatest cell surface is offered here. These cells are typically replete with rough endoplasmic reticulum (Fig. 27). The presence of endoplasmic reticulum, in addition to multivesicular bodies, lysosomes, and other organelles typical of a secretory cell, suggests that extracellular digestion may be occurring in the posterior midgut of *D. farinae*. A few free cells, similar to those in the anterior midgut, have been observed in the posterior midgut, but outside of the peritrophic membrane (Fig. 28). Assuming that no food is available outside the PM, the function of these free cells is questionable.

The peritrophic membrane-wrapped fecal material then passes posteriorly down the hindgut where some degree of water resorption probably takes place. While it has been noted that the cuticle of the posterior hindgut has numerous pore canals, it is yet to be determined what form of water-regulatory mechanism the house-dust mite utilizes. The type of epithelium found here is unlike that of the water-resorptive epithelium in many insects (Oschman and Wall, 1969). The fecal pellet of *D. farinae* (containing 3 to 5 individual balls) is held together presumably by the mucous-like material which is often observed covering the hindgut cuticle (Fig. 29). The fecal pellets remain intact in air, but break up in mineral oil.

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Proceedings of the New York Entomological Society

(Meetings held in Room 129 of the American Museum of Natural History unless otherwise indicated.)

Meeting of March 7, 1972

President Howard Topoff presided; 11 members and 13 guests were present. Dr. Ivan Huber of Fairleigh Dickinson University was elected to Active Membership. Mr. Mitchell C. Miller of the University of Georgia was proposed for Active Membership and Mrs. Joseph A. Mele of Fairleigh Dickinson University was proposed for Student Membership.

PROGRAM. **Hymenopterous Venom and Human Allergies.** Mr. Richard Heckman, substituting for Dr. Allen Benton, both of Pennsylvania State University, made the address, showing slides and a brief movie.

The meeting was adjourned at 9:40 P.M.

JOAN DEWIND, *Sec.*

Meeting of March 21, 1972

The meeting was called to order by President Howard Topoff at 8:15 P.M. Ten members were present.

The minutes of the meeting of March 7, 1972 were approved as read.

Mr. Mitchell C. Miller was elected to Active Membership. Mr. Miller is with the Department of Entomology of the University of Georgia. Mrs. Joseph A. Mile, of Fairleigh Dickinson University, was elected to Student Membership.

The Rev. David Blair Stiffler was proposed for Active Membership and Mr. Alfred W. Bennett, of Fordham, for Student Membership.

PROGRAM. Mr. Ginter Ekis of the Department of Entomology, Rutgers University, was the speaker—his subject—"Digestive, Excretory and Reproductive Organs of Clerid Beetles." Schematic drawings of internal structures as well as outer forms were shown through color slides of both Clerinae and Korynetinae orders.

The next meeting will be held April 4, 1972. The guest speakers will be Miss Beverly Greenspan and Mr. Arthur Arnold of Rockefeller University. The topic will be "Biology of the African Driver Ant," including slides and film.

The meeting was adjourned at 9:20 P.M.

BETTY WHITE, *Asst. Sec.*

Meeting of April 4, 1972

The meeting was called to order by President Howard Topoff at 8:15 P.M. 11 members and 4 guests were present.

Rev. David Blair Stiffler was elected to Active Membership and Mr. Alfred W. Bennett of Fordham University to Student Membership. Dr. David Alsop of the Department of Biology, Queens College, and Dr. Karl Maramorosch were proposed for Active Membership. Sister Lois J. Keller, of Fordham University, was proposed for Student Membership. The Journal of the New York Entomological Society is now under the editorship of Dr. Karl Maramorosch, Program Director for Insect Physiology and Virology at Boyce Thompson Institute.

A letter of appreciation from Mrs. C. H. Curran on behalf of her late husband was read to the members of the Society by President Howard Topoff.

PROGRAM. The guest speakers of the evening were Miss Beverly Greenspan and Mr. Arthur Arnold of Rockefeller University: topic—"Biology of the African Driver Ant,"

including slides and films. Referring to earlier studies of Dr. Schneirla, Mr. Arnold described his research concerning predatory and migratory habits of *Daryllus nigricans*. Essentially, Miss Greenspan discussed the amount of prey in relationship to size of ants; also, the association of Staphylinid beetles to *Daryllus nigricans*.

The next meeting will be held April 18, 1972. The guest speaker will be Fr. Daniel J. Sullivan, S. J. The topic will be "Bermuda—The Islands Darwin Missed."

The meeting was adjourned at 9:38 P.M.

Betty White, *Asst. Sec.*

Meeting of April 18, 1972

The meeting was called to order by Dr. Howard Topoff, President, at 8:15 P.M. 16 members and 11 guests were present.

The minutes of the meeting of April 4, 1972, were approved as read.

Dr. Karl Maramorosch, Editor of the *Journal of the New York Entomological Society* and Program Director for Insect Physiology and Virology at Boyce Thompson Institute, and Dr. David Alsop, of the Biology Department of Queens College, were elected to Active Membership and Sister Lois J. Keller, of Fordham University, was elected to Student Membership.

A competition initiated by Dr. Topoff to identify the "Mystery Scientist" from a slide photo baffled all. The correct answer was not Darwin, as guessed, but Robert Buckbee (former Publications Business Manager) with a beard.

The audience's attention was directed to the "Scientific Supplement" of *The Saturday Review* of April 15th, which contains an article by Eleanor Ford on army ants and includes the escapades of our illustrious president.

PROGRAM. Father Daniel J. Sullivan, S. J., spoke on "Bermuda—The Islands Darwin Missed." With slides, maps, and charts he described geology, geography, flora, and fauna of these Atlantic islands.

The speaker at the meeting of May 2, 1972, will be Dr. William W. Metterhouse, of the New Jersey Department of Agriculture, on the "Control of the Gypsy Moth."

The meeting was adjourned at 9:45 P.M.

Joan DeWind, *Sec.*

Meeting of May 2, 1972

The meeting was called to order by President Howard Topoff at 8:15 P.M. 16 members and 14 guests were present.

The previous meeting's minutes were approved as read.

PROGRAM. Mr. William W. Metterhouse of the New Jersey Department of Agriculture spoke on "Control of the Gypsy Moth," describing principally biological controls and their use, illustrating the moths, their spread and damage, and his experimental laboratories at Trenton, which Mr. Metterhouse invited all to visit.

Dr. Sullivan announced the next speaker: Albert J. Poelzl, who, with slides, will illustrate the "World of Nature." This will be the last meeting until fall, and will include a "year-end party with refreshments."

After an extensive question period, the meeting was adjourned at 9:50 P.M.

Joan DeWind, *Sec.*

Meeting of May 16, 1972

The meeting was called to order by President Howard Topoff at 8:15 P.M. 17 members and 8 guests were present.

The minutes of the meeting of May 2, 1972 were approved as read.

PROGRAM. Fun, frivolity, and refreshments preceded speaker Albert J. Poelzl's spectacularly beautiful slide show entitled "The World of Nature."

At 9:45 P.M., the meeting was adjourned until next fall.

JOAN DEWIND, *Sec.*

Meeting of October 3, 1972

President Howard Topoff called the meeting to order at 8:15 P.M. 13 members and 15 guests were present.

The minutes of the meeting of May 16, 1972 were approved as read.

The following names were proposed for Active Membership: Glenn K. Morris, Assistant Professor of Zoology, Erindale College, Clarkson, Ontario; Dr. Diane Young, Department of Zoology, Auburn University, Auburn, Alabama; L. H. Rolston, Department of Entomology, Louisiana State University; Michael J. Bentivegna, Jr., Bethpage, Long Island. Owner of pest-control firm; Robert B. Hutt, Washington. Interested in systematics; Dr. Charles C. Porter, Biology Department of Fordham University. Interested in systematics of Hymenoptera, especially Ichneumonidae; Marion W. Boesel, Zoology Department, Miami University, Oxford, Ohio.

PROGRAM. Father Sullivan introduced the speaker of the evening, Dr. James B. Kring. Dr. Kring described research he is doing on the behavior of aphids, with special reference to their vision, particularly related to their flight habits; he illustrated his talk with slides. (An abstract follows.)

Father Sullivan announced that Edwin Way Teale, author and photographic illustrator of many books on nature, and Society Member, will be the speaker on October 17th.

The meeting was adjourned at 9:25 P.M.

JOAN DEWIND, *Sec.*

BEHAVIOR OF APHIDS AND THEIR VISION

Aphids or plant lice are polymorphic plant parasites of the family Aphididae. M. D. Leonard has recorded over 450 species from New York. Some can live on only one kind of plant while others can develop on many different species. In this area aphids overwinter as eggs or as parthenogenetic, viviparous females in protected environments. In the spring wingless parthenogenetic females hatch from the eggs. Progeny of these stem mothers, depending on the species, are winged or wingless. The wingless forms produce aphids that will be winged if they are crowded or if the host is deficient.

Winged aphids reared under crowded conditions reject the plant on which they develop and fly to the sky. After one or two hours' flight aphids return to plants and attempt to find a suitable host. In leaving plants they are attracted to shortwave light and avoid plants or yellow surfaces. When aphids are searching for a host, many avoid surfaces that reflect shortwave light and alight on soil, plants, or yellow objects. Few alight on plants surrounded by shortwave reflecting surfaces (e.g., aluminum). This behavior has been used to protect plants. Such responses are visual and could result from changes in the eye, the central nervous system, or both. Winged aphids have ocelli, simple (three facets), and complex (many facets) compound eyes. Wingless aphids lack ocelli and may have simple eyes, complex eyes, or both. The structure and probably the function of each of these is different. Pigment movement occurs in the complex compound eye and may be related to the changing behavior of these insects to short- and longwave light.

JAMES B. KRING

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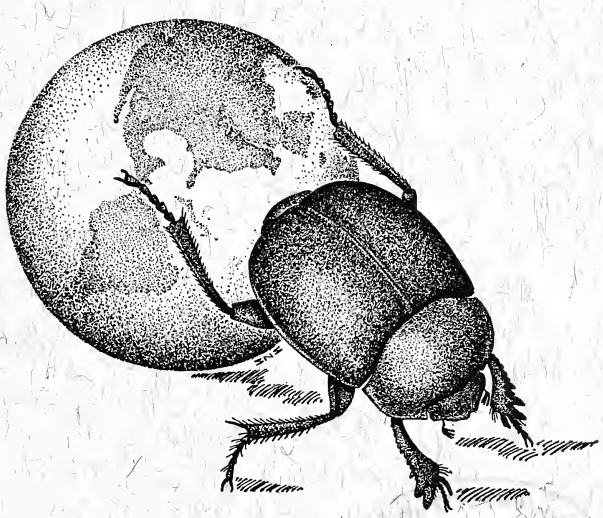

Devoted to Entomology in General

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CONTENTS

Aphids of New Jersey, A Few More Records (Homoptera: Aphididae)

MORTIMER D. LEONARD[1]

COLLABORATOR, AGRICULTURAL RESEARCH SERVICE,
U.S. DEPARTMENT OF AGRICULTURE, WASHINGTON, D.C.

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Abstract: At present, 242 species of aphids on 313 plants are known to occur in New Jersey. This paper is based on collections made in 1969, 1970, and 1971 and on several records omitted from my four previous papers on New Jersey aphids. Here are listed 52 species of aphids from 68 plants and records of five aphids and two food plants new to the state.

In New Jersey, 242 species of aphids on 313 plants are known to occur. This paper is based on collections made in 1969, 1970, and 1971 and on several records omitted from my four previous papers (Leonard, 1956; 1964; 1967; 1971) on New Jersey aphids. Here, I list 52 species of aphids from 68 plants. Five of the aphid and two of the food plant records are new to the state. The names of winged aphids collected from a yellow water-pan at Haddonfield (Leonard, 1972) are not included.

The aphid species are listed alphabetically by genus. An asterisk (*) indicates that the species was not included in the four previous papers. Detailed records of localities, dates, food plants, and collectors (indicated by initials) are given for each species. Records from the Co-operative Economic Insect Report (CEIR), published by the USDA Agricultural Research Service, are included. The following made collections:

H. W. Allen (HWA), USDA, Moorestown, N.J.
G. W. Angalet (GWA), USDA, Moorestown, N.J.
M. H. Brunson (MHB), USDA, Moorestown, N.J.
L. W. Coles (LWC), USDA, Moorestown, N.J.
Lemuel Craft (LC), Cornell University
W. H. Day (WHD), USDA, Moorestown, N.J.
L. D. DeBlois (LDD), N.J. Department of Agriculture, Trenton, N.J.
R. W. Fuester (RWF), USDA, Moorestown, N.J.
D. D. Leonard (DDL), Ridgewood, N.J.
M. D. Leonard (MDL), Washington, D.C.
F. N. Pagliaro (FNP), N.J. Department of Agriculture, Trenton, N.J.
L. L. Pechuman (LLP), Cornell University
S. W. Race (SWR), N.J. Coll. Agriculture
J. P. Reed (JPR), N.J. Dept. Agr., Trenton, N.J.

[1] Mail Address: 2480 16th Street, NW, Washington, D.C. 20009.

Mrs. Graham W. Rendell (GWR), Glen Rock, N.J.
E. A. Richmond (EAR), deceased, 14-VII-70, Moorestown, N.J.
Mary Rohwer (MR), Medford Lakes, N.J.
J. A. Stewart (JAS), USDA, Moorestown, N.J.
F. S. Stinson (FSS), N.J. Dept. Agriculture, Trenton, N.J.
H. L. Streu (HLS), N.J. Coll. Agriculture, New Brunswick, N.J.
H. E. Surface (HES), N.J. Dept. Agriculture
L. M. Vasvary (LMV), N.J. Coll. Agriculture, New Brunswick, N.J.
D. L. Winters (DLW), Haddonfield, N.J.

I am grateful to the specialists who identified the aphids. These are indicated by their initials:

Mortimer D. Leonard (MDL), Washington, D.C.
M. E. MacGillivray (MEM), Agriculture Canada, Fredericton, N.B., Canada
F. W. Quednau (FWQ), Environment Canada, Sillery, Quebec, Canada
A. G. Robinson (AGR), University of Manitoba, Winnipeg, Manitoba, Canada
L. M. Russell (LMR), ARS, USDA, Washington, D.C.
A. N. Tissot (ANT), University Florida, Gainesville, Florida

Again, Dr. S. G. Shetler, Dept. Botany, Smithsonian Institute, Washington, D.C., kindly named some of the plants. The plants are listed alphabetically by genus. Plant species not reported in previous lists are marked with an asterisk (*).

LIST OF APHIDS

Acyrthosiphon pisum (Harris), Pea Aphid. ". . . This aphid caused very little injury in NEW JERSEY." [in 1969 on alfalfa].—CEIR, 1970 (**20:** 139).

G. W. Angalet reported on populations in 1971: "The pea aphid for the third year in a row proved to be of no economic importance in New Jersey, Delaware, eastern Pennsylvania, eastern Maryland and southeastern New York. An occasional alfalfa field was encountered where pea aphid populations reached 200 aphids per sweep in late May and early June but this population does not seem to harm healthy alfalfa and the highest populations of aphids found were heavily parasitized by *Aphidius ervi ervi* Haliday and declined in numbers within a few days." (Angalet, 1971*a*.)

"The aphid populations during this quarter [July–September] remained at low levels in New Jersey, Delaware and eastern Pennsylvania until late September when there was a rapid increasing population. Parasitization of pea aphids was not an important factor during the past 3 months with most samples showing a percentage of less than 1%. Cloudy wet weather delayed the build-up of parasites that had occurred in past seasons. Predators were common in all of the alfalfa fields surveyed and in some fields were unusually abundant for this time of the year and had to be considered a factor in the control of the pea aphid population encountered." (Angalet, 1971*b*.)

Acyrthosiphon (*Aulacorthum*) *solani* (Kltb.), Foxglove Aphid. Ridgewood, 22-VI-69, on *Philadelphus* sp. (MDL, DDL, coll). In addition to those records

from Glen Rock reported by Leonard, 1971, the following collections were made by GWR:—on *Anthurium schezeriana*, 1-XII-67, 2 apterae;—II-68, a few on flower stalks;—on two hybrids of *Leliocattleya*, 4 apterae and nymph, 1-XII-67;—on the buds and flowers of the orchid hybrid, Pansy Orchid *Miltonidium* (*Miltonia* × *Onedium*), late November, 1970;—on *Hibiscus rosasinensis*, May, 1970, 1 alata and about 30 apterae and nymphs on young leaves, buds, and flower stalks;—on Gesneriads: August, September, 1970, *Streptocarpus* hybrid, 15 apterae and nymphs on flowers and flower stems; *Sinningia* "Dollbaby × *Gloxinia* "Pink Flake" and *Sinningia* "Cindy," 30 apterae and nymphs on flowers; *Sinningia eumorpha* × *Reichsteineria leucotricha*, a number of apterae and nymphs; *Gloxinia* hybrid in terranium and indoors, June, 1969, many apterae and nymphs on leaves; *Columnea perscrassa*, 1-XII-67, several apterae and nymphs; February, 1968, heavy on leaves, a few on flowers of *Columnea* hybrid "Mary Anne"; June, 1969, on the *Columnea* hybrid *Caryuga*.

Aphis craccivora Koch. Sommerville, 29-VI-69, on *Deutzia gracilis* (FSS coll MDL det with query); Fairton, 13-VIII-70, aptera and nymphs on *Asparagus plumosus* (GWA coll LMR det).

Aphis fabae Scopoli, Bean Aphid. Ridgewood:—VII-67, abundant on *Philadelphus* sp. (DDL coll); 22-V-69, moderate on *Philadelphus* sp. (MDL, DDL, DLW coll); 28-VI-70, on *Rudbeckia hirta* (DDL coll MacG det); Haddonfield, 14-VI-69, a number of alatae, apterae, and nymphs on stems of *Viburnum opulus* var. *roseum* (MDL, DLW coll); Moorestown, 24-V-68, many on *Euonymus alatus* and *E. atropurpureus* (EAR coll FWQ det).

Aphis gossypii Glover, Cotton or Melon Aphid. Moorestown:—XI-66, common on *Hibiscus* sp. in greenhouse (WHD coll); 26-V-68, about 35 alatae, apterae, and nymphs on *Celastrus scandens* (EAR coll).

Aphid illinoisensis Shimer, Grapevine Aphid. Ridgewood, 22-VI-69, a few on cultivated grape (MDL, DDL, DLW coll); 3 & 4-VII-70, two long tendrils of same grapevine heavily infested (DDL coll).

Aphis nerii B. de F., Oleander and Milkweed Aphid. Siklerville, 22-X-69, on *Asclepias* sp. (RWF coll).

Aphis pomi de Geer, Apple Aphid. Sommerville, 29-VI-67, heavy on tips of curled leaves of *Chaenomeles japonica* (FSS coll); Moorestown, 14-VII-67, heavy on terminals of *C. japonica* (HWA coll); Haddonfield, 16-VI-69 and mid-V-70, light on two terminals of *C. speciosa* with many ants (MDL coll).

"Abundant in New Jersey, *D. plantaginea* and *A. pomi* curled leaves in many commercial apple orchards by early May [1970]. Aphidices in early cover sprays reduced numbers so that injury was not significant."—CEIR, 1971 (**21:** 219).

". . . winged forms and nymphs continue abundant on terminal leaves in many southern area apple orchards. (Ins.-Dis. Newsltr.)."—CEIR, 1971 (**21:** 433).

Aphis rumicis L., Dock Aphid. Moorestown, 19-XI-69, a few on *Rumex crispa* (WHD coll); Haddonfield, 20-V-69, several on *Rumex* sp. (WHD coll).

Aphis spiraecola Patch, Spiraea Aphid. Haddonfield: late May 1970, on *Spiraea Vanhouttei*; many shoots encrusted with aphids; reported to be abundant early in season in 1971, scarce by mid-season (MDL coll).

Brachycaudus maidiradicis (Forbes), Corn Root Aphid. "Corn Root Aphid (*Anuraphis maidiradicis*) was found for the first time on corn in NEW JERSEY on 8-VIII-69, in a field near Blawenburg, Somerset County:"—CEIR, 1970 (**20:** 121).

Haddonfield, 9-X-70, on roots of grass (MDL coll P. W. Mason det); 25-X-70, many on roots of a single *Plantago major* in a lawn (DLW coll MDL det). Attended by ants, *Acanthomyops claviger* (Roger).

Brevicoryne brassicae (Linnaeus), Cabbage Aphid. ". . . was light and easy to control in NEW JERSEY during spring."—CEIR, 1970 (**20:** 165).
". . . Light to moderate on cabbage in several Burlington County fields. (Ins.-Dis. Newsltr.)."—CEIR, 1971 (**21:** 451).

Calaphis betulaecolens (Fitch). Red Lion, 30-VI-66, on *Betula populifolia* (LLP coll FWQ det); Wycoff, 1-VII-67, on *Betula* sp. (MDL, DDL coll FWQ det).

Calaphis betulella Walsh. Haddonfield, 6-VI-69, on *Betula populifolia* (DLW coll FWQ det).

**Calaphis* (*Calipterinella*) *callipterus* (Hartig). On *Betula pendula*—Ridgewood: 21-VI-69, 1 aptera (MDL, DDL coll FWQ det);—VI-69, 30 alatae, apterae, nymph (DDL coll FWQ det); 19-X-69, 2 apterae (DDL coll FWQ det). On *B. populifolia*.—Haddonfield: 6 and 11-VI-69, several apterae, nymphs, alatae (DLW coll FWQ det); 23-V-70, 18 specimens (MDL, DLW coll FWQ det); Medford Lakes: 16-V-64, 3 specimens (MR coll FWQ det).

**Calaphis leonardi* Quednau. On *B. populifolia*.—Medford Lakes, 16-V-64, 19 specimens (MR coll FWQ det). Haddonfield, from one tree: 6-VI-69, 4 alatae (DLW coll FWQ det); 15 to 20-VI-69, 2 alatae (MDL coll FWQ det); 23-V-70, 13 specimens (MDL, DLW coll FWQ det); 21-V-70, 5 specimens (MDL coll FWQ det); 5-VII-70, about 50 alatae, a few immature alatae (DLW coll); 2-VIII-70, no aphid could be found. On *Betula pendula*—Ridgewood, 21-VI-69, 9 alatae (DDL, MDL, DLW coll FWQ det). On *Betula* sp.—Franklin Lakes, 16-X-66 (MDL, LWC coll FWQ det).

**Calaphis neobetulella* Quednau. Haddonfield, 25-V-69, 1 alata on *Betula* sp. (DLW coll FWQ det).

Capitophorus elaeagni (Del Guercio), Oleaster, Thistle Aphid. Haddonfield, a few apterae on *Polygonum persicaria* (MDL coll MDL det). Ridgewood, 19-IX-70, 2 apterae, 1 nymph on *Polygonum* sp. (DDL coll).

Capitophorus hippophaes (Walker), Polygonum Aphid. Haddonfield, 15 and 16-X-70, apterae, nymphs, scarce on a few leaves of several large plants of

Polygonum cuspidatum (MDL coll), attended by ants, *Prenolepis imparis* (Say) and *Lasius neoniger* Emery.

Cinara pinea (Mordvilko). Moorestown, 11-V-68, 2 apterae on *Pinus sylvestris* (EAR coll ANT det).

Cuernavaco (*Brachycorynella*) *aspargi* (Mordv.), Asparagus Aphid. This little aphid was described by Mordvilko in 1928 as *Brachycolus asparagi.* Apparently it is not a common aphid. Börner (1952) reported that it occurred sporadically in Central Europe. Szelegiewicz (1961) redescribed the species and stated that it is known from the USSR and southern Poland. In a letter, dated March 4, 1970, Dr. D. Hille Ris Lambers, Bennekom, Netherlands, stated that although asparagus is widely grown in his country, he has been unable to find the aphid there. Likewise, at about the same time, Dr. V. F. Eastop, British Museum (Natural History), London, wrote that he had never seen this aphid even as a student when he had made observations on the asparagus beetle.

In North America, the asparagus aphid was first reported in 1970: "AN APHID (*Brachycolus asparagi* Mordvilko)—NEW YORK—Single alate collected on redtop (*Agrostis alba*) at Orient, Long Island, July 20, 1969, by R. Latham. Determined by F. W. Quednau. This is the first record of *B. asparagi* in North America. This aphid is native to the Mediterranean area and eastern Europe. Asparagus is the only recorded host. Feeding by *B. asparagi* causes seedlings to shrivel or die, and is responsible for severe dwarfing of older plants. (Leonard). NEW JERSEY—Aphids first noted on asparagus plants in Rutgers University horticultural greenhouse at New Brunswick, Middlesex County, in August 1969. Specimens collected November 20, 1969, at this location by J. P. Reed determined by F. W. Quednau. This is a new State record and first known infestation of *B. asparagi* in North America. Aphids found nearby on 2 horticultural farms at East Brunswick in late August and early September 1969. Aphids caused severe rosetting of brush, and damaged young growth, resulting in shortening of internodes. No chlorosis was observed. Aphids fed on cladophylls (modified leaves) and under bracts. Plants in greenhouse and on university farms sprayed during August and September. Last import of asparagus material from Europe (England and Holland) made in 1959. As of February 16, 1970, no *B. asparagi* or recent injury observed in any of the horticultural greenhouses. (Race)."—CEIR, 1970 (**20:** 156).

Other records from New Jersey soon followed:
"ASPARAGUS APHID (*Brachycolus asparagi*)—NEW JERSEY—Nymphs and winged forms stunted and rosetted asparagus and weeds at New Brunswick, Middlesex County. Also collected in Burlington County for a new county record. Determined by L. M. Russell. (Ins.-Dis. Newsltr.)."—CEIR, 1970 (**20:** 539).

"CEIR **20**(31): 539—ASPARAGUS APHID (Brachycolus asparagi)—NEW JERSEY—. . . stunted and rosetted asparagus and weeds . . . should read . . .

stunted and rosetted asparagus and *volunteer asparagus plants . . .* "—CEIR, 1970 (**20:** 561).

"ASPARAGUS APHID (*Brachycolus asparagi*)—NEW JERSEY—Collected on asparagus in Monmouth, Ocean, Cumberland (Centerton), and Gloucester (Swedesboro and Mullica Hill) Counties. Determined by L. M. Russell. These are new county records. (Ins.-Dis. Newsltr.). Specimens collected July 30 in Salem County determined by L. M. Russell for new county record. Now known to occur in 7 counties, including Middlesex and Burlington. (PPD)."—CEIR, 1970 (**20:** 584).

"ASPARAGUS APHID (*Brachycolus asparagi*)—NEW JERSEY—Adults taken from wild asparagus at Rocky Hill, Somerset County, by R. R. Jackowski August 6. Determined by L. M. Russell. This is a new county record. (PPD)." —CEIR, 1970 (**20:** 627).

"ASPARAGUS APHID (*Brachycolus asparagi*)—NEW JERSEY—Eggs on leaves of asparagus plants at Somerset, Somerset County. Found by J. P. Reed October 1, 1970. First report of eggs laid by this aphid in North America. Eggs small and shiny black. (Race)."—CEIR, 1970 (**20:** 737).

In 1971, the occurrence of this aphid in North America was summarized: "ASPARAGUS APHID (*Brachycolus asparagi*) was first identified from NEW JERSEY in February 1970 although asparagus research plots had been treated in August 1969 to control damaging aphid populations, which undoubtedly were this species. It first appeared during late June in experimental plantings at East Brunswick, Middlesex County; damage was severe enough to warrant control by early July. This aphid was found in Monmouth County and elsewhere in Middlesex County by July 23, in Burlington, Ocean, Comberland, and Gloucester Counties by August 7, and in Salem, Mercer, and Somerset Counties by August 14. Severe stunting, rosetting of brush, and stickiness from much honeydew were evident in many heavily infested fields. Overwintering eggs, probably of this species, were first observed on brush at Somerset, Somerset County, on October 1. By late August many aphids in many fields were parasitized. Middlesex County by July 23, in Burlington, Ocean, Cumberland, and Gloucester County fields. Asparagus aphid was found on asparagus in Bucks and Montgomery Counties for a new State record in PENNSYLVANIA."—CEIR, 1971 (**21:** 205). In addition it was collected in New York,—CEIR, 1970 (**20:** 773) Virginia,—CEIR, 1970 (**20:**759), and Pennsylvania,—CEIR, 1970 (**20:** 658, 699).

Angalet (1971*a*) reported on the occurrence of the aphid in New Jersey in 1971: "The asparagus aphid was again found in Burlington, Salem, Gloucester and Cumberland Counties, New Jersey, during the quarter. As in 1970 a few asparagus bushes were destroyed by the aphid but the aphid again disappeared before there was a build-up of economic populations. Some growers did spray

against the aphid but in the great majority of the asparagus fields observed no insecticidal treatments were found to be necessary. The primary aphid parasites, *Diaeretiella rapae* (McInt.) and *Lysephlebius testaceipes* (Cress.) were recovered from all of the asparagus fields investigated. . . . Disease was a greater factor in the control of the asparagus aphid this year than during 1970. . . . Predators were found to be abundant wherever the asparagus aphid was found and predation, as during 1971, must be considered the major factor in the control of the asparagus aphid. Even on asparagus bushes which had light populations of the aphid, several species of predators in all stages were common . . ."

Several additional records of the occurrence of the asparagus aphid were reported in 1971 and include records from Delaware,—CEIR, 1971 (**21:** 709) and Maryland,—CEIR, 1971 (**21:** 660) as well as those from New Jersey—CEIR, 1971 (**21:** 376, 473, 512, 548, 569, 633, 709).

Dactynotus ambrosiae (Thomas), Brown Ambrosia Aphid. Centerton, light infestation in experimental plots of head lettuce, at Rutgers University South Jersey Vegetable Research Farm, 27-X-69 (JPR coll FWQ det). Haddonfield, 24-IX-64, a few on *Ambrosia trifida* (MDL coll MDL det). Crosswicks, 9-X-69, several on *Ambrosia trifida* (RWF coll).

**Drepanosiphum platanoides* (Schrank), Sycamore Maple Aphid. Cinnaminson, common on *Acer pseudoplatanus*, 2-VI-71 and abundant on same tree, 27-VI-71, (LWC coll).

Dysaphis plantaginea (Passerini), Rosy Apple Aphid. ". . . Numbers were light in most NEW JERSEY areas [in 1969 on apples]; injury was insignificant."—CEIR, 1970 (**20:** 198). Abundant in 1970 (see *Aphis pomi* above).

Dysaphis tulipae (B de F), Tulip Bulb Aphid. Saddlebrook, 9-XI-69, on stored wedgewood iris bulbs (LMV coll). First record since 1942.

Euceraphis deducta Baker. Haddonfield, on *Betula populifolia*: 21-V-70 (MDL coll FWQ det); 23-V-70 (MDL, DLW coll FWQ det).

Euceraphis lineata Baker. On *Betula populifolia* (MDL, DDL coll FWQ det): Summit, 22-VI-63; Haddonfield, 5-VII-70.

Euceraphis punctipennis (Zett.). Ridgewood, 21-VI-69, 3 alatae on *Betula pendula* (MDL, DDL, DLW coll); Haddonfield, 6, 15-VI-69 (DLW coll).

Hamamelistes spinosus Shimer. Haddonfield, 25-V-69, 81 alatae and 10 apterae, on *Betula populifolia* (DLW coll FWQ det).

Hyadaphis foeniculi (Passerini), Honeysuckle and Parsnip Aphid. Ridgewood, 20-X-62, many on wild *Daucus carota* (MDL, DDL coll).

Macrosiphoniella sanborni (Gillette), Chrysanthemum Aphid. Moorestown, 30-VI-69, scarce on garden "mums" (HWA coll).

Macrosiphum sp. (possibly new). Sutton Road, Lebanon, RD # 2, males, oviparae, 1 apterous vivipara on *Erigeron canadensis* (DDL coll AGR det). '71

Macrosiphum euphorbiae (Thomas), Potato Aphid. Glen Rock,—VI-69, abundant on tall, bearded iris and *Dicentra* sp. (MR coll). Ridgewood, 22-VI-69,

2 alatae, 2 apterae on *Philadelphus* sp. (MDL, DDL, DLW coll); on *Lithospermum* sp: 1 alata, 1 aptera, 22-VI-69 (MDL, DDL, DLW coll), many, in all stages 21-VI-71 (DDL coll); on *Rhododendron* sp. (DDL coll) and Rose (DDL coll MacG det), 20-VI-70. Moorestown, 30-VI-69, many on *Asclepias* sp., several on *Iris* sp. and *Ipomoea purpurea* (WHD coll). Centerton, 29-X-69, light infestation of all stages on head lettuce (JPR coll). Swedesboro, 5-VI-67, alatae, apterae, and nymphs on *Asparagus officinalis* (MHB coll LMR det).

Macrosiphum rosae (Linnaeus), Rose Aphid. Moorestown, 16-X-69, about 25 apterae, nymphs on one rose stem (MDL coll). Haddonfield, scarce on cultivated rose between 1969 and 1971 (DDL).

**Masonaphis lambersi* MacGillivray. Ridgewood, 20-VI-70, on *Rhododendron* sp. (DDL coll MacG det).

Masonaphis pepperi MacGillivray. New Lisbon, 15-VI-70, about 4 apterae, nymphs on cultivated *Vaccinium corymbosum* (Marucci coll MacG det).

**Masonaphis rhokalaza* (Tissot & Pepper). Ridgewood (MacG det)—on *Rhododendron* spp: 4-VIII-68 (DDL coll), 22-VI-69. (MDL, DDL, DLW coll), 20-VI-70 (DDL coll)—on wild *Azalea* sp., 22-VI-69 (MDL, DDL, DLW coll).

**Monellia hispida* Quednau. Haddonfield, (MDL coll TLB det): 30-V-47, 1 alata on *Carya* sp.; 16 to 30-IX-62, 1 alata in yellow water-pan.

Myzocallis melanocera Boudreaux & Tissot. Princeton, 19-V-64, several on *Quercus* sp. (LWC coll).

Myzocallis punctata (Monell), Clear-winged Oak Aphid. Princeton, 19-V-64, several on *Quercus* sp. (LWC coll).

Myzocallis ulmifolii (Monell). See *Tinocallis ulmifolii* (Monell).

Myzus persicae (Sulzer), Green Peach Aphid. Glen Rock (GWR coll FWQ det):—II-68, on *Columaea percrassa*; -VIII, IX-70, on flowers of *Hibiscus rosa-sinensis cooperi*. Moorestown: (WHD coll).—11-XI-69, a few on Chinese cabbage—19-XI-69, 7-XII-69, on leaves of *Rumex crispus*—18-XII-69, about 30 apterae, nymphs on red clover; (EAR coll).—5-XI-69, 1 aptera, 2 nymphs, 1 immature alata, on cultivated *Chrysanthemum* sp.—19-V-70, 2 apterae, 5 nymphs on *Euonymus alatus*. Centerton, 14 alatae, 15-IX-68; 16 alatae, 21-IX-68, in yellow water-pan in a squash field (SRR coll). Jacobstown, 17-IV-70, apterae and nymphs on *Asparagus officinalis* (ET coll LMR det). New Brunswick 21-IV-71, on greenhouse tomatoes, extremely difficult to control (SRR coll); 11-XI-71, on greenhouse chrysanthemums, possibly the number one problem in growing potted chrysanthemums. Hackettstown, 11-XI-71, a low infestation on greenhouse chrysanthemums (HES coll).

Reports of the species in CEIR for the period 1969–1971 are summarized as follows:

1969—"GREEN PEACH APHID (*Myzus persicae*) started to build up on all vegetable crops in NEW JERSEY during late spring and early summer.

Midsummer rains and a fungus disease kept this pest in check the rest of the season. Generally, populations and damage were much lighter than in previous years. Incidence of mosaic type viruses transmitted by this species was generally much lighter than in past years."—CEIR 1970 (**20:** 167). ". . . was typically abundant without noticeable injury on stone fruits in the spring."—CEIR, 1970 (**20:** 199).

1970—". . . In NEW JERSEY it damaged a sweetpotato planting in Burlington County during late July; by August 7 it was eliminated by heavy numbers of *Hippodamia convergens* (convergent lady beetle)."—CEIR, 1971 (**21:** 205). "Abundant in many peach orchards in southern NEW JERSEY, many leaves were cupped by May 15 due to *M. persicae* feeding. Numbers declined by early July due to widespread migrations to alternate hosts. No lasting injury to peach occurred."—CEIR, 1971 (**21:** 220). "This pest was troublesome and damaging to eggplant in many Cumberland and Gloucester County, NEW JERSEY, plantings by late July. Thousands of winged forms were observed hovering above plants in one field near Vineland on July 29. By mid-August, adequate rainfall helped reduce populations to more manageable levels. Populations became heavy by late July in New Jersey. Buildup was partly due to lower than average early summer rainfall."—CEIR, 1971 (**21:** 197).

1971—"*Myzus persicae* (green peach aphid) winged forms on eggplant, pepper, and tomato seedlings throughout State; nymphs abundant beneath leaves."—CEIR, 1971 (**21:** 431) "Potentially heavy population of *M. persicae* on eggplant indicated. Winged forms observed on potato leaves in several Burlington and Salem County fields."—CEIR, 1971 (**21:** 450). "Heavy damaging foliage of potato planting near Lumberton, Burlington County."—CEIR, 1971 (**21:** 547).

Nearctaphis bakeri (Cowen), Clover Aphid. Moorestown, 18-VIII-69, about 40 apterae, nymphs on red clover (WHD coll).

Neosymydobius annulatus Koch. Haddonfield, 15 to 20-VI-69, on *Betula populifolia* (MDL coll).

Ovatus crataegarius (Walker), Mint Aphid. Haddonfield, 14-VI-69, scarce, on spearmint (DLW coll).

Periphyllus californiensis Shinji, California Maple Aphid. Trenton, 6-V-64, heavy on leaves and twigs of *Acer palmatum* var. *dissectum* (FNP coll MDL det). This is the collection that Leonard recorded in CEIR, 1969 (**19:** 26). Although it is the first record from New Jersey, Essig (1952) records it also from California, Washington, Oregon, New York, Washington, D.C., Pennsylvania. Takahashi (1919) described the species from *A. palmatum.*

Periphyllus lyropictus (Kessler), Norway Maple Aphid. Haddonfield, 15-VI-69, moderate on *Acer platanoides,* shade trees in the town (MDL coll).

Phyllaphis fagi (Linnaeus) Haddonfield, 213 Rhodes Ave., 15-VI-69, abundant on *Fagus sylvatica nigra*; some leaves heavily infested mid-May 1970; few

aphids mid-October 1970, mid-May and late October, 1971 (MDL coll MDL det).

Pleotrichophorus glandulosus (Kaltenbach). Haddonfield, 18-X-70, scarce, on a few small *Artemisia vulgaris* (MDL coll MDL det).

Prociphilus erigeronensis (Thomas), White Aster Root Aphid. Haddonfield, 20-VI-69, on the roots of *Artemisia vulgaris* (DLW coll).

Rhopalosiphum maidis (Fitch), Corn Leaf Aphid. ". . . Counts were generally light [1969] in NEW JERSEY and not so troublesome as in recent years except in several Camden County fields."—CEIR, 1970 (**20:** 110).

Therioaphis maculata Buckton, Spotted Alfalfa Aphid. Surveys for this species have been made in New Jersey since 1966. In 1969, spotted alfalfa aphid was found in only three of seven alfalfa fields surveyed in Cumberland and Gloucester Counties, in October and November. The highest population was 20 aphids per 100 sweeps. Early survey records suggested that the aphid did not overwinter in New Jersey. However, in 1971 aphids were found as early as April 20, on alfalfa at Medford (an average of 1 per 100 sweeps) and for the first time were found as far north as Blairtown and Hope in Warren County by July 17. ". . . There is no reason to believe that the spotted alfalfa aphid cannot continue to extend its range northward if it can overwinter in northern New Jersey."—(Angalet, 1971*b*).

Therioaphis trifolii (Monell), Yellow-Clover Aphid. This aphid was rare in May, 1971 in New Jersey and was found only in five of twenty fields surveyed in central and southern part of the State. Populations remained low between July and September. ". . . The dominant parasite of the yellow clover aphid in New Jersey continued to be *Praon exsoletum palitans* which made up more than 90% of the parasite collections made during the Quarter. There was a slight increase in the number of *Trioxys complanatus* during August and *Aphelinus semiflavus* became rare. One of the clover fields from which the 3 species of parasites were recovered was in Warren County in north New Jersey proving that these parasites of the yellow clover aphid as well as the spotted alfalfa aphid are present throughout the state and were present in New Jersey on the yellow clover aphid prior to the establishment of the spotted alfalfa aphid in New Jersey during 1966." (Angalet, 1971*b*).

LIST OF FOOD PLANTS

Acer palmatum var. *dissectum* (Japanese Red Maple)
  Periphyllus californiensis
Acer platanoides (Norway Maple)
  Periphyllus lyropictus
**Acer pseudoplatanus* (Sycamore Maple)
  Drepanosiphum platanoides
Alfalfa—see *Medicago sativa*
Ambrosia trifida (Giant Ragweed)
  Dactynotus ambrosiae
Anthurium schezeriana
  Acyrthosiphon (*Aulacorthum*) *solani*
Apple—see *Malus sylvestris*
Artemisia vulgaris (Mugwort)
  Pleotrichophorus glandulosus
  Prociphilus erigeronensis
Asclepias sp. (Milkweed)
  Aphis nerii

Macrosiphum euphorbiae
Asparagus Fern—see *Asparagus plumosus*
Asparagus officinalis (Garden Asparagus)
Cuernavaca asparagi
Macrosiphum euphorbiae
Myzus persicae
**Asparagus plumosus* (Fern Asparagus)
Aphis craccivora
Cuernavaca asparagi
Macrosiphum euphorbiae
Myzus persicae
Azalea sp.
Masonaphis rhokalaza
Betula sp.
Calaphis betulaecolens
Calaphis callipterus
Calaphis leonardi
Calaphis neobetulella
Betula pendula (White Birch)
Calaphis leonardi
Betula populifolia (Gray or Yellow Birch)
Calaphis betulaecolens
Calaphis betulella
Calaphis callipterus
Calaphis leonardi
Euceraphis deducta
Euceraphis lineata
Hamamelistes spinosus
Neosymydobious annulatus
Birch, White—see *Betula pendula*
Birch, Gray or Yellow—see *Betula populifolia*
Bittersweet—see *Celastrus scandens*
Blackeyed Suzan—see *Rudbeckia hirta*
Bleedingheart—see *Dicentra*
Blueberry, Highbush—see *Vaccinium corymbosum*
Brassica chinensis (Chinese Cabbage)
Myzus persicae
Brassica oleracea capitata (Cabbage)
Brevicoryne brassicae
Cabbage, Chinese—see *Brassica chinensis*
Cabbage—see *Brassica oleracea capitata*
Carrot, Wild—see *Daucus carota*
Capsicum frutescens
Myzus persicae
Celasteus scandens (Bittersweet)
Aphis gossypii
Chaenomeles japonica (Flowering Crab)
Aphis pomi
Chaenomeles speciosa
Aphis pomi
Chrysanthemum sp.
Macrosiphoniella sanborni
Myzus persicae
Columnea hybrids
Acyrthosiphum (*Aulacorthum*) *solani*
Columnea percrassa
Acyrthosiphon (*Aulacorthum*) *solani*
Myzus persicae
Corn—see *Zea mays*
Cucurbita maxima (Squash)
Myzus persicae
Daucus carota (Wild Carrot)
Hyadaphis foeniculi
Deutzia gracilis
Aphis craccivora
Dicentra sp. (Bleedingheart)
Macrosiphum euphorbiae
Dock—see *Rumex*
Eggplant—see *Solanum melogena*
Erigeron canadensis (Horseweed Fleabane)
Macrosiphum sp.
Euonymus alatus (Winged Euonymus)
Aphis fabae
Myzus persicae
Euonymus atropurpureus (Eastern Wahoo)
Aphis fabae
Fagus sylvatica nigra
Phyllaphis fagi
Giant Ragweed (*Ambrosia trifida*)
Gloxinia hybrid
Acyrthosiphon (*Aulacorthum*) *solani*
Grape—see *Vitis*
Grass—see *Brachycaudus maidiradicis*
Gromwell—see *Lithospermum*
Head Lettuce—see *Lactuca sativa capitata*
Hibiscus sp.
Aphis gossypii
Hibiscus rosa-sinensis (Rose-of-China)
Acyrthosiphon (*Aulacorthum*) *solani*
Myzus persicae
Horseweed Fleabane—see *Erigeron canadensis*
Ipomoea batata (Sweetpotato)
Myzus persicae
Ipomoea purpurea (Morningglory)
Macrosiphum euphorbiae
Iris sp.
Dysaphis tulipae
Macrosiphum euphorbiae

Lactuca sativa capitata (Head Lettuce)
Dactynotus ambrosiae
Macrosiphum euphorbiae
Leliocattleya hybrid
Acyrthosiphon (*Aulacorthum*) *solani*
Lithospermum sp. (Gromwell)
Macrosiphum euphorbiae
Lycopersicon esculentum (Tomato)
Myzus persicae
Malus sylvestris (Apple)
Aphis pomi
Dysaphis plantaginea
Maple, Japanese Red—see *Acer palmatum dissectum*
Maple, Norway—see *Acer platanoides*
Maple, Sycamore—see *Acer pseudoplatanus*
Medicago sativa (Alfalfa)
Acyrthosiphon pisum
Therioaphis maculata
Mentha spicata (Spearmint)
Ovatus crataegarius
Milkweed—see *Asclepias*
Miltonidium hybrid
Acyrthosiphon (*Aulacorthum*) *solani*
Mockorange—see *Philadelphus*
Morningglory—see *Ipomoea purpurea*
Mugwort—see *Artemisia vulgaris*
Oak—see *Quercus*
Peach—see *Prunus persica*
Pepper—see *Capsicum frutescens*
Philadelphus sp. (Mockorange)
Aphis fabae
Acyrthosiphon (*Aulacorthum*) *solani*
Macrosiphum euphorbiae
Pine, Scotch—see *Pinus sylvestris*
Pinus sylvestris (Scotch Pine)
Cinara pinea
Plantago major
Brachycaudus maidiradicis
Polygonum sp. (Smartweed)
Capitophorus elaeagni
Polygonum cuspidatum
Capitophorus hippophaes
Polygonum persicaria (Heartsease)
Capitophorus elaeagni
Potato—see *Solanum tuberosum*
Prunus persicae (Peach)
Myzus persicae
Quercus sp. (Oak)
Myzocallis melanocera
Myzocallis punctata
Red Clover—see *Trifolium pratense*
Rhododendron sp.
Macrosiphum euphorbiae
Masonaphis lambersi
Masonaphis rhokalaza
Rosa sp.
Macrosiphum euphorbiae
Macrosiphum rosae
Rudbeckia hirta (Blackeyed Suzan)
Aphis fabae
Rumex sp. (Dock)
Aphis rumicis
Rumex crispa (Curled Dock)
Aphis rumicis
Myzus persicae
Sinningia eumorpha × *Reichsteineria leucotrichia*
Acyrthosiphon (*Aulacorthum*) *solani*
Sinningia × *Gloxinia*
Acyrthosiphon (*Aulacorthum*) *solani*
Solanum melogena (Eggplant)
Myzus persicae
Solanum tuberosum (Potato)
Macrosiphum euphorbiae
Myzus persicae
Spiraea Vanhouttei
Aphis spiraecola
Streptocarpus hybrid
Acyrthosiphon (*Aulacorthum*) *solani*
Smartweed—see *Polygonum*
Spearmint—see *Mentha spicata*
Squash—see *Cucurbita maxima*
Tomato—see *Lycopersicon esculentum*
Trifolium pratense (Red Clover)
Myzus persicae
Nearctaphis bakeri
Therioaphis trifolii
Sweetpotato—see *Ipomoea batata*
Tomato—see *Lycopersicon esculentum*
Vaccinium corymbosum (Highbush blueberry)
Masonaphis pepperi
Viburnum opulus var. *roseum*
Aphis fabae
Vitis sp. (Grape)
Aphis illinoisensis
Zea mays
Brachycaudus maidiradicis

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Revision of the Schizomida (Arachnida)

J. Mark Rowland
Department of Biology, and The Museum, Texas Tech University,
Lubbock, Texas

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Abstract: The family group and generic nomenclature of the arachnid order Schizomida are reviewed. A new subfamily is created, one genus synonymized, and the generic status of African species corrected. All family group and generic taxa are diagnosed, and a key to the extant subfamilies and genera is provided.

SYSTEMATIC HISTORY

Currently there are two familial and nine generic names applied to the order Schizomida. The purpose of this paper is to examine the applicability and usage of these names.

Calcitronidae and its two monotypic genera are wholly extinct and known only from Pliocene calcite deposits in Arizona. The works of Petrunkevitch (1945, 1955) and Pierce (1950, 1951) provide all the information available on these taxa.

The largely extant family Schizomidae has seven generic names applied to it. *Calcoschizomus* Pierce (1951) is apparently wholly extinct, known only from the same deposits as the Pliocene calcitronids. A summary of the history and the origin of the names of these taxa will clarify their usage.

Cambridge (1872) described the first schizomid and erected for it the family Tartarides, genus *Nyctalops*, and trivial name *crassicaudata*. In this work he also described *N. tenuicaudata*. The latter name was subsequently removed to synonymy by Pocock (1900) on the basis that *N. tenuicaudata* was actually the female of *N. crassicaudata*. Evidence is convincing that this revision is sound, although Pocock (1893) had earlier assigned *N. tenuicaudata* to another genus. Further, Cook (1899), by authority of first revisor, designated *crassicaudata* as type of the genus.

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Previous to Pocock's work Thorell (1888) elevated Cambridge's family Tartarides to tribal status and introduced the new family name Schizonotoidae. He proved that the name *Nyctalops* is a junior homonym and had been previously occupied (Hagler, 1832). In its place he provided *Schizonotus*, the nominate genus of Schizonotoidae. The spelling of the latter family name was emended to Schizonotidae by Pocock (1893). The work of Cook (1899) shows that the name *Schizonotus* is also a junior homonym, being preoccupied (Ratzeburg, 1852). In its place he used the name *Schizomus*. For the family name Schizonotidae, which was based on the junior homonym, he used the new family name Hubbardiidae, which contained a new nominate genus *Hubbardia*, however the type genus remained *Schizomus*.

Thorell (1889) erected the new genus *Tripeltis* on the basis of two new species, *T. grassii* and *T. cambridgei*, the former being originally designated as type species of the genus. The work of Cook (1899) however, shows that *Tripeltis* is a junior homonym, being previously occupied (Cope, 1886). For *Tripeltis* he provided the name *Triplomus*. Cook's revision does not stand, however, since Kraepelin (1899) offered the name *Trithyreus* for *Tripeltis* for similar reasons, just one month before Cook.

Cook's (1899) work includes data on two important schizomids. The first, and the main point of his paper, was the description of the new genus and species *Hubbardia pentapeltis*, however Hansen and Sorensen (1905) dispelled the criteria for generic distinction of this species and placed it with *Trithyreus*. Second, he mentioned a new animal which he had presented at a meeting of the Entomological Society of Washington two years previously. A printed description of *Artacarus liberiensis* never appeared under his authorship and, consequently, it was treated as a *nomen nudum* by Kraepelin (1897) and Hansen and Sorensen (1905). Kraus (1960) has located the original type series and has described the species and placed it in *Schizomus*.

Of *Nyctalops* Cambridge, *Schizonotus* Thorell, *Schizomus* Cook, *Artacarus* Cook, *Tripeltis* Thorell, *Triplomus* Cook, *Trithyreus* Kraepelin, and *Hubbardia* Cook, only *Schizomus* and *Trithyreus* remain valid. *Nyctalops*, *Schizonotus*, and *Tripeltis* are junior homonyms applied to this group. *Artacarus* and *Hubbardia* are junior subjective synonyms, and *Triplomus* is a junior objective synonym.

The original classification of Cambridge (1872) included the family name Tartarides; there was no nominal genus, but the type genus *Nyctalops* was fixed by monotypy. Thorell (1888) elevated Tartarides to tribal status, but did not use a nominate-type family name. He used the new name Schizontoidae, which is invalid because the nominate genus *Schizonotus* was later shown to be a junior homonym. Family Hubbardiidae, which Cook (1899) offered to replace Schizonotidae, was also not allowable because its nominate type genus was later

decided to be a junior subjective synonym of *Schizomus*. The family name Schizomidae has been erroneously attributed to Chamberlin (1922). Hansen and Sorensen (1905) offered the name Schizomoidae to replace Hubbardiidae. The original spelling was emended to Schizomidae by Gravely (1915). The family name Tartarides should have been conserved from the start by Thorell and given its proper suffix, but since the name has been out of general usage, the name Schizomidae should be used.

In the same publication that Chamberlin made his belated revision of family names he also described a new genus and species of schizomid from Puerto Rico. He characterized his new genus *Stenochrus* by the lack of the mesopeltidial plates which are present in all other known species. A reexamination of the type series of *Stenochrus portoricensis* reveals that this species does indeed have the mesopeltidial plates that Chamberlin reported to be absent. Most of the specimens in the type series are strongly bent upward, causing the metapeltidial plate to become unnaturally closely associated with the posterior margin of the carapace (propeltidium). This flexure results in the mesopeltidial plates being reflected underneath the metapeltidium. I examined all of the specimens available and in all but one was able to find at least some evidence of the mesopeltidial plates, though in some it is rather obscure. In light of these observations this animal fits perfectly well in the genus *Schizomus*. Hereafter this species should be referred to as *Schizomus portoricensis* (Chamberlin, 1922).

Since 1922 three Recent genera have been described. *Megaschizomus* Lawrence (1969) is based on two African species, *Agastoschizomus* Rowland (1971) and *Heteroschizomus* Rowland (1973) are based on Mexican species. I have examined paratypes of the African *Megaschizomus mossambicus* (Lawrence) and have found a remarkable similarity between the latter genus and *Agastoschizomus*. While they bear the basic differences allowing their generic distinction I have found it most reasonable to place these two genera in a common subfamily of Schizomidae, separate from *Trithyreus*, *Schizomus*, and the extinct *Calcoschizomus*. I designate the new subfamily Megaschizominae based on the nominate and type genus *Megaschizomus*, the type species of which is *Schizomus mossambicus* Lawrence (1958). I have discussed this combination with Dr. Lawrence, who has seen specimens of *Agastoschizomus lucifer*, and he agrees with this decision.

Lawrence (1969), in his revision of the African schizomids, makes the decision that there do not exist good criteria for maintenance of both *Trithyreus* and *Schizomus*. Unfortunately, Lawrence apparently missed the earlier revision of a similar nature by Mello-Leitao (1931). Mello-Leitao reasoned that the two genera should be reduced to subgenera and that only the genus *Schizomus* should stand. While I find his criteria faulty, and do not accept this general revision, he nonetheless produced a revision that is applicable to African fauna.

I do not question Lawrence's decision to unite applicable African species

into one genus, but it seems he, like Mello-Leitao, has picked the younger generic name to survive. *Trithyreus* Kraepelin dates to March, 1899, whereas *Schizomus* Cook dates to April, 1899. Under the law of priority a genus group taxon formed by the union of two or more genus group taxa takes the oldest valid name among those of its components; Art. 23(e), ICZN. My nominal objective revision of African species requires a reevaluation of a secondary homonym renamed in Lawrence's and Mello-Leitao's revisions. The union of the two genera in Africa caused *T. cavernicola* Hansen (1926) to become *S. cavernicola* (Hansen), a name combination which previously existed from Gravely (1912). Both revisors correctly changed the junior *cavernicola* to *S. hanseni* and took authorship. But since *Trithyreus* is the proper genus the junior secondary synonym *T. cavernicola* Hansen must be reestablished as the valid name of the taxon. The names *S. hanseni* Lawrence and *S. hanseni* Mello-Leitao then become junior objective synonyms and mutual primary homonyms.

A number of specific new combinations must be designated, and as a result of Lawrence's and Mello-Leitao's work *Artacarus liberiensis* Cook must be treated as a synonym of *Trithyreus* rather than *Schizomus*.

African Schizomidae Hansen and Sorensen, 1905

Subfamily Schizominae Hansen and Sorensen, 1905

1. *Trithyreus liberiensis* (Cook), 1899 NEW COMBINATION
   Artacarus liberiensis Cook, 1899
   Schizomus liberiensis, Kraus, 1960
   Schizomus liberiensis, Lawrence, 1969
2. *Trithyreus similis* (Hirst), 1913 NEW COMBINATION
   Schizomus similis Hirst, 1913
   Schizomus similis, Mello-Leitao, 1931
   Schizomus similis, Lawrence, 1969
3. *Trithyreus latipes* (Hansen), 1905 NEW COMBINATION
   Schizomus latipes Hansen, 1905
   Schizomus latipes, Mello-Leitao, 1931
   Schizomus latipes, Lawrence, 1969
4. *Trithyreus montanus* (Hansen), 1910 NEW COMBINATION
   Schizomus montanus Hansen, 1910
   Schizomus montanus, Mello-Leitao, 1931
   Schizomus montanus, Lawrence, 1969
5. *Trithyreus africanus* Hansen, 1905
   Trithyreus africanus Hansen, 1905
   Schizomus africanus, Mello-Leitao, 1931
   Schizomus africanus, Lawrence, 1969
6. *Trithyreus brevicauda* Hansen, 1921
   Trithyreus brevicauda Hansen, 1921
   Schizomus brevicauda, Mello-Leitao, 1931
   Schizomus brevicauda, Lawrence, 1969

7. *Trithyreus cavernicola* Hansen, 1926
   Trithyreus cavernicola Hansen, 1926
   Schizomus hanseni Mello-Leitao, 1931 NEW SYNONYMY
   Schizomus hanseni Lawrence, 1969 NEW SYNONYMY
8. *Trithyreus ghesquierei* Giltay, 1935
   Trithyreus ghesquierei Giltay, 1935
   Schizomus ghesquierei, Lawrence, 1969
9. *Trithyreus parvus* Hansen, 1921
   Trithyreus parvus Hansen, 1921
   Schizomus parvus, Mello-Leitao, 1931
   Schizomus parvus, Lawrence, 1969
10. *Trithyreus machadoi* (Lawrence), 1958 NEW COMBINATION
    Schizomus machadoi Lawrence, 1958
    Schizomus machadoi, Lawrence, 1969
11. *Trithyreus schoutedeni* Roewer, 1954
    Trithyreus schoutedeni Roewer, 1954
    Schizomus schoutedeni, Lawrence, 1969
12. *Trithyreus nidicolus* (Lawrence), 1969 NEW COMBINATION
    Schizomus nidicolus Lawrence, 1969
13. *Trithyreus vadoni* (Lawrence), 1969 NEW COMBINATION
    Schizomus vadoni Lawrence, 1969
14. *Trithyreus mediocriter* (Lawrence), 1969 NEW COMBINATION
    Schizomus mediocriter Lawrence, 1969
15. *Trithyreus madagassus* (Lawrence), 1969 NEW COMBINATION
    Schizomus madagassus Lawrence, 1969
16. *Trithyreus tenuipes* (Lawrence), 1969 NEW COMBINATION
    Schizomus tenuipes Lawrence, 1969
17. *Trithyreus virescens* (Lawrence), 1969 NEW COMBINATION
    Schizomus virescens Lawrence, 1969
18. *Trithyreus pauliani* (Lawrence), 1969 NEW COMBINATION
    Schizomus pauliani Lawrence, 1969
19. *Trithyreus vinsoni* (Lawrence), 1969 NEW COMBINATION
    Schizomus vinsoni Lawrence, 1969
20. *Trithyreus milloti* (Lawrence), 1969 NEW COMBINATION
    Schizomus milloti Lawrence, 1969
21. *Trithyreus remyi* (Lawrence), 1969 NEW COMBINATION
    Schizomus remyi Lawrence, 1969
22. *Trithyreus benoiti* (Lawrence), 1969 NEW COMBINATION
    Schizomus benoiti Lawrence, 1969

Subfamily Megaschizominae Rowland, NEW SUBFAMILY

23. *Megaschizomus mossambicus* (Lawrence), 1958
    Schizomus mossambicus Lawrence, 1958
    Megaschizomus mossambicus, Lawrence, 1969
24. *Megaschizomus zuluanus* (Lawrence), 1947
    Schizomus zuluanus Lawrence, 1947
    Megaschizomus zuluanus, Lawrence, 1969

SYSTEMATICS

Order Schizomida Petrunkevitch, 1945

Colopyga Cook, 1899

Family Schizomidae Hansen and Sorensen, 1905

Tartarides Cambridge, 1872, Ann. and Mag. Nat. Hist., Ser. 4, **10**:410. (nom. obl.)

Schizonotidae Thorell, 1888, Ann. Mus. Civ. Genova, **26**:358. [nom. correct. Pocock, 1893 (ex Schizonotoidae Thorell, 1888, nom. imperf.)] (nom. based on jun. hom.)

Hubbardiidae Cook, 1899, Proc. Ent. Soc. Wash., **4**:249. (nom. obl.) (nom. based on jun. subj. syn.)

Schizomidae Hansen and Sorensen, 1905, Ark. fur Zool., **2**:4. [nom. correct. Gravely, 1915 (ex Schizomoidae Hansen and Sorensen, 1905, nom. imperf.)]

Schizomidae Chamberlin, 1922, Proc. Biol. Soc. Wash., **35**:11. (jun. prim. hom.)

TYPE: *Nyctalops crassicaudata* Cambridge, 1872.

DIAGNOSIS: Tarsus of leg one, seven-segmented; tarsi of legs two to four, three-segmented; flagellum one to two segmented in males, one to four segmented in females.

Subfamily Schizominae Hansen and Sorensen, 1905 [nom. transl. Rowland, herein (ex Schizomidae Hansen and Sorensen, 1905)].

DIAGNOSIS: Chelicerae with six to ten teeth on fixed finger; flagellum one segmented in males, one segmented in females (though two to three annulations may be present, there is no dividing membrane between segments).

Genus *Schizomus* Cook, 1899

Nyctalops Cambridge, 1872, Ann. and Mag. Nat. Hist., Ser. 4, **10**:410. (jun. hom.) Type; *N. crassicaudata* (SD Cook, 1899)

Schizonotus Thorell, 1888, Ann. Mus. Civ. Genova, **26**:358. (jun. hom.) [nom. subst. pro *Nyctalops* (non *Nyctalops* Wagler, 1832)]

Schizomus Cook, 1899, Proc. Ent. Soc. Wash., **4**:249. [nom. subst. pro *Schizonotus* (non *Schizonotus* Ratzeburg, 1852)]

Stenochrus Chamberlin, 1922, Proc. Biol. Soc. Wash., **35**:11. (jun. subj. syn.) Type; *S. portoricensis* Chamberlin, Monotypy. NEW SYNONYMY

TYPE: *Nyctalops crassicaudata* Cambridge, 1872, = *Schizomus crassicaudatus* (Cambridge), 1872.

DIAGNOSIS: Metapeltidium entire (some species of African *Trithyreus* have metapeltidium entire); not present in Africa.

→

FIG. 1. Mesal aspect of chelicera of *Schizomus mexicanus* Rowland, 1971, a typical representative of the Schizominae. Note the number of teeth on fixed digit.

FIG. 2. Mesal aspect of chelicera of *Agastoschizomus lucifer* Rowland, 1971, a representative of the Megaschizominae. Note the number of teeth on fixed digit.

FIG. 3. Lateral aspect of flagellum of female *Schizomus* sp., a typical representative of the Schizominae. Note the presence of annulations, and absence of segmentation.

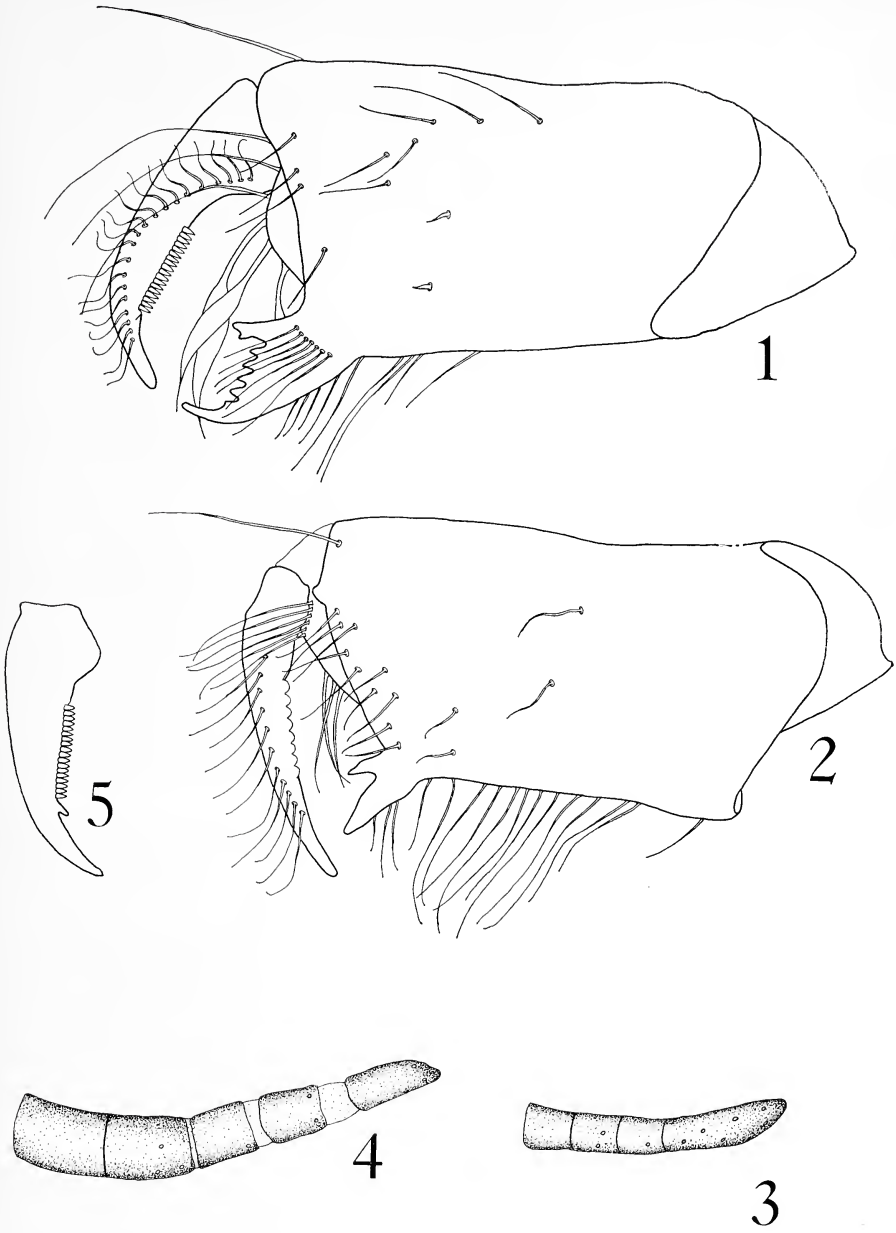

Fig. 4. Lateral aspect of flagellum of female *Agastoschizomus lucifer*. Note the presence of segmentation, marked by the occurrence of dividing membranous areas.

Fig. 5. Mesal aspect of movable finger of chelicera of *Megaschizomus mossambicus* (Lawrence), 1958, a representative of the Megaschizominae. Note the internal tooth file which is absent in *Agastoschizomus* (Fig. 2).

Genus *Trithyreus* Kraepelin, 1899

Tripeltis Thorell, 1889, Ann. Mus. Civ. Genova, **27**:554. (jun. hom.) Type; *T. grassii* (OD)
Trithyreus Kraepelin, 1899, in Das Tierreich, **8**:234. [nom. subst. pro *Tripeltis* (non *Tripeltis* Cope, 1886)]
Triplomus Cook, 1899, Proc. Ent. Soc. Wash., **4**:250. (jun. obj. syn.) [nom. subst. pro *Tripeltis* (non *Tripeltis* Cope, 1886)]
Hubbardia Cook, 1899, Proc. Ent. Soc. Wash., **4**:250. (jun. subj. syn.) Type; *H. pentapeltis* Cook, Monotypy
Artacarus Cook, 1899, Proc. Ent. Soc. Wash., **4**:254. (jun. subj. syn.) Type; *A. liberiensis* Cook, Monotypy
Schizomus Cook, 1899, Proc. Ent. Soc. Wash., **4**:250. [jun. subj. syn. (in part)]

TYPE: *Tripeltis grassii* Thorell, 1889 = *Trithyreus grassii* (Thorell), 1889.

DIAGNOSIS: Metapeltidium divided (some species of African *Trithyreus* have metapeltidium entire); all African species of this subfamily belong in this genus.

Genus *Calcoschizomus* Pierce, 1951

Calcoschizomus Pierce, 1951, Bull. So. Cal. Acad. Sci., **50**:41. Type; *C. latisternum* Pierce, Monotypy

DIAGNOSIS: Flagellum not annulated or segmented; Pliocene.

Genus *Heteroschizomus* Rowland, 1973

Heteroschizomus Rowland, 1973, Occas. Papers Mus., Texas Tech Univ., 11. Type; *H. goodnightorum* Rowland, 1973 (OD)

DIAGNOSIS: Abdominal segments seven to eleven extremely elongate.

Subfamily Megaschizominae Rowland, NEW SUBFAMILY

DIAGNOSIS: Chelicerae with two to three teeth on fixed fingers; flagellum one to two segmented in males, three to four segmented in females.

Genus *Megaschizomus* Lawrence, 1969

Megaschizomus Lawrence, 1969, J. Nat. Hist., **3**:257. Type; *Schizomus mossambicus* Lawrence, 1958 (OD) = *Megaschizomus mossambicus* (Lawrence), 1958

DIAGNOSIS: Chelicerae with three teeth on fixed finger, movable finger with internal tooth file; flagellum two segmented in males, three segmented in females.

Genus *Agastoschizomus* Rowland, 1971

Agastoschizomus Rowland, 1971, Ass. Mex. Cave Stud. Bull., **4**:13. Type; *A. lucifer* Rowland, Monotypy

DIAGNOSIS: Chelicerae with two teeth on fixed finger, movable finger without internal tooth file; flagellum one segmented in males, four segmented in females.

Family Calcitronidae Petrunkevitch, 1945

Calcitronidae Petrunkevitch, 1945, Am. Jour. Sci. **243**:323.

TYPE: *Calcitro fisheri* Petrunkevitch, 1945.

DIAGNOSIS: Tarsus of leg one, seven-segmented; leg two, five-segmented; legs three and four, four-segmented; flagellum three to seven segmented.

Genus *Calcitro* Petrunkevitch, 1945

Calcitro Petrunkevitch, 1945, Am. Jour. Sci. **243**:323. Type; *C. fisheri* Petrunkevitch, Monotypy

DIAGNOSIS: Flagellum three segmented; Pliocene.

Genus *Onychothelyphonus* Pierce, 1950

Onychothelyphonus Pierce, 1950, Bull. So. Cal. Acad. Sci. **49**:102. Types; *O. bonneri* Pierce, Monotypy

DIAGNOSIS: Flagellum seven segmented; Pliocene.

The following key separates the extant family group and generic taxa of the Schizomidae.

1. Chelicerae with 6 to 10 teeth on the fixed finger (Fig. 1); flagellum 1 segmented (there may be two or three annulations present on the female's flagellum, but they have no dividing membranous area) (Fig. 3) ..... 2. Schizominae Hansen and Sorensen

   Chelicerae with 2 to 3 teeth on fixed finger (Fig. 2); flagellum 1 to 2 segmented in males, 3 to 4 segmented in females (Fig. 4) ..... 3. Megaschizominae Rowland, NEW SUBFAMILY

2. Metapeltidium entire; not African 4

   Metapeltidium divided into two lateral plates by a median suture; all African species are in this genus ..... *Trithyreus* Kraepelin

3. Chelicerae with 3 teeth on fixed fingers; flagellum 2 segmented in males, 3 segmented in females; chelicerae with an internal tooth file on movable finger (Fig. 5) ..... *Megaschizomus* Lawrence

   Chelicerae with 2 teeth on fixed finger; flagellum 1 segmented in males, 4 segmented in females; chelicerae without an internal tooth file on movable finger (Fig. 2) ..... *Agastoschizomus* Rowland

4. Abdominal segments seven to eleven similar to other abdominal segments .. *Schizomus* Cook

   Abdominal segments seven to eleven extremely elongate ..... *Heteroschizomus* Rowland

DISCUSSION

The poorly diagnosed genera *Schizomus* and *Trithyreus* have been criticized by various authors. The question of generic rank for the single character used in the diagnosis has been an argument of some (Hansen and Sorensen, 1905; Mello-Leitao, 1931). However, a more objective criticism is that the taxa based on this character probably do not typify discrete phyletic units. Indeed, I have found that this character may vary within specimens of the same species. Dr. Lawrence has decided along these lines that African species exclusive of *Megaschizomus* should be relegated to a single genus. While I do not question this judgment I have not extended this revision to North American forms. It will be necessary to assess the schizomid fauna of the South Pacific, West Indies, South America, and Central America before a revision of these problematic genera in North America can be determined.

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Pupal Color Dimorphism and its Environmental Control in *Papilio polyxenes asterius* Stoll (Lepidoptera: Papilionidae)

David A. West

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

William M. Snellings

Interdepartmental Program in Toxicology, Horace H. Rackham School of Graduate Studies, The University of Michigan, Ann Arbor, Michigan 48104

Thomas A. Herbek

6227 W. Franklin St., Richmond, Virginia 23226

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Abstract: The color dimorphism of pupae of the swallowtail butterfly *Papilio polyxenes* is thought to be an adaptation to variable surroundings in which the insect pupates. Laboratory experiments suggest that pupal coloration is determined by an interaction between photoperiod during larval development and background color immediately before and during pupation. Short photoperiod evokes brown pupal color regardless of background, a result consistent with the situation in nature, where short photoperiod presages a long overwintering period. Long photoperiod permits flexibility of pupal color development, allowing green or brown pupal color depending on the background color, or on the intensity of light reaching the underside of the larva just before pupation. Some "mistakes" occur, and the failure of natural selection to have eliminated all such inappropriate responses may be due to their selective advantage in some years.

DISCUSSION

The pupae of many species of Lepidoptera, especially butterflies, are variable or polymorphic in color, often matching to a high degree the color of the substrate to which they are attached. The concealing coloration has variously been attributed to a direct adaptation of the developing pupa to its background, or to a developmental response triggered by temperature, humidity, or photoperiod during late larval or prepupal life (Poulton, 1890, 1892; Brecher, 1921; Ford, 1953; Sheppard, 1958; Wiltshire, 1958; Hidaka, 1961*b*; Clarke and Sheppard, 1972). The pupae of swallowtail butterflies are often dimorphic, being either green or brown in the North American species *Battus philenor* (L.), *Papilio troilus* L., *P. polyxenes*, *P. brevicauda* Saunders, *P. bairdii* Edwards, and *Graphium marcellus* (Cramer), among others (Forbes, 1960; our unpublished observations), in *P. machaon* L. of Europe (Clarke, 1954; Cribb, 1970) and

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in *P. protenor demetrius* Cr. of Japan (Ohnishi and Hidaka, 1956), while the Japanese species *P. xuthus* has an orange form as well (Ishizaki and Kato, 1956).

Although a photoperiodic influence could act over the whole of the larval period (about two weeks in *P. polyxenes*), a larva chooses its attachment site only about a day before pupation. If background color is to influence pupal color it must act rapidly. There is no evidence of a genetic basis to the color dimorphism in *P. machaon* (Clarke, 1954) or in *P. polytes* (Clarke and Sheppard, 1972).

The proximate factor responsible for brown pupal color in *P. xuthus* (Hidaka, 1961*a*) is the action of a hormone released by the prothoracic ganglion during the prepupal period. Without this hormone, the release of which is controlled by stimuli mediated by the brain, a pupa will be green.

The two experiments reported here attempted to identify the environmental factors responsible for determining pupal coloration in the North American species *P. polyxenes*. This swallowtail has two or three broods between April and October in the central Appalachians and overwinters as pupae. The larvae are thus exposed to two contrasting sets of environmental variables: long day length and the availability of food plant after a short pupation (May–August); and shorter day length and an uncertain availability or absence of food plant except after a long pupation (September, October). Furthermore, overwintering pupae are exposed to predation against brown or gray backgrounds, while summer pupae are usually in green surroundings, but may have green or brown immediate backgrounds. Considering how poorly camouflaged a green pupa is against the backgrounds of winter, while in summer such a pupa would often be more cryptic than would a brown one, we expected to find some environmental factor(s) that would trigger development of the appropriate color, whether the factor be temperature or photoperiod, or perhaps the color of the substrate to which the prepupal insect attaches. This expectation is based on the assumption that background matching is of selective value. Although this seems the simplest assumption, there is in fact very little direct evidence (e.g., Hidaka, Kimura and Onosaka, 1959).

In Experiment 1 we tested the effects on pupal color of photoperiod and temperature, using ranges of both that were comparable to, or slightly more extreme than, those encountered in nature. Stimulated by Prof. Sheppard's observations in *B. philenor* (Clarke and Sheppard, 1972), we tested the effect of substrate color during the prepupal period in Experiment 2.

MATERIALS AND METHODS

Experiment 1. The eggs came from three females, two of them (681-1 and 681-2) sibs from a brood reared in variable conditions in October 1968. That brood contained 19 green and 29 brown pupae. Female 681-1 came from a green pupa, 681-2 from a brown one. Both females were hand-paired to one

Table 1. Experiment 1: effects of temperature and photoperiod on pupal coloration in *Papilio polyxenes*.

Photoperiod	Temperature	Female Parent	Pupal Color	
			green	brown
Long	Warm	681-1	15	0
		681-2	15	0
		691	15	0
	Cool	681-1	8	0
		681-2	16	2
		691	20	0
Short	Warm	681-1	2	13
		681-2	2	13
		691	2	13
	Cool	681-1	0	15
		681-2	0	16
		691	0	15

wild-caught male (method of Clarke and Sheppard, 1956). The third female (691) came from the wild after insemination in May 1969, and all materials originated from Montgomery and Giles Counties, Virginia. At this latitude day length reaches nearly 15 hours in June and is about 11 hours in mid-October.

Within three days of hatching we distributed the larvae haphazardly to the four treatments. The larvae were kept in round, clear plastic dishes (15 × 3.8 cm) with tight lids and filter paper bottom liners and were given fresh leaves of wild carrot (*Daucus carota* L.) in abundance daily. We kept 15 larvae per dish at first but thinned to 5 per dish in the last two larval instars. The dishes were sterilized every other day in dilute sodium hypochlorite solution. Few larvae died in the warm treatments, but as many as a third of those in the cool treatments died in late larval life or as prepupae. They were not obviously diseased but seemed to have suffered some sort of arrested development because of the cool temperature.

Our treatments were of two photoperiods, Long (16 hr) and Short (8 hr), and of two temperature ranges, Warm (18°C night, 29°C day) and Cool (7°C night, 18°C day); all larvae, however, were on the same daily temperature cycle, i.e., 16 hr high, 8 hr low, the larvae on short days being placed in lighttight boxes during their "night." The humidity of the dishes was not controlled but was always close to saturation because of the fresh food plant and the tight lids. We used Percival environmental chambers, illuminated by eight 40-watt cool white high-output fluorescent lamps and four 25-watt incandescent lamps. As an insect pupated it was scored and removed.

Experiment 2. Eggs were collected from three wild-caught females taken in Montgomery Co., Va., in May 1970, and all larvae were reared in the Warm temperature regime used in Experiment 1, but the temperature and day-night cycles were synchronous. Other conditions were essentially the same as those in Experiment 1. When a larva started to wander in late 5th instar it was removed from the rearing dish and assigned for pupation randomly to one of the treatment canisters. These were round, clear plastic containers (18 × 18 cm) with fairly tight opaque lids. They contained either green twigs, brown twigs, a green log, or a brown log, the green objects being spray-painted flat forest-green and aged in the sun for a few days. The brown objects were left natural, and all had intact bark. The logs were 6 to 8 cm in diameter, 15 to 18 cm long, of black locust or apple; the twigs were about 0.5 cm in diameter, generally branched, and of wild cherry. Some food had to be added for a last feeding, but the larvae soon settled on pupation sites, either on the objects or on the walls of the canisters. Pupae were scored and removed to plastic dishes in the same environmental chamber in which they had been kept throughout the experiment. Some of the larvae were left in the rearing dishes for a direct comparison with the results of Experiment 1.

RESULTS AND DISCUSSION

Effect of temperature and photoperiod. Experiment 1 (Table 1) suggests an overwhelming importance of photoperiod, with all three broods responding in the same way, and Long day length evoking predominantly green pupae. Using the percent green pupae, transformed by the method of Mosteller and Youtz (1961), an analysis of variance and the F-test reveals a weak interaction between temperature and photoperiod (P just less than 0.05); but taking the two temperatures separately and testing by chi square, there is a highly significant effect of photoperiod in each temperature range ($P < 0.001$ in each). In Experiment 2 (Table 2) the comparable effect of photoperiod can be tested for those pupae forming on canister walls and in the rearing boxes. The influence of day length is again striking ($\chi^2_1 = 48.7$; $P < 0.001$). On Short days the responses on the clear plastic backgrounds are homogeneous in the two experiments (Fisher's exact test, $P = 0.46$), with nearly all pupae being brown. On Long days, however, the proportion of green pupae was slightly higher in Experiment 1 than in Experiment 2 (Fisher's exact test, $P = 0.045$).

Effect of background. In Experiment 2 (Table 2) nearly all larvae on short days developed into brown pupae (68/73) whatever the background of pupation. On Long days, however, there was a striking difference between those pupating on clear plastic dishes and canister walls or slender twigs on the one hand (60 green:13 brown), and on logs on the other (no green:13 brown). There is homogeneity between twig colors (Fisher's exact test, $P = 0.22$) and between

Table 2. Experiment 2: effects of photoperiod and background color on pupal coloration in *Papilio polyxenes*.

Photoperiod	Background	Pupal Color		
		green		brown
Long	Green twigs	10		1
	Brown twigs	14		8
	Green log	0		1
	Brown log	0		12
	Canisters	29		2
	Rearing dishes	7		2
Short	Green twigs	0		6
	Brown twigs	0		11
	Green log	0	1*	15
	Brown log	1		4
	Canisters	0		7
	Rearing dishes	2	1*	25

* Intermediate color.

twigs and clear plastic ($\chi^2_1 = 2.6$; $P > 0.10$). Pooling the results on plastic and on twigs, and comparing them to the results on logs, reveals a strong difference ($\chi^2_1 = 31.6$, $P < 0.001$). The similarity of results on clear plastic and on twigs may be accounted for by the importance of bright light reaching the undersides; on plastic or on slender twigs much light comes through, or by, the substrate. There is, in fact, a suggestion that brown twigs stimulated a slightly larger proportion of brown pupae than did green twigs. It may be that the effective background of a pupa on a slender twig is not the twig itself (see below). Clarke and Sheppard (1972) found in *Battus philenor* that twigs under 12 mm in diameter influenced pupal color in favor of that matching twig color, but brown twigs did so only to a degree. The twigs in our experiments were all considerably thinner than 12 mm, but Clarke and Sheppard do not give a lower limit to twig size, so that the question of the importance of light passing by the twig to the underside of the prepupa must remain open.

Although nearly all pupae that formed after exposure to Short day length were brown, there was a great deal of variation in the shade of brown, and some pupae had greenish patches; in fact there was often an excellent match to the human eye between the shade of brown of a pupa and that of its immediate background. This was in marked contrast to brown pupae formed after Long photoperiod, in which the shade of brown was nearly uniform.

Pupal color and diapause. Among pupae forming after Long photoperiod there were 60 green and 26 brown; for those eclosions that were recorded, 42 green

and 13 brown pupae completed development after a short pupation (7 to 13 days, with a mean of 9.3 days). For the remainder, precise eclosion times were not recorded, and some died, but none entered diapause. The proportions of the colors in these two groups are the same ($\chi^2_1 = 0.43$; $P > 0.50$). Among pupae formed after Short photoperiod only 2 eclosed after brief pupation, and both were green. The only other green pupa evidently died, and the remaining 68 brown or intermediate pupae entered diapause and had not eclosed a month after pupation. In *P. xuthus* (Ishizaki and Kato, 1956), the orange form of brown always enters diapause, while the other forms of brown and green usually do not. Thus in these two species there seems to be a diapause phenotype, orange in *P. xuthus* and variable brown in *P. polyxenes*. In our experiments green pupae did not enter diapause, nor did brown pupae that formed under "summer" photoperiod; the only pupae that entered diapause were brown ones reared in "autumn" photoperiod.

These results suggest a complex adaptive response of larvae about to pupate; in autumn Short day length is overriding and stimulates the development of brown pupae regardless of background color, but the insects are able to vary the shade of brown. In midsummer, Long day length permits the expression of a brown-green alternative, but there is little flexibility in the development of the shade of brown. (In fact, we cannot say whether it is day length or night length that is critical.) The selective advantage of brown pupae in autumn presumably comes from their long exposure, against dull backgrounds, to predators during the overwintering diapause. In midsummer, however, the backgrounds are more varied and the duration of pupation short. Selection might be expected to favor a matching to immediate background, since the background will not change over the 10-day pupal period, but there may be little to gain, from a selective point of view, in matching the shade of that background on which an insect pupates.

There remains the problem of those insects that make "mistakes." Three pupae out of 73 that were reared on Short photoperiod were green. In fact, as pointed out above, these "mistakes" did not enter diapause. Clarke and Sheppard (1972) suggested that such mistakes may be favored by apostatic selection. The results of experiments with artificial baits support this suggestion (Allen and Clarke, 1968). In addition, in *P. polyxenes*, the success of these late season "mistakes" will vary from year to year, but in some seasons the insects will be able to complete another generation before winter. Thus environmental variation may promote the maintenance of Short day length "mistakes" in *P. polyxenes*.

The corresponding "mistakes" among pupae formed after Long photoperiod raise the question of cryptic coloration in a swallowtail or other butterfly pupa. A green pupa on a green leaf is clearly "protected," as is a brown one on a brown tree trunk. On slender stems, however, the value of matching the color of the stem is less obvious, since the background against which a predator views

a pupa may be more the mass of surrounding vegetation than the stem itself. For example, resemblance to a green leaf, even on a brown stem, may lower the risk of predation under some circumstances, but until the predators are identified this must be speculative. As suggested above, it may be the intensity of light reaching the underside of a prepupa that determines whether or not it develops into a green or brown pupa, but this must also remain a speculation until the critical experiments have been done.

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Laetulonthus, a New Genus for *Philonthus laetulus* Say (Coleoptera: Staphylinidae)

IAN MOORE AND E. F. LEGNER[1]

DIVISION OF BIOLOGICAL CONTROL, CITRUS RESEARCH CENTER AND AGRICULTURAL EXPERIMENT STATION, UNIVERSITY OF CALIFORNIA, RIVERSIDE 92502

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INTRODUCTION

Philonthus laetulus Say must be removed from *Philonthus* and placed in a new genus because of its unarmed anterior tibiae and strongly deflexed superior lateral carina of the prothorax.

Say first described this species thinking that it probably was the *Staphylinus blandus* of Gravenhorst, but noting some discrepancies between his specimen and Gravenhorst's description he proposed the name *laetulus* should they prove to be distinct.

The following key to the genera is modified from Moore (1965).

KEY TO THE GENERA OF THE STAPHYLININAE OF AMERICA NORTH OF MEXICO

1. Superior lateral line of pronotum not deflexed in front so that the large lateral setigerous puncture is on it or separated from it at most by little more than the width of the puncture 2
   Superior lateral line of pronotum deflexed in front so that the large lateral setigerous puncture is distant from it by at least three times the width of the puncture 4

2(1). Last segment of labial palpi not or very little narrower than penultimate, subfusiform or aciculate; anterior tarsi usually with pale spatulate setae beneath ..... *Philonthus* Stephens
   Last segment of labial palpi narrower than penultimate, cylindrical; tempora longer than eyes, subparallel; pronotum elongate 3

3(2). Anterior tarsi broadly dilated, with pale spatulate setae beneath; pronotum with a series of four discal punctures each side of mid-line ..... *Gabronthus* Tottenham
   Anterior tarsi not dilated; without pale spatulate setae beneath; pronotum with a series of five discal punctures each side of mid-line ..... *Gabrius* Curtis

4(1). Prosternum not carinate 5
   Prosternum strongly longitudinally carinate 10

5(4). Basal impressions of basal tergites not more coarsely punctured than rest of tergite 6
   Basal impressions of basal tergites much more coarsely punctured than rest of tergite ..... *Neobisnius* Ganglbauer

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[1] Staff Research Associate and Associate Entomologist, respectively, Division of Biological Control, Department of Entomology, University of California, Riverside 92502.

6(5). First segment of posterior tarsi as long as last segment 7
First segment of posterior tarsi shorter than last segment ..... *Erichsonius* Fauvel
7(6). Anterior tarsi dilated (second segment wider than long), with dense pale spatulate setae beneath 8
Anterior tarsi slender (second segment longer than wide); without pale spatulate setae beneath; posterior femora of male usually spinose beneath ..... *Belonuchus* Nordman
8(7). Last segment of maxillary palpi not more than three times as long as wide 9
Last segment of maxillary palpi more than four times as long as wide ..... *Hesperus* Fauvel
9(8). Anterior tibiae spinose on outer edge ..... *Cafius* Curtis
Anterior tibiae not spinose on outer edge ..... *Laetulonthus* NEW GENUS
10(4). Mesosternum longitudinally carinate ..... *Ontholestes* Ganglbauer
Mesosternum not longitudinally carinate 11
11(10). Last segment of labial palpi subfusiform ..... *Staphylinus* Linnaeus
Last segment of labial palpi subsecuriform ..... *Ocypus* Samuelle

Laetulonthus NEW GENUS, MOORE & LEGNER

FORM. Moderate size, elongate, parallel. Integuments shining, not coarsely sculptured.

HEAD orbicular, narrowed behind to form a neck which is delimited by a distinct nuchal constriction. Eyes moderate, not protruding. Antennae eleven-segmented, slightly thickened apically; their fossae located at the front margin of the head just inside the bases of the mandibles, not under a ridge; first three segments semi-glabrous, segments four through eleven densely pubescent. Mandibles curved, pointed; with a central tooth; with a shallow groove on the upper surface near the outer edge. Clypeus truncate. Labrum deeply bilobed, with six or eight long setae at apical edge. Maxillary palpi four-segmented; first segment short, curved; second segment a little more than twice as long as wide, curved, thickened at apex; third segment about as long as but not quite as wide as second; fourth segment a little longer than and slightly narrower than third, subcylindrical, pointed at apex. Outer lobe of maxillae longer than inner lobe, each densely ciliate at apex. Labial palpi three-segmented, the segments of about equal length, each a little more than twice as long as wide, third segment subcylindrical, somewhat narrowed at apex. Ligula membranous, entire. Mentum three times as wide as long, widest at base. Gular sutures widely separated in front, united from near the middle to the base. Infra-orbital carina lacking.

THORAX. Pronotum subquadrate, with a dorsal series of three discal punctures each side of mid-line; superior lateral carina deflexed so that the large lateral setigerous puncture is removed from it by about four times the width of the puncture. Prosternum large, tumid centrally, divided transversely by a carina. Trochantin small. Hypomera slender, the superior and inferior lateral carinae united before the anterior angles. Prothoracic epimera lacking. Mesosternal process extending about a third of the distance between the middle coxae. Middle coxae separated. Mesosternum with a curved longitudinal carina delimiting the base of the mesosternal process. Elytra subquadrate, elytral epipleura not delimited by a carina. Scutellum large, punctate. Anterior and middle coxae large, exserted; posterior coxae transverse. Anterior tibiae without spines except at apices; middle and posterior tibiae with large scattered spines throughout. Tarsi five-segmented, first three segments of anterior tarsi moderately broadly dilated, with pale spatulate setae beneath. Posterior tarsi with first and fifth segments of about equal length, second through fourth segments shorter, decreasing in length.

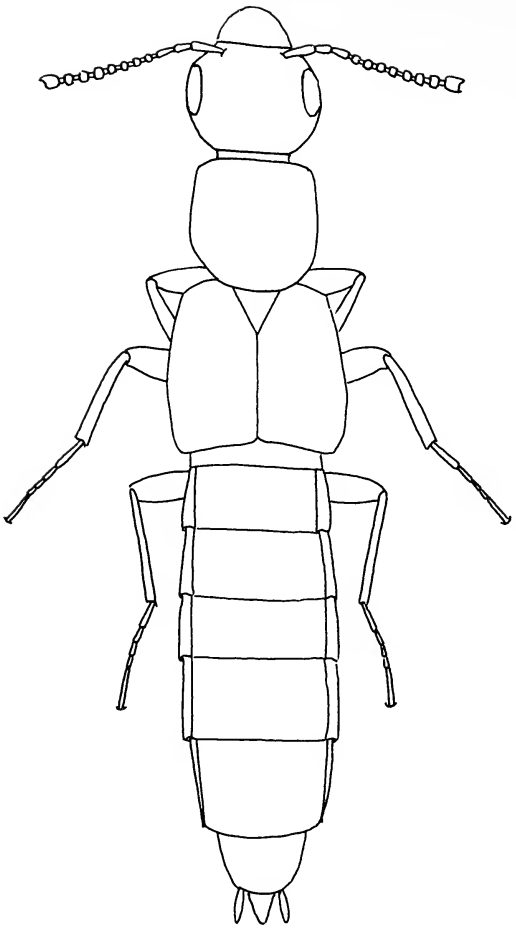

FIG. 1. Habitus of *Laetulonthus laetulus* (Say), male.

ABDOMEN with first three visible tergites shallowly impressed at base; first five visible sternites with two paratergites each side. First visible sternite without a keel between the coxae.

TYPE SPECIES *Staphylinus laetulus* SAY

NOTES. The single species in this genus has usually been included in the genus *Philonthus* from which it differs widely in that the large lateral setigerous puncture of the pronotum is removed from the lateral margin by about four times the width of the puncture whereas in *Philonthus* it is either on the lateral carina or removed from it by no more than the width of the puncture. In *Laetulonthus* the anterior tibiae are without spines on the outer edge. The anterior tibiae are strongly spinose on the outer edge in *Philonthus*.

Laetulonthus laetulus (SAY)

Staphylinus laetulus Say, 1834, Trans. Am. Philos. Soc., **14:** 449.
Philonthus laetulus, Horn, 1884, Trans. Am. Entomol. Soc., **11:** 184.

DESCRIPTION OF MALE:

COLOR piceus with the pronotum, prosternum, coxae, trochanters, femora, first three and bases of fourth and fifth abdominal segments ferruginous.

HEAD orbicular, about one-fourth wider than long, with a few scattered punctures on disc and behind eyes, surface with very fine strigulose ground sculpture throughout. Antennae with first segment as long as next two together; second and third segments subequal in length; fourth segment as wide as and half as long as third; fifth through tenth segments as long as fourth, each slightly wider than preceding so that tenth is three-eighths wider than long; eleventh as wide as and twice as long as tenth, asymmetrically pointed.

THORAX. Pronotum very slightly narrower than head, as wide as long, quadrate, anterior angles narrowly rounded, sides gently arcuate, hind angles broadly rounded, apex nearly straight, base broadly arcuate. Anterior tibiae moderately broadly dilated.

ELYTRA conjointly three-tenths wider than pronotum, one-tenth wider than long, rather coarsely punctured throughout, the punctures separated by about three or four times their diameters, surface between the punctures minutely rough, shining, but without definite ground sculpture.

ABDOMEN as wide as elytra, punctured a little more finely and a little more sparsely than elytra, surface with very faint strigulose ground sculpture. Beneath slightly more coarsely punctures and more coarsely strigulose than above. Apex of sixth visible sternite with a moderately large triangular emargination surrounded by a fine membrane.

FEMALE. Head as wide as pronotum. Anterior tarsi slightly dilated. Apex of sixth sternite entire.

DISTRIBUTION. Has been collected from Canada to Georgia and west to Missouri and Texas.

HABITAT. Has been taken in Missouri by C. A. Frost from under bark of pine logs in September.

REMARKS. This species has been compared with *Philonthus blandus* which it resembles in configuration and color but which differs from it not only in the generic characters but in the pronotum having a series of three discal punctures on each side and in having the anterior tarsi undilated and without pale spatulate setae beneath and in many other details.

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The Anthomyiidae and Muscidae of Mt. Katahdin, Maine (Diptera)

H. C. HUCKETT

LONG ISLAND VEGETABLE RESEARCH FARM, CORNELL UNIVERSITY,
RIVERHEAD, NEW YORK 11901

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Abstract: A preliminary survey was made of the anthomyiid and muscid flies on the upper regions of Mt. Katahdin during the early summer of 1957, 1958, 1959, from a base on Chimney Pond at 2,914-feet elevation. Sixty-nine species and one subspecies were recognized as belonging to the family Anthomyiidae *sens. str.*, and 112 species to the Muscidae, a total that included the unpublished records of 3 muscid species that were not found during the foregoing visits. The species *Chirosia setifer*, *Spilogona browerí*, *S. concomitans*, *S. katahdin*, *Lispocephala aemulata*, *Mydaea grata*, and *Phaonia cauta* are described as new to science, and *Delia tarsifimbria* (Rondani), as newly recorded from North America.

INTRODUCTION

In the early summer of 1957 to 1959, from mid-June to mid-July, I had the opportunity, aided by the experienced support of Dr. A. E. Brower, Forest Entomologist of the State of Maine, of visiting Chimney Pond on Mt. Katahdin for the purpose of making a preliminary survey of the species belonging to the families Anthomyiidae and Muscidae, exclusive of the subfamily Scatophaginae. At the time it was already becoming apparent that changes in the immediate vicinity around Chimney Pond were imminent owing to the increasing number of persons utilizing the camp facilities. It was felt that any extension or modernizing of camp accommodation might detrimentally affect the environment and with it the delicate balance existing with the flora and fauna surrounding the Pond, at least insofar as such changes might render precarious the habitats of the present anthomyiid and muscid populations. Thus it seemed more pressing that a record should be made and preserved of the existing number of species and their abundance, not only of the Pond, but also of the surrounding basin and beyond.

The biotic and physical features of Mt. Katahdin have been sufficiently described and illustrated by Blake (1926, 1931) and Leavitt (1954) so that there remains only to mention the following particulars. Mt. Katahdin is an isolated mountain mass of irregular form arising abruptly out of the surrounding lowlands of central Maine; it represents a northern outpost of the Appalachian Range in the United States. It is situated at lat. 45°55′N, long. 69°55′W, about 25 miles from Millinocket. In elevation the higher summits rise to 5,267 feet at Baxter Peak, an altitude that lies just above the zone of timber growth.

I made my headquarters in the bunkhouse at Chimney Pond, from whence all trails lead conveniently upward, downward, or across the whole South Basin. An outline of these trails may be found in the Appalachian Mountain Association Guide to Mt. Katahdin. The various locations at which collections were made are shown on the accompanying map.

In 1957 I spent 17 days at the camp, from June 29 to July 15, during which period collecting was possible to some extent on most of the days, in windy weather and despite the rain. In 1958 the camp was reached on June 14, two weeks earlier by the calendar than in 1957, in the expectation that seasonal conditions would also be more advanced, thereby providing an opportunity for collecting specimens that had possibly escaped capture the previous year owing to the later start. As it happened, it was found on arrival that seasonal conditions had not advanced and were considerably retarded, and continued so for the remaining days. Collecting on the Saddle plateau and vicinity was seriously curtailed, it being noted that specimens were taken only on June 29, July 3, and July 7. Camp was broken on July 8. It was, all together, a disappointing season for carrying on the work because of the prevailing high winds and low temperatures. In 1959 operations commenced on July 1 and ended on July 20 under more favorable conditions. Only three days were lost on account of all-day rains.

PREVIOUS RECORDS

A search of the literature indicated that there were only a few scattered references to species of Anthomyiidae and Muscidae from Mt. Katahdin. Johnson (1925) in his records of Diptera in the New England states listed 5 nominal muscid species; Blake (1926) in his treatise on the biota of Mt. Katahdin, 6 muscid species; Huckett (1932, 1965), 2 species of *Spilogona*; and Chillcott (1961), 2 species of *Fannia*. All the records cited by the above authors were confirmed by the capture of additional specimens in the present survey with the exception of four, namely, *Spilogona aerea* (Zetterstedt) and *S. tetrachaeta* (Malloch) of Johnson's list, and *Schoenomyza litorella* (Fallén) and *Coenosia flavicoxa* Stein in Blake's records. Through the kindness of Dr. R. L. Jeanne of Boston University I was able to examine Johnson's specimens under *tetrachaeta*, and found that they had been misnamed, and were identical with those of *Spilogona suspecta* (Malloch).

In addition, I have included in the following list of species several unpublished records of specimens taken on Mt. Katahdin that are deposited in the collections of the United States National Museum (USNM) and of Cornell University (CU), and which I have had the privilege of examining. Such records are cited in brackets, and contain 3 species of Muscidae that are not represented in the present survey, namely, *Hoplogaster intacta* (Walker), *Lispocephala erythrocera* (Robineau-Desvoidy), *Quadrularia annosa* (Zetterstedt).

RESULTS OF THE SURVEY

In the present work 69 species and 1 subspecies of Anthomyiidae and 112 species of Muscidae are recognized. Among the Anthomyiidae are included one hitherto unknown species and one European species unrecorded from North America, namely, *Delia tarsifimbria* (Rondani); among the Muscidae, six species are introduced as new to science, of which three belong to the genus *Spilogona*, and one each to the genera *Lispocephala*, *Mydaea*, and *Phaonia*.

ABBREVIATIONS

For purposes of brevity, the various localities from which the present records were obtained have been assigned a letter, such as A, B, C, and also for each species the number of specimens from all localities have been combined.

The names of localities follow:

A. Roaring Brook and camp
B. Basin Pond
C. Pamola Pond
D. Chimney Pond trail
E. Dry Pond
F. North Basin trail
G. Hamlin Ridge trail
H. Chimney Pond
I. Chimney Pond and camp
J. South Basin
K. Cathedral trail
L. Cleftrock pool
M. Lower Saddle trail
N. Upper Saddle trail
O. Saddle plateau
P. Saddle Spring
Q. Thoreau Spring trail
R. Caribou Spring trail
S. Caribou Spring
T. Klondike Pond
U. North Basin
V. North Basin Pond

List of species with locality records

FAMILY ANTHOMYIIDAE *sens. str.*

Fucellia tergina (Zetterstedt) = *F. intermedia* Lundbeck (Hennig, 1966: 18)
10 ♂, 5 ♀. H, L, N, R, V.
Pycnoglossa flavipennis (Fallén)
2 ♂, 1 ♀. A, M.
Chirosia filicis (Huckett) *N. COMB.*
1 ♀. E.
Chirosia setifer n. sp.
2 ♂, 3 ♀. E, J, T.
Hylemya alcathoe (Walker)
25 ♂, 1 ♀. A, D, E, F, I, J, T.
Hylemyza partita (Meigen) = *Anthomyza lasciva* Zetterstedt (Hennig, 1969: 245)
13 ♀. C, E, I, J, N, S.
Botanophila inornata (Stein)
1 ♂. I.
Delia alaba (Walker)
10 ♂, 5 ♀. B, E, H, J.
Delia brassicae (Bouché)
4 ♂. I.

Delia cupricrus (Walker) = *Hylemyia coenosiaeformis* Stein (Huckett, 1971)
10 ♂, 2 ♀. E, H, J, N, T.
Delia echinata (Séguy)
2 ♂. J, M.
Delia egleformis (Huckett)
321 ♂, 14 ♀. D, E, I, J, M, N, V.
Delia exigua (Meade)
3 ♂, 4 ♀. C, D, I, N.
Delia lineariventris (Zetterstedt)
3 ♂, 2 ♀. H, N, T.
Delia platura (Meigen)
44 ♂, 18 ♀. B, D, E, I, J, M, N, O, P. (1 ♀, Mt. Katahdin, 4,800 ft. Aug. 1913, C. P. Alexander, CU)
Delia tarsata (Ringdahl)
76 ♂, 4 ♀. H, J, M, N, P, S, T.
Delia tarsifimbria (Rondani)
21 ♂, 3 ♀. J, M, N.
Pegohylemyia acquiescens Huckett
76 ♂, 13 ♀. B, D, E, F, J, I, L, M-N, O.
Pegohylemyia fugax (Meigen)
19 ♂, 7 ♀. E, I, J, M, N, O.
Pegohylemyia hucketti Ringdahl
3 ♂, 2 ♀. J, N, T.
Pegohylemyia profuga (Stein)
4 ♂, 3 ♀. B, H, M-N, P, Q, V.
Pegohylemyia sericea (Malloch)
9 ♂, 5 ♀. D, E, H, J, M, O.
Paregle aestiva (Meigen)
9 ♂, 6 ♀. B, C, D, I, J, O.
Paregle cinerella (Fallén)
1 ♀. M-N.
Paregle radicum (Linnaeus)
21 ♂, 1 ♀. I, J.
Lasiomma abietis (Huckett)
6 ♂, 14 ♀. D, E, F, I, J, L, M-N, O.
Lasiomma anthracinum (Czerny)
5 ♂, 8 ♀. D, E, I, J.
Lasiomma octoguttatum (Zetterstedt)
20 ♂, 7 ♀. D, E, I, J, M, N, O, Q.
Acrostilpna atricauda (Zetterstedt)
61 ♂, 15 ♀. B, C, D, E, F, I, J, L, M, N, O-P, U.
Acrostilpna latipennis (Zetterstedt)
10 ♂, 2 ♀. B, D, F, H, J, M, N, T, V.
Acrostilpna restorata Huckett
26 ♂, 4 ♀. C, D, E, M, N, O-P, R, S.
Crinurina cuneicornis (Zetterstedt)
94 ♂, 69 ♀. B, C, D, E, I, J, M, N, O-P, S.
Macrophorbia houghi Malloch
1 ♂. D.

Eremomyioides cylindrica (Stein)
4 ♂, 3 ♀. H, J, N.
Pegomya bicolor (Wiedemann)
1 ♀. J.
Pegomya connexa Stein
5 ♂, 12 ♀. D, E, H, J, M-N.
Pegomya corrupta Huckett
1 ♂, 1 ♀. D, O.
Pegomya flavipalpis (Zetterstedt)
10 ♂, 1 ♀. D, H, J, L, N.
Pegomya frigida (Zetterstedt)
1 ♂. E.
Pegomya geniculata (Bouché)
6 ♂, 2 ♀. D, E, J, M-N, U.
Pegomya gilva (Zetterstedt)
3 ♂, 1 ♀. A, D, H.
Pegomya indicta Huckett
1 ♂. M-N.
Pegomya labradorensis Malloch
5 ♂, 3 ♀. B, D, E, H, J, M-N.
Pegomya lunatifrons (Zetterstedt)
27 ♂, 8 ♀. D, H, J, M, N. (1 ♀, Mt. Katahdin, "Camp Kennedy," 3,000 ft. Aug. 1902, USNM)
Pegomya pilosa Stein
80 ♂, 4 ♀. B, D, E, F, H, J, M, N, V.
Pegomya rufipes (Fallén)
1 ♀. O.
Pegomya solitaria Stein
1 ♂, 1 ♀. H, J.
Pegomya tenera obscurior Collin
6 ♂. F, H, J.
Pegomya univittata (von Roser)
2 ♂. J.
Pegomya vittigera (Zetterstedt)
1 ♀. E.
Pegomya winthemi (Meigen)
1 ♀. E.
Nupedia infirma (Meigen) = *dissecta* of authors, not Meigen (Ackland, 1965: 207)
376 ♂, 140 ♀. A, B, D, E, F, I, J, K, M, N, O-P, T, V.
Nupedia nigroscutellata (Stein)[1]
113 ♂, 76 ♀. B, C, D, E, I, J, M, N, P.
Nupedia patellans (Pandellé)
12 ♂, 41 ♀. E, H, J.
Pseudonupedia intersecta (Meigen)
20 ♂, 6 ♀. B, D, E, H, J, N, O-P, V.

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[1] Of male specimens, 98 were regarded as a pale variant of *nigroscutellata*, and to be identical with the type-specimen of *Pegomya slossonae* Malloch. Females exhibited no differences.

Hydrophoria alpina Huckett
1 ♀. H.
Hydrophoria conica (Wiedemann)
33 ♀. D, E, I, J, M, N.
Hydrophoria implicata Huckett
2 ♂, 1 ♀. B, J, M-N.
Hydrophoria packardi Malloch
3 ♂, 1 ♀. D, J, N.
Hydrophoria proxima Malloch
3 ♂. C, D.
Hydrophoria uniformis Malloch
1 ♀. N.
Anthomyia oculifera Bigot
1 ♂. J.
Anthomyia pluvialis (Linnaeus)
1 ♀. C.
Leucophora johnsoni (Stein)
1 ♀. M-N.
Leucophora marylandica (Malloch)
2 ♀. E, N.
Leucophora sociata (Meigen)
1 ♂. B.
Paraprosalpia brunneigena (Schnabl) = *Prosalpia incisa* Ringdahl (Hennig, 1969: 11)
3 ♂, 4 ♀. D, H, J.
Paraprosalpia littoralis (Malloch)
6 ♂, 3 ♀. B, J, M, N.
Paraprosalpia pilitarsis (Stein)
13 ♂. E, H, J.
Paraprosalpia silvestris (Fallén)
36 ♂, 59 ♀. A, B, C, D, E, F, I, J, K, M, N, O, P, Q, R, T. (1 ♀, Mt. Katahdin, 4,500 ft. Aug. 1902, USNM)

FAMILY MUSCIDAE

Schoenomyza chrysostoma Loew
3 ♀. H. (2 ♂, 9 ♀, Mt. Katahdin, Aug. 1913, C. P. Alexander, CU)
Coenosia tigrina (Fabricius)
3 ♂, 3 ♀. H, N.
Limosia atrata (Walker)
1 ♀. H.
Limosia conforma Huckett
1 ♂, 2 ♀. E, N. (1 ♂, 6 ♀, Mt. Katahdin, summit, VIII-19-02, USNM)
Limosia fuscifrons (Malloch)
9 ♀. D, I, J.
Limosia nigrescens (Stein)
1 ♂, 2 ♀. E, N, S. (1 ♂, 3 ♀, Mt. Katahdin, 5,100 ft. Aug. 1913, C. P. Alexander, CU)
Limosia triseta (Stein)
20 ♂, 40 ♀. D, E, F, H, J, M, O, Q. (1 ♀, Mt. Katahdin, 5,100 ft. Aug. 1913, C. P. Alexander, CU)
Hoplogaster intacta (Walker)
(2 ♀, Mt. Katahdin, Aug. 1913, C. P. Alexander, CU)

Hoplogaster minor Huckett
6 ♂, 15 ♀. E, H, J, M, N, V.
Hoplogaster morrisoni Malloch
1 ♂. P.
Hoplogaster octopunctata (Zetterstedt)
1 ♀. T.
Macrorchis ausoba (Walker)
13 ♂, 1 ♀. D, I, J, N.
Lispocephala aemulata n. sp.
1 ♂. J.
Lispocephala alma (Zetterstedt)
3 ♀. D, E.
Lispocephala erythrocera (Robineau-Desvoidy)
(2 ♀, Mt. Katahdin, 5,100 ft. Aug. 1913, C. P. Alexander, CU)
Lispocephala varians Malloch
1 ♀. H.
Pentacricia aldrichii Stein
1 ♀. I.
Lispe cotidiana Snyder
1 ♂. D.
Lispe tentaculata (De Geer)
4 ♂, 2 ♀. B.
Lispoides aequifrons (Stein)
8 ♂, 3 ♀. D, I, J, M-N.
Spilogona alticola (Malloch) ♂
54 ♂. A, B, D, E, F, I, J, M, N.
Spilogona alticola—contractifrons complex ♀ ♀
133 ♀ + 2 ♀? B, D, E, F, I, J, L, M, N, O-P, Q, S, V.
Spilogona arctica (Zetterstedt)
638 ♂, 298 ♀. B, D, E, F, I, J, K, L, M, N, O-P, Q, R, T, V.
Spilogona argenticeps Malloch
146 ♂, 67 ♀. B, D, E, F, I, J, L, M, N, O, S, V.
Spilogona broweri n. sp.
25 ♂, 1 ♀. D, E, F, H, J, M, V.
Spilogona caroli (Malloch)
9 ♂, 11 ♀. D, F, I, J, L, M, N.
Spilogona concomitans n. sp.
1 ♂, 1 ♀. H, J.
Spilogona contractifrons (Zetterstedt) ♂
27 ♂. A, D, E, F, H, K, M, N. (1 ♂, Mt. Katahdin, 5,100 ft. Aug. 1913, C. P. Alexander, CU)
Spilogona forticula Huckett
30 ♂, 21 ♀. D, E, F, H, J, L, M, V.
Spilogona gibsoni (Malloch)
15 ♂, 30 ♀. A, D, E, F, H, J, M, N, O-P, Q, V.
Spilogona hypopygialis Huckett
7 ♂, 4 ♀. D, T.
Spilogona katahdin n. sp.
4 ♂, 2 ♀. E, H, J, T.

Spilogona magnipunctata (Malloch)
60 ♂, 62 ♀. C, D, E, F, I, J, M, N, O, Q, R, V.
Spilogona monacantha Collin
207 ♂, 34 ♀. B, D, E, I, J, L, M, N, V.
Spilogona nigriventris (Zetterstedt)
12 ♂, 1 ♀. H, J.
Spilogona obscuripennis (Stein)
1 ♂. T.
Spilogona placida Huckett
33 ♂, 6 ♀. E, H, J, M, N.
Spilogona semiglobosa (Ringdahl)
7 ♂, 30 ♀. D, E, I, J, M, N.
Spilogona setilamellata Huckett
3 ♂. N, S.
Spilogona sororcula (Zetterstedt)
5 ♂, 2 ♀. F, H, J, M, N.
Spilogona suspecta (Malloch)
7 ♂, 4 ♀. E, F, L, P, Q, V. (1 ♂, Mt. Katahdin, summit, Aug. 19, 1902 USNM; 1 ♀, Mt. Katahdin, 5,100 ft. Aug. 1913, C. P. Alexander, CU; 2 ♂, Mt. Katahdin, Aug. 18, 1923, I. H. Blake, BU)
Spilogona trigonifera (Zetterstedt)
15 ♂, 14 ♀. D, E, I, J, M, N, P.
Pseudolimnophora nigripes (Robineau-Desvoidy)
4 ♂. I, J.
Helina fulvisquama (Zetterstedt)
1 ♂, 9 ♀. E, F, H, J, M, N, P.
Helina maculipennis (Zetterstedt)
1 ♂, 8 ♀. C, E, I, J, N.
Helina rothi Ringdahl
2 ♂, 2 ♀. E, M-N, O.
Quadrularia annosa (Zetterstedt)
(2 ♂, 4 ♀, Mt. Katahdin, "Camp Kennedy," 3,000 ft. Aug. 1902; 1 ♀, Mt. Katahdin, summit, 5,215 ft. Aug. 19, 1902, both USNM)
Quadrularia laetifica (Robineau-Desvoidy)
5 ♂, 1 ♀. D, L, M-N, O, Q.
Hebecnema affinis Malloch
44 ♂, 6 ♀. B, E, I, J, T.
Hebecnema nigricolor (Fallén)
3 ♂. J, M-N.
Myospila meditabunda (Fabricius)
4 ♂, 24 ♀. B, C, D, E, I, J, M, O, P.
Mydaea furtiva Stein
3 ♂, 26 ♀. D, E, F, I, J, M, N, O-P, T.
Mydaea grata n. sp.
1 ♂, 3 ♀. F, H, J.
Mydaea neglecta Malloch
4 ♀. D, F, J, M-N.
Mydaea nubila Stein
2 ♂, 2 ♀. C, D, J.

Mydaea obscurella Malloch
32 ♂, 21 ♀. A, D, E, F, H, J, M, N, P.
Mydaea palpalis Stein
123 ♂, 2 ♀. B, D, E, F, I, J, L, M, N, T.
Mydaea sootryeni Ringdahl
5 ♂. J.
Fannia abrupta Malloch
50 ♂, 70 ♀. B, D, E, F, I, J, M, N, O, Q, V.
Fannia aethiops Malloch
67 ♂, 39 ♀. D, I, J, M, N.
Fannia bifimbriata Collin
1 ♂. E.
Fannia brevipalpis Chillcott
25 ♂. D, E, M-N.
Fannia brooksi Chillcott
1 ♂. H.
Fannia canicularis (Linnaeus)
17 ♂, 2 ♀. F, I, J, M, N.
Fannia ciliatissima Chillcott
3 ♂, 1 ♀. H, J.
Fannia flavibasis Stein
3 ♂. H.
Fannia immaculata Malloch
5 ♂, 2 ♀. D, E, I, J, V.
Fannia immutica Collin
2 ♀. F.
Fannia manicata (Meigen)
4 ♂. I. (1 ♀, Mt. Katahdin, 4,800 ft. Aug. 1913, C. P. Alexander, CU)
Fannia melanura Chillcott
1 ♀. A. (1 ♀, Mt. Katahdin, summit, 5,215 ft. Aug. 1902, USNM)
Fannia metallipennis (Zetterstedt) = *Homalomyia kowarzi* Verrall (Hennig, 1962: 619)
20 ♂, 2 ♀. A, B, D, H, J.
Fannia mutica (Zetterstedt)
1 ♂, 1 ♀. H, J.
Fannia nidicola Malloch
1 ♀. V.
Fannia postica (Stein)
2 ♂, 24 ♀. B, E, H, J, M, N, O.
Fannia rondanii (Strobl)
2 ♂. J, V.
Fannia scalaris (Fabricius)
17 ♂, 1 ♀. D, I, V.
Fannia sociella (Zetterstedt)
47 ♂, 36 ♀. B, D, E, H, J, M-N, O, V.
Fannia spathiophora Malloch
1 ♂, 11 ♀. D, I, J.
Coelomyia subpellucens (Zetterstedt)
167 ♂, 122 ♀. B, D, E, I, J, M, N, O, Q, T, V.
Azelia gibbera (Meigen)
1 ♂. J.

Hydrotaea cristata Malloch
1 ♀. H.
Hydrotaea houghi Malloch
3 ♀. E, I, N.
Hydrotaea militaris (Meigen)
29 ♂, 219 ♀. B, C, D, E, F, G, I, J, L, M, N, O, P, Q, R, S, T, V.
Hydrotaea pilipes Stein
1 ♀. P.
Hydrotaea pilitibia Stein
2 ♀. J, Q.
Hydrotaea spinifemorata Huckett
5 ♂, 13 ♀. B, E, F, J, M, N, O-P.
Hydrotaea unispinosa Malloch
1 ♀. E.
Lasiops albibasalis (Zetterstedt)
54 ♂, 37 ♀. E, F, I, J, L, M, N, O, Q, R, V. (1 ♀, Mt. Katahdin, summit, 5,215 ft. Aug. 19, 1902, USNM)
Lasiops hirtulus (Zetterstedt)
26 ♂, 50 ♀. F, H, M, N, O-P, Q, R, S, T. (1 ♀, Mt. Katahdin, 5,200 ft. Aug. 1913, C. P. Alexander, CU)
Lasiops innocuus (Zetterstedt)
242 ♂, 150 ♀. B, D, E, F, I, J, M, N, O-P, Q, R, S, T, V.
Lasiops rufisquama (Schnabl)
3 ♂, 1 ♀. E, F, I, J.
Lasiops spiniger (Stein)
264 ♂, 269 ♀. B, D, E, F, I, J, K, L, M, N, O-P, Q, R, T, V. (1 ♀, Mt. Katahdin, 4,800 ft., 1 ♀, at 5,100 ft., both Aug. 1913, C. P. Alexander, CU; 1 ♂, 2 ♀, Mt. Katahdin, "Camp Kennedy," 3,000 ft. Aug. 1902, 1 ♂, Mt. Katahdin, 3,400 ft. Aug. 14, 1902, both USNM)
Alloeostylus diaphanus (Wiedemann)
4 ♂, 2 ♀. F, H, J, N, P. (2 ♀, Mt. Katahdin, "Camp Kennedy," 3,000 ft. 1902, USNM)
Dendrophaonia querceti (Bouché)
1 ♀. J.
Phaonia apicata Johannsen
5 ♂, 3 ♀. A, E, F, J, M.
Phaonia bysia (Walker)
2 ♀. E, M.
Phaonia cauta n. sp.
2 ♂. J.
Phaonia curvipes (Stein)
18 ♂, 13 ♀. B, C, E, H, J.
Phaonia errans (Meigen)
1 ♂. D.
Phaonia errans var. *luteva* (Walker)
1 ♀. F.
Phaonia protuberans Malloch
55 ♂, 59 ♀. C, D, I, J, M, N, O-P, Q, R, S, V.
Phaonia rugia (Walker)
20 ♂, 32 ♀. B, C, D, E, M, N, O, Q, R, T.
Phaonia serva (Meigen)
19 ♂, 24 ♀. B, C, D, E, F, I, J, M-N, Q, S.

Phaonia soccata (Walker)
1 ♀. Q.
Phaonia tipulivora Malloch
2 ♂, 1 ♀. D, I, R.
Lophosceles cinereiventris (Zetterstedt)
353 ♂, 246 ♀. B, C, D, E, I, J, L, M, N, O-P, S, T, V.
Lophosceles frenatus (Holmgren)
2 ♂, 1 ♀. H, M-N.
Muscina flukei Snyder
1 ♂, 19 ♀. C, D, E, I, J, M, N, P.
Muscina stabulans (Fallén)
1 ♂, 1 ♀. D, I.
Mesembrina latreillii Robineau-Desvoidy
3 ♀. H, J, N.
Morellia micans (Macquart)
3 ♂, 9 ♀. C, F, H, J, M-N, R, T.
Morellia podagrica (Loew)
34 ♂, 40 ♀. A, B, C, D, E, F, G, I, J, L, N, O, Q, R, T.
Pyrellia cyanicolor (Zetterstedt)
1 ♂, 12 ♀. C, D, E, J, M, N, T.
Musca domestica Linnaeus
6 ♂, 3 ♀. I, M.

Chirosia setifer, NEW SPECIES

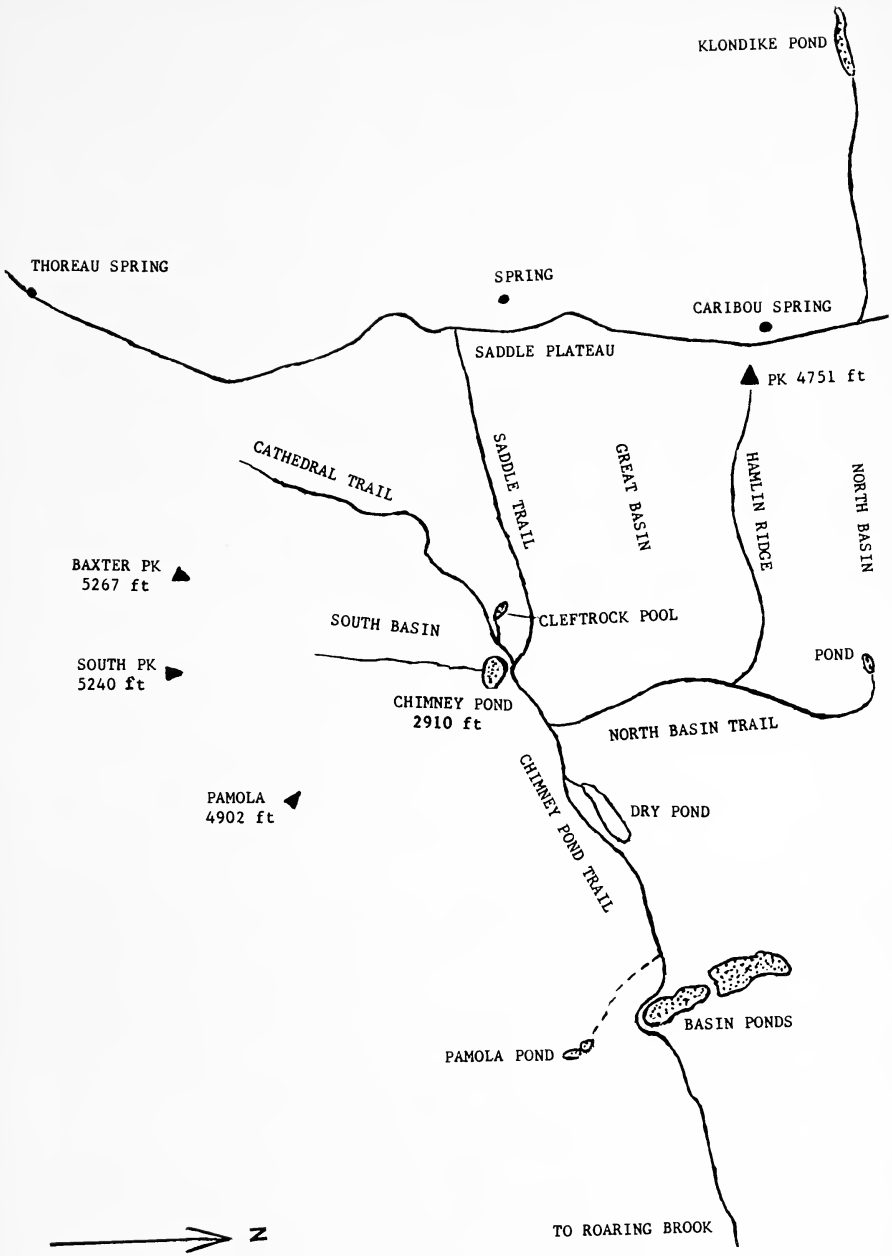
Male. Black, subshining, mesonotum and abdomen with brownish pruinescence, head with parafrontals brownish, parafacials, cheeks and face gray, interfrontalia purplish black and with a whitish sheen when seen from in front, second antennal segment brownish, third black, palpi dark brown, haustellum dull. Abdomen with restricted subtriangular marks. Legs black, pulvilli whitish. Wing-veins and calyptrae yellowish, knobs of halteres yellow.

Eyes broadly separated at vertex, wider apart than distance between first pair of dorsocentral bristles, interfrontalia as wide as breadth of third antennal segment, height of cheek and length of aristal hairs respectively about equal to half the antennal width, vertical bristles long and erect, 2 pairs of reclinate paraorbitals and 3 pairs of parafrontal bristles, profrons prominent, parafacials narrow and receding ventrad, proboscis swollen. Mesonotum without stripes, 2 pairs of presutural acrostical bristles, the series being narrowly separated, prealar slightly longer than half length of posterior notopleural bristle, scutellum with ventral hairs, sternopleurals 1:2, all long. Abdomen slender, depressed, slightly tapering on caudal region as seen from above, hypopygium nonswollen, processes of sternum 5 broad and bluntly rounded at apex, weakly bristled.

Fore tibia notably setulose ventrad, with 1 or 2 *ad*, 2 *pv*, mid femur with extensive series of *av* setae, 3 proximal *pv*, mid tibia with 1 *ad*, 2 *pd*, 2 *pv*, hind femur with 5 or 6 *av*, 3 or 4 proximal short *pv*, hind tibia with 4 *av*, 4 *ad*, 3 *pd*, 4 or 5 semierect *post* setulae, apical *pv* robust.

Wings with costal setulae irregularly coarse, semierect on proximal half of costa, costal thorn as long as *r-m* cross-vein.

Female. Similar to male except for sexual characters, interfrontalia evenly broad to vertex, as wide as length of third antennal segment; abdomen black, shiny, sparsely dusted and without medial stripe; caudal pair of ocellar bristles upright, prealar variable in length, not as long as posterior notopleural bristle; abdomen with discal bristles on terga 3, 4, 5. Fore



Sketch map showing collecting localities on Mt. Katahdin. Distances from Chimney Pond to Basin Pond are 1.2 miles; to the Saddle, 1.2 miles; to North Basin Pond, 1.3 miles; to Thoreau Spring, 2.6 miles; to Caribou Spring, 2.1 miles; to Klondike Pond, 3.0 miles (A.M.C. Katahdin Guide, 1956).

tibia normal, with 1 *ad*, 2 *post*, 1 mid *pv*, apical *pv* robust, mid femur with 4 short *av*, 3 *pv*, mid tibia with robust *ad*, 3 or 4 *pd*, 1 *pv*, hind femur with 5 *av*, 2 *pv*, hind tibia with 4 or 5 *av*, 4 or 5 *ad*, 3 or 4 *pd*, 1 semierect *post* setula, apical *pv* strong.

Length, 4.5 to 5 mm.

HOLOTYPE AND ALLOTYPE: ♂ and ♀, Mt. Katahdin, Klondike Pond, 3,500 feet, July 12, 1959 (USNM). Syntypes: 1 ♀, same data as holotype; 1 ♂, Mt. Katahdin, South Basin, 3,000 feet, July 6, 1959; 1 ♀, Mt. Katahdin, Dry Pond, 2,800 feet, July 10, 1959 (both HCH).

The male of *Chirosia setifer* has a slender, depressed abdomen, and may be separated from males of similar character by the broad frons with femalelike bristling. In both sexes there are two pairs of reclinate paraorbital bristles and two long caudal sternopleurals, arista distinctly pubescent.

I have tentatively followed Collin (1955) in restricting the genus *Pycnoglossa* Coquillett (1901) to the single species *Musca flavipennis* Fallén, and along with Collin (loc. cit.) and Hennig (1966: 251–268) have regarded the remaining species in *Pycnoglossa* as akin to those in *Chirosia* Rondani on account of their similar habits and behavior as recorded.

Spilogona broweri, NEW SPECIES

Male. Head with parafrontals and cheeks gray, parafacials whitish pruinescent, the broad interfrontalia with a whitish sheen when seen from in front, haustellum shiny; mesonotum and scutellum deep seal brown, subshining, humeral callosities gray when seen from behind; abdomen gray, terga 1 + 2 dark brown, tergum 3 with a pair of subquadrate and tergum 4 with subtriangular marks, each with or without a medial stripe, the subquadrate marks may be fused lightly across dorsum, tergum 5 with a pair of narrow submedial marks. Legs black, pulvilli whitish. Wings clear, upper calyptral scale white, lower slightly dulled and margin pale brown, knobs of halteres yellow.

Frons at vertex as wide as distance between first pair of dorsocentral bristles, interfrontalia evenly broad caudad, wider than breadth of third antennal segment, inner pair of vertical bristles robust and erect, parafrontals narrow and bristled as in female, with 2 pairs of reclinate paraorbitals and 3 pairs of incurving parafrontal bristles, anterior pair of ocellar bristles robust, parafacials narrow and receding ventrad, vibrissae strong, eyes tall, cheeks reduced in height to one-half the width of third antennal segment, the latter nearly twice as long as wide, at apex nearly reaching a level with oral margin, artista minutely pubescent; mesonotum without stripes, acrosticals coarse, irregularly set, one or two presutural pairs bristly, 3 pairs of postsutural dorsocentral bristles, notopleural depression without setulae, predorsal interspatial mesopleural bristle (*lückenborste*) absent, scutellum with declivities hairless, sternopleurals 1:2, abdomen subovate and slightly depressed, processes of sternum 5 shiny and broadly maintained distad, blunt at apex, sparsely bristled.

Fore tibia with 1 or 2 weak *post*, mid femur with 3 or 4 proximal *pv*, mid tibia with or without a setulose *ad*, 1 or more *pd*, hind femur with 2 to 4 *av* on distal half, 2 to 4 short *pv* on proximal half, hind tibia with 2 *av*, 1 or 2 *ad*, apical *av* robust. Wings with costal setulae coarse, costal thorn weak, veins R_{1+5} and M_{1+2} gradually diverging toward wing margin, *m-cu* cross-vein upright.

Length, 4 mm.

The type series from Mt. Katahdin is as follows.

HOLOTYPE: ♂, Chimney Pond trail, 2,800–3,000 feet, June 27 to 30, 1958 (USNM). Syntypes: Chimney Pond trail, 1 ♂, July 1, 1 ♂, July 4, 1957, 2 ♂, same data as holotype (all USNM); North Basin Pond 2 ♂, July 17, 1959 (USNM), 1 ♂, July 7, 1959 (HCH); Chimney Pond, 4 ♂, June 30 to July 15, 1957 (A. E. Brower; CNC), 2 ♂, July 9, 1959 (HCH); South

Basin, 2 ♂, July 10, 1957 (A. E. Brower; CNC), 1 ♂, July 6, 1959 (HCH); Saddle trail, 2 ♂, July 3 to 13, 1 ♂, July 4 to 12, 1957 (CNC); Dry Pond, 2 ♂, July 10, 1959 (HCH); North Basin trail, 1 ♂, July 5, 1959, and Hamlin Ridge trail, 1 ♂, July 13, 1959 (both HCH).

Spilogona browerí is related to *S. forticula* Huckett, from which it differs in having the male thorax seal brown, and the abdomen, from base to apex, not deeply formed. In both species the antennae are longer and cheeks narrower than in *arctica*, *contractifrons*, or *alticola*. I have in addition a male and female, the only female specimen unfortunately, taken on the Chimney Pond trail on July 2, 1958, that I regard as belonging to *browerí*. Both specimens are quite teneral, the frons of the male having collapsed. The female specimen differs from that of *forticula* by its darker color, the mesonotum having three suffused brown stripes. Named in honor of Dr. A. E. Brower, whose field assistance and generous cooperation served on many occasions to lighten the work of carrying out this survey.

Spilogona concomitans, new species

Male. Head as in *browerí*, interfrontalia with a brownish sheen when seen from in front, parafrontals, parafacials, face and cheeks brown, haustellum polished; thorax dull brown, mesonotum shiny when seen from behind, with 3 faint stripes, humeral callosities pale brown; abdomen slate gray, shiny, terga 1 + 2 brown, terga 3 and 4 with brownish subtriangular marks confined to dorsum, and with an interrupted mid-dorsal stripe, tergum 5 with reduced submedial marks. Legs black, pulvilli brownish. Wings tinged, calyptrae yellowish, knobs of halteres yellow.

Frons broad and bristled as in *browerí*, with 6 or 7 pairs of parafrontal bristles, parafacials narrow and receding ventrad, cheeks nearly as high as width of third antennal segment, the latter 1.5 times as long as wide. Mesonotum with paired series of short acrosticals, the mid presutural pair bristly, posterior notopleural bristle with hairs at base, scutellum with preapical hairs on declivities, 3 pairs of postsutural dorsocentral bristles, sternopleurals 1:2. Abdomen stout and thickened, processes of sternum 5 dull, broad and truncated at apex, weakly bristled.

Fore tibia with mid *post*, mid femur with 3 or 4 *pv* on proximal half, mid tibia with 1 *ad*, 2 *pd*, hind femur with full series of *av*, and proximal series of *pv*, hind tibia with 1 *av*, 2 *ad*, and 1 weak mid-*post*. Wings with costal thorns weak, veins R_{4+5} and M_{1+2} diverging slightly toward margin of wing, *m-cu* cross-vein upright.

Length, 3.75 mm.

Female. Paler brown than male, parafacials and cheeks grayish when viewed laterad, humeral callosities paler; abdomen ovate, lustrous, with paired expansive marks on terga 3 and 4, ovipositor with recurrent spinules on subanal sclerite. Legs bristled as in male, the proximal bristles of mid and hind femora sparse and finer.

Length, 4.25 mm.

HOLOTYPE: ♂, Mt. Katahdin, South Basin, 3,000 feet, July 11, 1957 (USNM).

ALLOTYPE: ♀, Mt. Katahdin, Chimney Pond, 2,950 feet, July 14, 1959 (USNM).

The species *Spilogona concomitans* resembles *S. browerí*, from which it differs in having parafrontals, parafacials and cheeks infuscated, antennae shorter and cheeks broader, posterior notopleural bristle with hairs at base, scutellum with preapical hairs on declivities, and hind femur with a full series of anteroventral bristles. I have in addition a male specimen with antennae and abdomen missing, that I regard as conspecific with *concomitans*, taken on Hamlin Ridge trail on July 13, 1959.

Spilogona katahdin, NEW SPECIES

Male. Gray, head with parafrontals, parafacials and cheeks silvery, occiput gray, interfrontalia black, haustellum dull; mesonotum and scutellum subshining, brownish, humeral callosities and pleura gray, mesonotum with 3 stripes; abdomen gray, terga 1 + 2 partly or entirely blackish on dorsum, tergum 3 with quadrate and tergum 4 subtriangular marks that do not extend to lateral margins of dorsum, and with or without a weak medial stripe, tergum 5 with trace of medial marking, hypopygium lightly dusted. Legs black, pulvilli tinged. Wings smoky, veins brown, *m-cu* cross-vein with or without pale infuscation, calyptrae yellowish, knobs of halteres yellow.

Eyes bare, narrower part of frons equal to distance between posterior ocelli inclusive, interfrontalia uninterrupted caudad, series of parafrontal bristles continued caudad to level with anterior ocellus, caudal pair reclinate, profrons half as long and cheek three-fourths as high as width of third antennal segment, the latter one and a half times as long as wide, parafacials in profile receding ventrad, artista minutely pubescent, proboscis thick; mesonotum with presutural acrosticals diverse and irregularly arranged, being bristly and setulose, posterior notopleural bristle with hairs near base, mesopleural series with fine supplementary predorsal bristle (*lückenborste*), 4 pairs of postsutural dorsocentral bristles, sternopleurals 1:2; abdomen conical, marks on tergum 3 longer than wide, on tergum 4 not extending to anterior border, sternum 1 with setulae, processes of sternum 5 broadly extended and bluntly rounded at apex, weakly bristled.

Fore tibia with weak *post*, mid femur with slender proximal *pv*, mid tibia with 1 *ad*, 2 *pd*, hind femur with entire series of *av*, those on proximal half much weaker, with 2 or 3 slender proximal *pv*, hind tibia with 3 *av*, 2 *ad*, 2 weak *pd*. Wings with short costal setulae and thorns, *m-cu* cross-vein upright and slightly bowed inward at middle.

Length, 5.5 mm.

Female. Dark gray, parafrontals gray, parafacials and cheeks whitish pruinescent, interfrontalia with a whitish sheen when seen from in front, frontal triangle dull and extending to frontal border, haustellum dull or with a large dull patch on ventral surface; mesonotum and scutellum gray; abdomen subovate, with a pair of ill-formed subtriangular marks on terga 3 and 4 respectively, that extend to lateral margins of dorsum, tergum 5 obscurely marked. Wings faintly tinged, *m-cu* cross-vein clouded.

Head with 2 pairs of reclinate paraorbital bristles, mesonotum with 3 pairs of bristly and several setulose presutural acrosticals; ovipositor with polished sclerites and fine setulae on anal plates. Legs bristled as in male, the *av* and *pv* on proximal half of hind femur weak. Otherwise similar to male except for sexual characters.

Length, 4.5 mm.

HOLOTYPE: ♂, Mt. Katahdin, Klondike Pond, 3,500 feet, July 12, 1959 (USNM).

ALLOTYPE: ♀, Mt. Katahdin, Dry Pond, 2,800 feet, July 10, 1959 (USNM). Syntypes: 1 ♂, same data as holotype. 1 ♂, Mt. Katahdin, South Basin, 3,000 feet, July 1, 1958 (CNC); 1 ♂, Chimney Pond, 2,914 feet, June 30 to July 15, 1957 (HCH); 1 ♀, South Basin, 3,000–3,500 feet, July 10, 1957 (HCH).

The species *Spilogona katahdin* possesses the habitus of *S. norvegica* Ringdahl, appearing dark gray, having the haustellum dull, and in the male the abdomen conical or slender. The male of *katahdin* differs from that of *norvegica* in having parafacials and cheeks narrower, and abdominal marks less extended. The above specimens in both sexes of *katahdin* possess fine hairs near base of posterior notopleural bristle, a fine predorsal interspatial bristle in the

mesopleural series, 2 or 3 pairs of bristly presutural acrosticals, and a few setulae on abdominal sternum 1.

Lispocephala aemulata, NEW SPECIES

Male. Gray, parafrontals brownish, interfrontalia black, parafacials, face and cheeks white, second and base of third antennal segments yellow, palpi pale yellow; mesonotum with two brown stripes, fuscous laterad, humerals gray, scutellum dingy and with inconspicuous brown marks at basal angles; abdomen yellowish testaceous on basal two segments, gray caudad, terga 1 + 2 and 3 with well-formed vitta, that become lineal and weak on terga 4 and 5, with a pair of brown spots on terga 3 to 5. Femora gray-black, narrowly fulvous at apices, tibiae and tarsi entirely fulvous. Wings tinged, cross-veins clear.

Frons with two pairs of paraorbital and three pairs of parafrontal bristles, arista short pubescent; mesonotum with 2 irregularly paired presutural acrostical bristles; abdomen robust, marginal and discal bristles weak, successively becoming stronger caudad, tergum 5 with 4 or 5 slender marginal bristles laterad, processes of sternum 5 shiny and broadly maintained to apical margin, inner border with a coarse series of fine setulae from base to apex, those on proximal half short, on distal half long, cerci slender and needlelike in form.

Fore tibia with a setulose mid *post*, mid tibia with 1 *post*, hind femur with entire series of *av*, hind tibia 1 *av*, 2 *ad*, 1 strong and 1 weak *pd*, with semierect *ant* setulae.

Length, 4 mm.

HOLOTYPE: ♂, Mt. Katahdin, South Basin, 3,000–3,500 feet, July 5, 1958 (USNM).

The male of *Lispocephala aemulata* has the cross-veins unclouded, and basal segments of abdomen yellowish testaceous. In *L. tinctinervis* Malloch, the male of which possesses an abdomen of similar color, both cross-veins are clouded, and inner margins of processes to sternum 5 marked by a chitinous projection (Malloch, 1935: 566; Fig. 2).

I have also compared *aemulata* with a male of *L. surda* (Zetterstedt) as treated by Collin (1963), a specimen of which was kindly furnished me by Mr. A. C. Pont of the British Museum (Natural History), and after he had examined the holotype of *aemulata*. I have concluded that the two taxa, although very similar, are not conspecific, *aemulata* differing in its paler aspect, as exemplified in the whitish parafacials, face and cheeks, and by the undarkened pellucid coloring of the two basal abdominal segments.

Mydaea grata, NEW SPECIES

Male. Black, parafrontals, parafacials and cheeks silvery pruinescent, antennae black, anterior border of second segment brown, palpi dark brown, paler basad. Thorax black, mesonotum viewed from behind lacking dust except between the inner pair of stripes on presutural region, outer pair of stripes obscure on postsutural region. Abdomen evenly yellowish gray, lustrous, without darker patches or checkering, with a lineal dorsocentral vitta. Coxae black, concolorous with thorax, femora and tibiae fulvous, tarsi dark brown, pulvilli tinged. Wings with veins brown, paler basad, calyptrae yellowish, knobs of halteres yellow.

Eyes closely approximated along frons, extensively so, parafrontals at narrowest width of frons contiguous, each equal to diameter of anterior ocellus, series of parafrontal bristles ending caudad at narrowest width of frons, profrons and cheek in profile each equal to one-third width of third antennal segment, the latter appendage 2.75 times as long as wide, longer aristal hairs equal to width of third antennal segment. Mesonotum with a broad band of weak acrosticals and one pair of robust bristles caudad, prealar bristle long, dorsocentrals 2–4, sternopleurals 1:2, hypopleura with setulae ventrad and above hind coxae.

Fore tibia with a fringe of semierect *pv* setulae, mid femur with short proximal *av* and stronger *pv*, mid tibia with 3 *post*, hind femur with 6 short *av* on distal half, and weak fine

av and *pv* on proximal half, hind tibia with 2 *av*, 2 *ad*, and semierect *post* setulae. Wings with *m-cu* cross-vein upright.

Length, 5 mm.

Female. Closely resembling the male except for sexual characters and weaker bristling on the femora; parafrontals, parafacials and cheeks whitish, second antennal segment mostly brown or black, mesonotum lustrous, and when seen from behind blackish laterad and devoid of outer pair of stripes on postsutural region. Tarsi black.

Parafrontals with 2 pairs of reclinate paraorbital and 4 or 5 pairs of parafrontal bristles. Fore tibia without *pv* series of semierect setulae, mid tibia with 3 *post*, mid femur with *av* and *pv* weak, setulose, hind femur with proximal *av* and *pv* weaker and sparse, hind tibia with 3 *av*, 2 or 3 *ad*.

Length, 6 mm.

HOLOTYPE: ♂, Mt. Katahdin, Chimney Pond, 2,914 feet, July 1–5, 1958 (USNM).

ALLOTYPE: ♀, same locality as holotype, July 3, 1959 (USNM). Syntypes: 1 ♀, Mt. Katahdin, North Basin trail, 2,800–3,200 feet, July 13, 1959; 1 ♀, Mt. Katahdin, South Basin, 3,000–3,500 feet, July 10, 1957 (both USNM).

The species *Mydaea grata* has a long prealar bristle, thus running in the keys to the couplet with *Mydaea urbana* (Meigen), and from which it may be distinguished by the weaker bristling on mid and hind femora, and the obsolescence of the outer pair of mesonotal stripes on postsutural region, when viewed from behind. The species *grata* is more closely related in habitus to *Mydaea detrita* (Zetterstedt), of which I have before me a male specimen determined by van Emden and kindly furnished by Mr. A. C. Pont, and a male and female from Sweden, the male identified by Ringdahl, all possessing stronger bristling on mid and hind femora.

I find that all the above specimens of *detrita* have one or more setulae on the hypopleural region adjacent to the hind coxa, and at variance with Hennig's (1956: 123) description of the male of *detrita*, namely "*Hypopleura nackt.*"

Phaonia cauta, NEW SPECIES

Male. Black, subshining, parafrontals, parafacials and cheeks silvery pruinescent, third antennal segment black, palpi dark brown; thorax black, sparsely dusted, mesonotum with four vittae, becoming obscured on postsutural region as viewed from behind, scutellum fulvous, more or less darkened basad; abdomen with whitish gray dust and a medial vitta. Fore femur fulvous, with or without infuscation, mid and hind femora and all tibiae fulvous, tarsi black, pulvilli tinged. Wings clear, faintly yellowish anteriorly, and denser basad, calyptrae and knobs of halteres yellow.

Eyes sparsely haired, frons at narrowest part as wide as distance between or including posterior ocelli, parafrontals here contiguous or lineally separated, with 4 pairs of parafrontal bristles, and 2 pairs of setulae opposite ocellar callosity, profrons and narrower part of cheek, in profile, respectively not longer nor higher than half width of third antennal segment, the latter appendage slightly longer than twice its width, longer aristal hairs slightly longer than width of third antennal segment; mesonotum with acrosticals setulose exclusive of caudal pair and one bristly presutural pair, prealar shorter than first dorsocentral bristle, dorsocentrals 2–3, sternopleurals 1:2, hypopleura hairless; abdomen subovate.

Fore tibia without *post*, mid femur with a series of sparsely set short *pv*, mid tibia with 3 *post*, hind femur with *av* series continued to basal region, and as weaker bristles on proximal half, with weak proximal *pv*, hind tibia with 2 or 3 *av*, 2 *ad*, 1 *pd*. Wings with *m-cu* cross-vein upright and slightly bowed inward at middle.

Length, 6 mm.

HOLOTYPE: ♂, Mt. Katahdin, South Basin, 3,200–3,500 feet, July 14, 1959 (USNM). Syntype: 1 ♂, same data as holotype.

The species *Phaonia cauta* has the third antennal segment entirely black, as in *P. apicalis* Stein, and from which it differs by having a shorter prealar bristle and longer hairs on the arista. The species *cauta* may be associated with the nearctic taxa *P. apicata* Johannsen and *P. bysia* (Walker), from both of which *cauta* may be separated by the entirely black third antennal segment, not yellowish at basal region. I have also taken *cauta* on Mt. Le Conte in the Great Smoky Mountains, 6 males and 26 females in May of 1958 and 1959.

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The Genus *Menecles* Stål (Hemiptera; Pentatomidae)

L. H. ROLSTON

DEPARTMENT OF ENTOMOLOGY, LOUISIANA STATE UNIVERSITY, BATON ROUGE, LOUISIANA

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Abstract: A diagnosis is given for the genus *Menecles*, *M. insertus* (Say) is redescribed, and a new species of the genus described from Texas.

Key words: Pentatominae, Pentatomini, new species, genitalia, stinkbug.

Menecles has been monotypic until now, represented by the widely distributed North American species, *M. insertus* (Say). This species is redescribed to emphasize the many differences between it and a new species from the Big Bend region of Texas. A diagnosis of *Menecles* is provided to facilitate its recognition among pentatomine genera.

MENECLES STÅL

STÅL, 1867, OFV. SVENSKA VET.-AK. FORH. XXIV NO. 7 P. 527

Body oval, sides subparallel, moderately convex dorsally, more strongly so ventrally. Head inserted deeply into thorax, basal third to half of eyes lying behind imaginary line connecting apex of anterolateral pronotal angles (Fig. 1). Apex of pronotum wider than head, on each side extending laterad of head by about ½ diameter of eye, behind vertex of head emarginate to depth subequal to ¼ maximum length of pronotum; anterolateral pronotal margins weakly convex, entire, explanate; humeri broadly rounded, not produced. Apical margin of corium extending obliquely posterolaterad from apex of scutellum to acute angle. Bucculae evanescent at base of head, subequal in length to first rostral segment. Subspatulate ostiolar rugae short, elevated at apex. Tibiae sulcate. Abdomen without tubercle or spine.

Menecles insertus (Say, 1832)

Pentatoma insertus Say, 1832, Desc. Het. Hem. p. 6

Menecles insertus; Stål, 1867, Ofv. Svenska Vet.-Ak. Forh. XXIV no. 7 p. 527; Blatchley, 1926, Het. p. 145 (desc.); Baker, 1931, Can. J. Res. 4(3): 199, 200 figs. 109–112 (genitalia); Froeschner, 1941, Amer. Mid. Nat. 26: 138 (biol. note); McDonald, 1966, Quaes. Ent. 2: 27, 111 figs. 232–6 (genitalia)

Menecles incertus; Van Duzee, 1904, Trans. Amer. Ent. Soc. XXX p. 52 (laps. cal.)

Dorsum with narrow, impunctate, median line extending from anterior margin of pronotum onto basal disk of scutellum, otherwise rather closely, uniformly punctate with black on sordid yellow to light castaneous background. Ventral surfaces concolorous with dorsum, punctation black, on head and thorax moderately dense, on abdomen dense, usually accretive; a large, median, black spot on each abdominal segment and pygophore, occasionally obsolete on first or first two basal segments, elongated among males on apical segment and pygophore, among females on apical two segments. Length 11.7 to 12.9 mm.

Width and length of head subequal, 2.5 to 2.6 mm. wide across eyes. Basal three and proximal portion of fourth antennae segments concolorous with head, distal portion of fourth and all of fifth fuscous; fourth segment perceptibly flattened; length of segments 0.6 to 0.7; 0.8 to 1.0; 1.1 to 1.3; 1.0 to 1.3; 1.6 to 1.7 mm., fifth segment substantially longer than fourth.

Pronotum 2.4 to 2.9 mm. long at meson, 2.5 to 2.7 times as wide at humeri. Length of scutellum about $\frac{1}{10}$ longer than width at base, 4.5 to 5.0 mm. long; clustered punctures in basal angles forming small, shallow fovea; membrane of hemelytra slightly brown, transparent, with reticulate venation. Connexivum rather broadly exposed, punctate with black, marked at basal and usually apical angles of each segment with large, diffuse, black spot.

Mesosternum largely covered on each side of median carina by subquadrate black spot. Legs dotted with black. Incisures at margin of abdomen bordered by diffuse black spot. Spiracles black.

Emargination of posterior margin of pygophore broad, sinuous, moderately deep, exposing inferior ridge from caudal view (Fig. 3). Proctiger with heavy, transverse, preapical ridge (Fig. 2). Cephalic margin of parameres subacutely produced above broad, shallow cup; apical hook somewhat triangular, finely denticulate on inner surface (Fig. 4). Lateral lobes of theca strongly produced laterad, not at all caudad (Fig. 6). Conjunctiva with long dorsal appendage, multiple lobes ventrally, none sclerotized at apex; median penal lobes quite large (Fig. 5).

Menecles **portacrus**, n. sp.

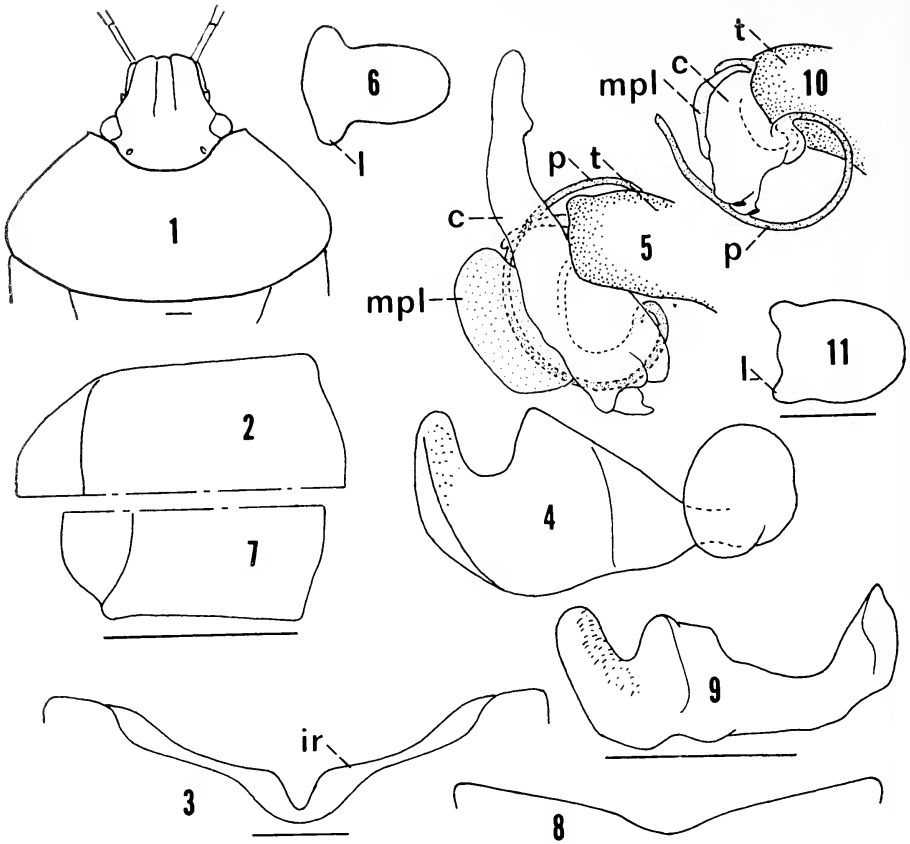
Dorsum bearing cross of two, narrow, impunctate lines, one traversing pronotum between humeri, other dividing pronotum along meson, usually continuing caudad onto basal disk of scutellum, extending cephalad as sparsely punctate fascia across vertex of head onto tylus; background yellowish brown with numerous darker spots on corium, punctured rather closely and uniformly with fuscous to black. Sordid yellow beneath, abdomen faintly tinged with orange and finely flecked with red; punctures mostly concolorous or dilute fuscous, of moderate size on head and thorax, nearly obscure on abdomen. Length 10.8 to 11.8 mm.

Head slightly broader than long, 2.5 to 2.7 mm. wide across eyes. Antennae sordid yellow marked with black dots on lateral surface of basal segment, these dots coalescing toward apex into streak; second segment streaked along lateral surface and circled at apex with black; distal $\frac{1}{2}$ of third, distal $\frac{2}{3}$ of fourth and fifth segments black; length of segments 0.6 to 0.7; 0.9 to 1.2; 1.0 to 1.3; 1.2 to 1.3; 1.4 to 1.5 mm.; fifth segment barely longer than fourth.

Pronotum 2.7 to 2.8 mm. long at meson, 2.4 to 2.5 times as wide across humeri. Width of scutellum at base subequal to length, 4.3 to 4.6 mm. long; punctures clustered in basal angles but not forming distinct fovea. Membrane of hemelytra brownish, transparent; veins simple or branched, occasionally forming cell. Moderately exposed connexivum fuscous with very margin, marginal spot in middle of each segment and punctures dark yellowish brown.

Thorax with five black spots on each side, one at base of each subcoxa, one on mesopleuron near distal end of supracoxal cleft, one on anterior border of propleuron behind eye. Sterna concolorous with pleura. Legs dotted with black. Submarginal row of two or four dots on most or all abdominal sternites; incisures immaculate; spiracles black.

Emargination of posterior margin of pygophore broad, shallow, V-shaped, not exposing inferior ridge from caudal view (Fig. 8). Preapical ridge of proctiger curving basad between obscurely developed tubercles (Fig. 7). Cephalic margin of parameres truncately produced basad of cup; cylindrical apical hook clearly striated on inner surface (Fig. 9). Lateral lobes of theca produced weakly laterad, more strongly caudad (Fig. 11); conjunctiva



FIGS. 1, 7–11. *M.* **portacrus**, n. sp. FIG. 1. Head and pronotum. FIG. 7. Proctiger, right half. FIG. 8. Posterior margin of pygophore, caudal view. FIG. 9. Right paramere. FIG. 10. Theca and related structures, lateral aspect; conjunctiva (c), median penal lobe (mpl), penisfilum (p), theca (t). FIG. 11. Theca, dorsal aspect; lateral lobe (1).

FIGS. 2–6. *M. insertus*. FIG. 2. Proctiger, left half. FIG. 3. Posterior margin of pygophore, caudal view; inferior ridge (ir). FIG. 4. Right paramere. FIG. 5. Theca and related structures, lateral aspect; conjunctiva (c), median penal lobes (mpl), penisfilum (p), theca (t). FIG. 6. Theca, dorsal aspect; lateral lobe (1).

bilobed on each side, each lobe terminating in small, dark, apical plate; median penal lobes of moderate size (Fig. 10).

TYPES. Holotype, male, labeled Lost Mines Trail, Big Bend Natl. Pk., Brewster Co., Tex. VII-14-50, 5800 ft., Ray F. Smith. Deposited in American Museum of Natural History. Rostrum damaged.

Paratypes, 3 females: The Basin, Big Bend National Park, Texas, VIII-15-1968. J. E. Hafernik (author's coll.); Green Gulch, Big Bend National Park, Texas, 5700 ft., July 24, 1968. J. E. Hafernik (Texas A&M Univ.); Chisos. M., IX-19-38, Tex. (b) D. J. & J. N. Knull Collrs. (Ohio State Univ.)

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Platypus rugulosus (Platypodidae) and *Xyleborus ferrugineus* (Scolytidae) and Certain Diseases of Coconut Palms in Puerto Rico[1]

KARL MARAMOROSCH,[2] L. F. MARTORELL,[3] JULIO BIRD,[3] AND PEDRO L. MELÉNDEZ[3]

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Abstract: Adult males of *Platypus rugulosus* Chapuis and adult females of *Xyleborus ferrugineus* (Fabr.) were found in the trunks of stem bleeding diseased coconut palms (*Cocos nucifera* L.) at Dorado Beach, Puerto Rico. The stem bleeding disease organism, *Ceratocystis paradoxa*, was recovered from the tissues of affected palms. The role of *P. rugulosus*, common on the island, and of the very rare *X. ferrugineus* in the decline of palms is obscure. Bud rot caused *Phytophthora palmivora* as well as water logged soil were also found to be affecting palms of various ages at the same location.

In December 1971, at the request of Dorado Beach Estate's horticulturist Roy G. Thomas, an inspection was made of dying coconut palms on the north shore of Puerto Rico approximately 28 miles west of San Juan. A comparison of records and detailed horticultural maps, which indicated the location of individual palms on the estate, showed that during the preceding years many palms had died and been replaced with mature palms at considerable expense. Since on several other Caribbean islands, and mainly on Jamaica, the highly contagious and devastating lethal yellowing disease has recently been found associated with mycoplasmalike organisms (6), the dying of coconut palms was of concern not only to the estate owners but also to others.

Preliminary observations indicated that the dying palms showed none of the typical signs of lethal yellowing disease. Neither did they resemble any of the diseased coconut palms affected by diseases of uncertain etiology, described in 1964 from different areas of the tropics (2). *Phytophthora palmivora* was isolated from the partly affected bud tissues of several young palms showing early symptoms of bud rot.

Other palms with small leaves and thin tapering trunks were found growing on water-drenched areas and many roots were visible on the soil surface. It was first thought that the soil might contain high amounts of mineral salts, but the results of conductivity tests indicated that the salt content was normal. The pH of soil from the root area of these palms was also found to be normal (6.05).

In other cases numerous brown to reddish spots were observed on the trunks

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[2] Boyce Thompson Institute, Yonkers, New York 10701.

[3] University of Puerto Rico, Agricultural Experiment Station, Río Piedras, Puerto Rico.

of affected, as well as of dead, palms. It was observed that where the outer reddish coloration was most intense, there were small tunnels leading inside the trunk. Small beetles were found within the tunnels. Several adult males of *Platypus rugulosus* Chapuis (Platypodidae) and adult females of *Xyleborus ferrugineus* (Fabr.) (Scolytidae) were the only inhabitants of the freshly bored tunnels.[4]

Trunk tissues of palms with the outer reddish coloration were sectioned longitudinally and transversely. Brownish red to dark brown coloration and partial to total decay of inner areas of the stem were characteristically associated with the bleeding palms. Small sections of tissue from interior areas of the trunk were surface sterilized and plated in various media. The fungus *Ceratocystis paradoxa* was isolated in every case. Partially invaded tissues also yielded the organism. Both the perfect as well as the imperfect stage (*Thielaviopsis paradoxa*) of the fungus were recovered from the inner tissues of the affected palms. The outer reddish discoloration, the interior symptoms of the malady, and the consistent isolation of *C. paradoxa* from infected material indicated that one of the most important diseases of palms in the Dorado Estate is stem bleeding. This malady has been described in various parts of the world and accepted to be caused by *C. paradoxa* (5).

It is known that beetles from the families Scolytidae and Platypodidae may attack weakened or diseased trees or plants, but these insects do not usually attack healthy trees. Most adult beetles are known to feed on the bark of trees while their larvae live in specially built galleries and feed on the mycelia of diverse ascomycetes (on the so-called ambrosia). The spores of the fungi are introduced in the galleries through the digestive tract of adult females. Whether the infestation at Dorado Beach Estates was an exception in which healthy trees were attacked is not possible to say at this time but instances of such occurrences have sometimes been known.

Apate monachus Fabricius, a bostrichid, is a common insect in Puerto Rico where it normally breeds in logs and dying trees. However, it came to be known as the "coffee tree borer" since it will attack living as well as dead coffee trees when population levels are high. This beetle has also been shown to attack many other tree species including mahogany, avocado, and tamarind (3, 4). Instances of similar behavior have been recorded locally in the case of certain buprestids and cerambycids.

In Puerto Rico, coconut palms as well as sugarcane stalks, coffee, trees of the genus *Inga*, and trees of the genus *Albizzia* have been attacked by other species of scolytids. In addition, many species of forest trees, guava fruits

[4] The identification of the two species was made by Dr. D. M. Anderson of the Insect Identification and Parasites Introduction Research Branch (now defunct), U.S. Department of Agriculture, ARS, Beltsville, Md., to whom the authors are indebted for his prompt assistance.

(*Psidium guajava*), oranges, and *Crotalaria* pods have been infested. However, *X. ferrugineus* is very rare in Puerto Rico and it has not been reported for over 85 years (1). *P. rugulosus*, on the other hand, is common in Puerto Rico. It has a very wide geographic distribution, i.e., from Baja California, to Argentina.

Research is under way to ascertain whether adults or larvae of the two species encountered can attack healthy palms and spread the causal agent of the stem bleeding disease.

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BOOK REVIEWS

Butterflies of the Australian region. Bernard D'Abrera. 1971. Lansdowne (distributed by Entomological Reprints. Specialists, Los Angeles, California). 415 pp. $39.95.

This is a systematic account of butterflies of the Australian region, prepared as an illustrated guide. Instead of using keys, the author has provided an illustrated guide, using type specimens from the British Museum as well as from his own collection. An introductory section deals with the place of butterflies in nature, mimicry and protective resemblance, variation, nomenclature and classification, and a short history of the collection and study of butterflies in the Australian region. The nine groups of butterflies, Papilionidae, Picridae, Danaidae, Nymphalidae, Libytheidae, Satyridae, Amathusiidae, Lycaenidae, and Riodinidae are pictured on 350 pages, followed by a selected bibliography and an index. To complete this work, the author traveled on field expeditions throughout the region, using with great skill his Asahi Pentax Spotmatic camera with a 50 mm Super Macro-Takumar lens and available light conditions. The photographs were made on Ektachrome and high-speed Ektachrome film and the stunning results have to be seen to be believed.

This work is written in a very readable and informative style. Over 3,000 color photographs are reproduced and the color rendition of these is amazingly good. The book is important because it fills a gap in entomological literature and is among the first publications on this subject in nearly 50 years. The unusually rich population of butterflies of the Australian area is covered thoroughly and authoritatively. The beauty of the volume is enhanced by the artistic outlay throughout the book. Identification of the many different species is made easy by the life-size, superb illustrations. The author of this useful book is to be congratulated not only for the enormous amount of essential information it contains but also for the timely publication, greatly needed at this time because of the half-century gap of information on this subject. I am told that the cost of a single large-color page, if printed in the Western Hemisphere, would surpass $1,000, and I have never seen a book so lavishly illustrated and comparatively priced. The secret probably lies, in part at least, in the choice of the printer, Dai Nippon Printing Co., Ltd., in Hong Kong. The printing is remarkably free of typographical errors. The book will be an essential reference and, in addition to libraries, might find numerous buyers among those who are interested in the sheer beauty of exotic butterflies. It certainly can be read with equal interest by both expert and layman.

K. Maramorosch

Maize Rough Dwarf: A Planthopper Virus Disease Affecting Maize, Rice, Small Grains and Grasses. Isaac Harpaz. 1972. Israel Universities Press, Jerusalem. 251 pp. $20.

The interactions between planthopper vectors and the virus that causes the important disease of maize, known as rough dwarf since 1949, are described in this monograph. The disease occurs in the Mediterranean area. The author, professor of entomology at the Faculty of Agriculture of the Hebrew University at Rehovot, Israel, was the first to establish the viral nature of the disease, and he also contributed significantly to its understanding and control. The geographic distribution of the vectors and the disease, the economic importance to corn-growing countries, symptomatology, host range of the virus in plants as well as in various species of planthoppers in which the virus multiplies, aspects of insect transmission and virus-vector interactions, including harmful effects on planthoppers, and virus purification and electron microscopy are discussed. Special attention is given to the morphology and biology of vector species, the epiphytology and the control of the disease. Work carried out in Italy, Czechoslovakia, Scandinavian countries, Britain, Germany, Japan, southeast Asia, the Soviet Union, Latin America, Africa, and Australia on planthopper vectors is

incorporated in this treatise. A great part of the author's research program has been supported financially by the U.S. Department of Agriculture. The author presents masterfully how a virus, which seemed to have been primarily a pathogen of planthoppers and had become adjusted to Old World cereal grasses so as to cause no appreciable damage, flared up and sometimes killed up to 70 percent of the newly introduced hybrid maize of American origin, when these varieties were introduced after World War II. Numerous tables, figures, color plates, and more than 330 references are provided. The book should be of special interest to entomologists and insect pathologists, as well as to virologists and plant pathologists.

K. MARAMOROSCH

Aphid Technology. H. F. van Emden, ed. 1972. Academic Press, London and New York. 344 pp. $18.50.

This book is the first book written on methods for studying one of the most important crop pests—aphids. Described in the eight chapters are the relevant aspects and techniques for collecting and storing of aphids, the biological properties of these insects and their host plant relationships, evaluations of aphid populations on plants, aerial sampling, natural enemies, measurement of the physical environment, population dynamics, and problems of data analysis. The authors, all prominent experts in their respective fields, were chosen from England, Canada, United States, Czechoslovakia, and Australia. An extremely valuable regionally classified list of bibliographical references, as well as bibliographies for identifying aphids, is included. This book will be indispensable to those who are interested in the important field of crop protection, as well as to all who are working with aphids. It should serve also as an excellent text for entomology students and teachers at colleges and universities. Pertinent references are listed at the end of each chapter and a subject and author index is provided for the whole volume. Illustrations are of fine quality.

K. MARAMOROSCH

Hewitson on Butterflies, 1867–1877. With a preface by Dr. L. G. Higgins. 1972. E. W. Classey Ltd. (distributed by Entomological Reprints Specialists, Los Angeles, California). 210 pp. $12.50.

The book contains original descriptions of ten genera and 403 species of butterflies, and is a reprint of the original descriptions, published by Hewitson in four parts and dealing with exotic Rhopalocera and Hesperidae: "Descriptions of one hundred new species of *Hesperidae*"; "Descriptions of some new species of Lycaenidae"; "Equatorial Lepidoptera collected by Mr. Buckley"; and "Bolivian Butterflies collected by Mr. Buckley." There are no figures in this book and no index is provided.

K. MARAMOROSCH

The Caddis Flies, or Trichoptera, of Illinois. Herbert H. Ross. 1944. Illinois Natural History Survey Bulletin 23. Reprinted by Entomological Specialists, Los Angeles, California. 1972. 326 pp. $9.95.

This is an exact reprint of the original publication which was out of print. If the author had added a complete bibliography of the vast literature on Trichoptera that has been published since World War II, this book would have been even more valuable.

K. MARAMOROSCH

Növenyvirusok, Vektorok, Virusatvitel. (Plant Viruses, Vectors, and Virus Transmission.) 1972. Jozsef Horvath (Hungarian Academy of Sciences). Akademiai Kiado, Budapest. 515 pp. In Hungarian (price: 92 florins).

This book, written by a crop-protection expert, is an up-to-date presentation of the relationships between plant pathogenic viruses and vectors. In addition to insect vectors, to which more than 100 pages are devoted, other transmitters, such as nematodes and fungi, are described in great detail. There are very good descriptions of interactions between aphids and viruses, as well as of relationships between viruses and leafhoppers, plant hoppers, mites, thrips, whiteflies, scale insects, mealy bugs, psyllids, woodlice, grasshoppers, earwigs, beetles, and others. Other chapters deal with methods of field and laboratory experimentation, serology, purification, chemical properties of viruses, and control of virus diseases including vector control. Each chapter is followed by a list of "Recommended literature," comprising the most important publications of the world literature. An English table of contents is provided, as well as an author and subject index for the whole volume. The book is very well illustrated.

Some of the recent findings concerning the mycoplasmalike agents of plant diseases, transmitted by leafhoppers and psyllids, are also discussed in this treatise.

Karl Maramorosch

Australian Butterflies. Charles McCubbin. 1971. Thomas Nelson, Ltd. Dai Nippon Printing Co., Hong Kong. 206 pp. (Distributed by Entomol. Repr. Specialists, Los Angeles, Calif.) $30.

This is a large volume weighing about five pounds. It is, therefore, a bit heavy to pick up, but once you start reading it, you will find it much more difficult to put down.

Charles McCubbin has produced a vital, fascinating book which makes a momentous contribution to neophytes as well as scientists. Mr. McCubbin's magnificent water color paintings of the insects and their food plants are superbly reproduced; there are also representations of larvae, pupae, and most interesting likenesses of localities where described specimens have been observed or taken.

His descriptions of Distribution, Life-History and Flying Period, with frequent notes of interest and importance, complete a superb document that must be seen to be believed. No one interested in entomological natural history should be without it.

Bernard Heineman

Noctuidae of North America. A. R. Grote. 1971. E. W. Classey, Ltd., Hampton, Middlesex, England. 85 pp. (Distributed by Entomol. Repr. Specialists, Los Angeles, Calif.) $16.95.

Written in 1882 by A. R. Grote, this is a profound book. It is fortunate that E. W. Classey of Hampton, England, reprinted it with an excellent bio-biographical foreword by R. S. Wilkinson.

Grote's earliest deep study of the Noctuidae took place over 100 years ago; in fact, his first papers on Lepidoptera were published in 1862.

The book contains much of importance and the illustrations excite one's interest, but there is no description of insect life history and food plants, which tends to detract. The last paragraph, however, tells the story of "A Colony of Butterflies" which needs to be read by everyone interested in conservation.

Bernard Heineman

BOOK NEWS

Bees: Their Vision, Chemical Senses, and Language. Karl von Frisch. Rev. edition 1972 (October). Cornell University Press, Ithaca and London. xviii + 157 pp., 76 figs., photographs. $2.45.

This is the same book that Cornell University Press published a year ago in a hard-cover edition for $7.50. See review by Father Daniel J. Sullivan in the March 1972 [Vol. 53 (1):54–55] issue of J.N.Y.E.S. The paper is of good quality and one can only hope that the soft-cover edition will help popularize this important classic work of Professor von Frisch.

KARL MARAMOROSCH

Proceedings of the New York Entomological Society

(Meetings held in Room 129 of the American Museum of Natural History unless otherwise indicated.)

Meeting of October 17, 1972

President Howard Topoff called the meeting to order at 8:15 P.M. 22 members and 24 guests attended.

The minutes of the meeting of October 3, 1972 were approved.

The following were elected to Active Membership: Glenn K. Morris, Assistant Professor of Zoology, Erindale College, Clarkson, Ontario; Dr. Diane Young, Department of Zoology, Auburn University, Auburn, Alabama; L. H. Rolston, Department of Entomology, Louisiana State University; Michael J. Bentivegna, Jr., Bethpage, Long Island, owner of pest-control firm; Robert B. Hutt, Washington. Interested in systematics; Dr. Charles C. Porter, Biology Department of Fordham University. Interested in systematics of Hymenoptera, especially Ichneumonidae; Marion W. Boesel, Zoology Department, Miami University, Oxford, Ohio.

PROGRAM. Edwin Way Teale, speaker, Society Member, naturalist, natural history author and photographer, was introduced by Dr. James Forbes. Mr. Teale showed a group of his remarkably beautiful slides entitled "Wild Life Farm," centered on his northeastern Connecticut home and dedicated to study of the natural history of the area.

Father Sullivan announced that because of election day there would be no meeting on November 7th. Dr. Charles C. Porter, of the Biology Department of Fordham University, our newly elected Member, will speak on "Ichneumon Wasps of the Argentine Desert" at our next meeting, November 21st. Members will be informed by postcard; there is a possibility of rescheduling.

The meeting was adjourned at 9:25 P.M.

JOAN DEWIND, *Sec.*

Meeting of November 21, 1972

President Howard Topoff presided; 8 members and 8 guests were present. Edward J. Rogers, Jr., student at the University of California, whose interest is in systematics, was proposed for Student Membership.

PROGRAM. **Ichneumonid Wasps of the Argentine Desert.** Dr. Charles C. Porter, Department of Biological Sciences, Fordham University, New York, discussed ichneumonids

of the sub-Andean desert and illustrated his talk with slides of the fauna, flora, and topography.

Joan M. DeWind, *Sec.*

Meeting of December 5, 1972

President Howard Topoff presided; eighteen members and five guests were present. Mr. Edward J. Rogers, Jr., of the University of California, Berkeley, California, was elected to Student Membership.

PROGRAM. **Tiger Beetles of the United States.** Dr. John Stamatov described species distribution, habitats, and his collection procedures, showing samples from his collection.

The meeting was adjourned at 9:15 P.M.

Joan M. DeWind, *Sec.*

Meeting of December 19, 1972

Dr. Howard Topoff presided. Eleven members and four guests were present. Barbara Paparesta, of New York, was proposed for Active Membership and Kevin J. McGrath, student at Fordham University, was proposed for Student Membership.

PROGRAM. Mr. and Mrs. Bernard Heineman, Society members, illustrated their travelog, "Nature Lovers in Hawaii, Fiji and New Zealand," with beautiful slides taken on their recent trip.

Joan M. DeWind, *Sec.*

INDEX TO SCIENTIFIC NAMES OF ANIMALS AND PLANTS VOLUME LXXX

Generic names begin with capital letters. New genera, species, subspecies, and varieties are printed in italics. The following items and articles are not indexed: synonymy in "The *Penenirmus* (Mallophaga:Ischnocera) of the Picidae (Aves:Piciformes)," by Robert C. Dalgleish, pp. 83–104; "Aphids of New Jersey, A Few More Records (Homoptera:Aphididae)," by Mortimer D. Leonard, pp. 182–194; "Revision of the Schizomida (Arachnida)," by J. Mark Rowland, pp. 195–211; and the locality records in "The Anthomyiidae and Muscidae of Mt. Katahdin, Maine (Diptera)," by H. C. Huckett, pp. 216–233.

INVITATION TO MEMBERSHIP

The New York Entomological Society was founded in 1892 and incorporated the following year. It holds a distinguished position among scientific and cultural organizations. The Society's **Journal** is one of the oldest of the leading entomological periodicals in the United States. Members and subscribers are drawn from all parts of the world, and they include distinguished professional naturalists, enthusiatic amateurs, and laymen for whom insects are only one among many interests.

Your are cordially invited to apply for membership in the Society or to subscribe to its **Journal** which is published quarterly. Regular meetings are held at 8:00 P.M. on the first and third Tuesdays of each month from October through May at the American Museum of Natural History, the headquarters of the Society. A subject of general interest is discussed at each meeting by an invited speaker. No special training in biology or entomology is necessary for the enjoyment of these talks, most of which are illustrated. Candidates for membership are proposed at a regular meeting and are voted upon at the following meeting.

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Active member: Full membership in the Society, entitled to vote and hold office; with **Journal** subscription $9.00

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I wish to apply for ..... membership (see classes above).

My entomological interests are: .....

If this is a student membership, please indicate school attending and present level.

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— Send application to Secretary —

JOURNAL of the NEW YORK ENTOMOLOGICAL SOCIETY

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Genetic symbols: follow recommendations of Demerec, et al. (Genetics **54**: 61, 1969)

Biochemical abbreviations: follow rules of the U.I.P.A.C. -I.U.B. (J. Biol. Chem. **241**: 527, 1966)

Enzyme activity: should be expressed in terms of international units. (Enzyme Nomenclature. Elsevier Pub. Co., 1965)

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8. ORDERS and inquiries for back issues and complete sets should be sent to our agent: S-H Service Agency, Inc., 866 Third Ave., New York, N.Y. 10022.

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of the

New York
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Devoted to Entomology in General

VOLUME LXXXI

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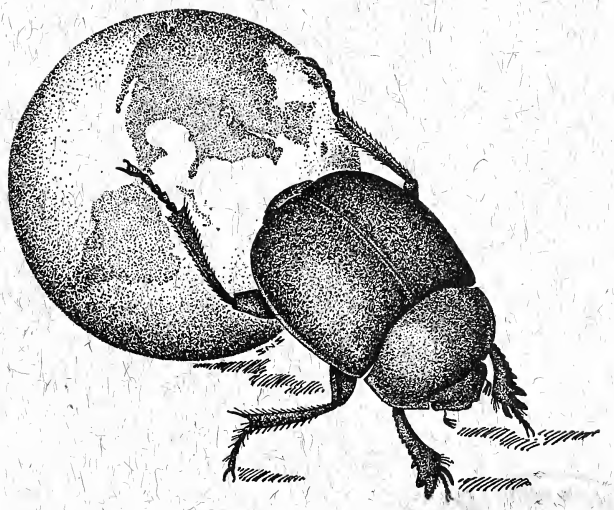

Devoted to Entomology in General

The New York Entomological Society
Incorporating The Brooklyn Entomological Society
Incorporated May 21, 1968

The New York Entomological Society
Organized June 29, 1892—Incorporated February 25, 1893
Reincorporated February 17, 1943

The Brooklyn Entomological Society
Founded in 1872—Incorporated in 1885
Reincorporated February 10, 1936

The meetings of the Society are held on the first and third Tuesday of each month (except June, July, August and September) at 8 P.M., in the AMERICAN MUSEUM OF NATURAL HISTORY, 79th St. & Central Park W., New York, N. Y. 10024.

Annual dues for Active Members, $4.00; including subscription to the Journal, $9.00.

Members of the Society will please remit their annual dues, payable in January, to the Treasurer.

Officers for the Year 1972

Trustees

Mailed May 18, 1973

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Journal of the New York Entomological Society

VOLUME LXXXI MAY 18, 1973 No. 1

CONTENTS

CHANGE OF EDITORS

The members of the New York Entomological Society wish to express their sincere thanks to Dr. Lucy W. Clausen for her diligent and faithful service as Editor-in-Chief of the Journal of the N.Y. Entomological Society. The Editor-in-Chief of our Journal has one of the most demanding jobs asked of any of our members. In 1972 Dr. Clausen completed her tenure in this office. She had handled this chore with tact, skill, and devotion, and deserves special recognition for her services to our Society. Dr. Clausen has worked many long hours for the Journal and for the profession. Her desire to maintain high standards in a scientific publication has been tempered by a reasonable attitude and a wish to encourage authors at every possible opportunity. Her devoted work as Editor-in-Chief is deeply appreciated.

Dr. Karl Maramorosch assumed the responsibilities of Editor-in-Chief in the summer of 1972. Serving with him as Associate Editors are Dr. Lawrence E. Limpel and Helen McCarthy.

As Program Director of the Insect Physiology and Virology lab at Boyce Thompson Institute since 1962, and earlier as faculty member of Rockefeller University, Karl Maramorosch has been exploring his interest in the insect transmission of viruses and mycoplasmalike agents. After receiving his Ph.D. from Columbia University in 1949, he participated in many international surveys to find effective ways of protecting crops. His work has taken him to Rumania, the Netherlands, the Philippines, India, Yugoslavia, U.S.S.R., and Africa.

Dr. Maramorosch is a past Chairman of the Biology Section of the Entomological Society of America, the Virology Committee of the American Phytopathological Society, and the Microbiology Division of the New York Academy of Sciences. He has edited books on "Biological Transmission of Disease Agents" (1962), "Insect Viruses" (1968), "Viruses, Vectors, and Vegetation" (1969), "Comparative Virology" (1971), and five volumes of "Methods in Virology" (1964–1971).

Presently Program Director of the Biocidal Chemicals lab at Boyce Thompson Institute, Lawrence Limpel has been investigating the effects of experimental chemicals from Diamond Shamrock as insecticides and herbicides. Dr. Limpel received his Ph.D. from the University of Wisconsin in 1957 and was senior author of two publications on iodine metabolism in insects.

In addition to papers on weed control by dimethyl tetrachloroterephthalate, Dr. Limpel has been co-author on papers concerning a new foliage-protectant fungicide, a portable step-logarithmic sprayer, and a seeder for greenhouse use. In 1972, he and two colleagues were granted a patent on insecticidal oximino organophosphate esters.

Dr. Limpel is a member of the Entomological Society of America and the Northeastern Weed Control Conference. He has co-authored many papers that have appeared in the proceedings of several weed control conferences on the relative efficiency of herbicides.

At present an editor with Avon Cosmetics, Helen McCarthy has just completed seven years as a freelance editor for the college departments of four major publishers. During this time she has also edited for other accounts such as the Joint Technical Advisory Committee of the Institute of Electrical Engineers; the Food and Agriculture Organization of the United Nations; Merck, Sharp & Dohme; Doremus & Company, the largest financial advertising agency in the United States; and Hill and Knowlton, the largest public relations agency.

After graduating from Hunter College in 1955 with a B.A. in English, Ms. McCarthy copyedited technical manuscripts at Electronics Research Laboratories (the electrical engineering lab of Columbia University). This background led to her becoming associate editor at Federal Scientific Corporation from 1958 to 1962, when she went into general book publishing.

In her spare time, Ms. McCarthy is writing a play.

Undescribed Species of Crane Flies from the Himalaya Mountains (Diptera: Tipulidae), XXI[1, 2]

Charles P. Alexander

Received for Publication October 10, 1972

Abstract: Six new species of crane flies are described, two from the western Himalayas, *Paradelphomyia* (*Oxyrhiza*) **pugilis**, and *Limnophila* (*Brachylimnophila*) **garhwalensis**, from Kumaon; four from the eastern Himalayas, Kameng, Assam, *Dolichopeza* (*Sinoropeza*) **fasciventris**, *Orimarga* (*Orimarga*) **suspensa**, *Hexatoma* (*Eriocera*) **paragnava**, and *H.* (*E.*) **perhirsuta**.

Dolichopeza (*Sinoropeza*) **fasciventris**, n.sp.

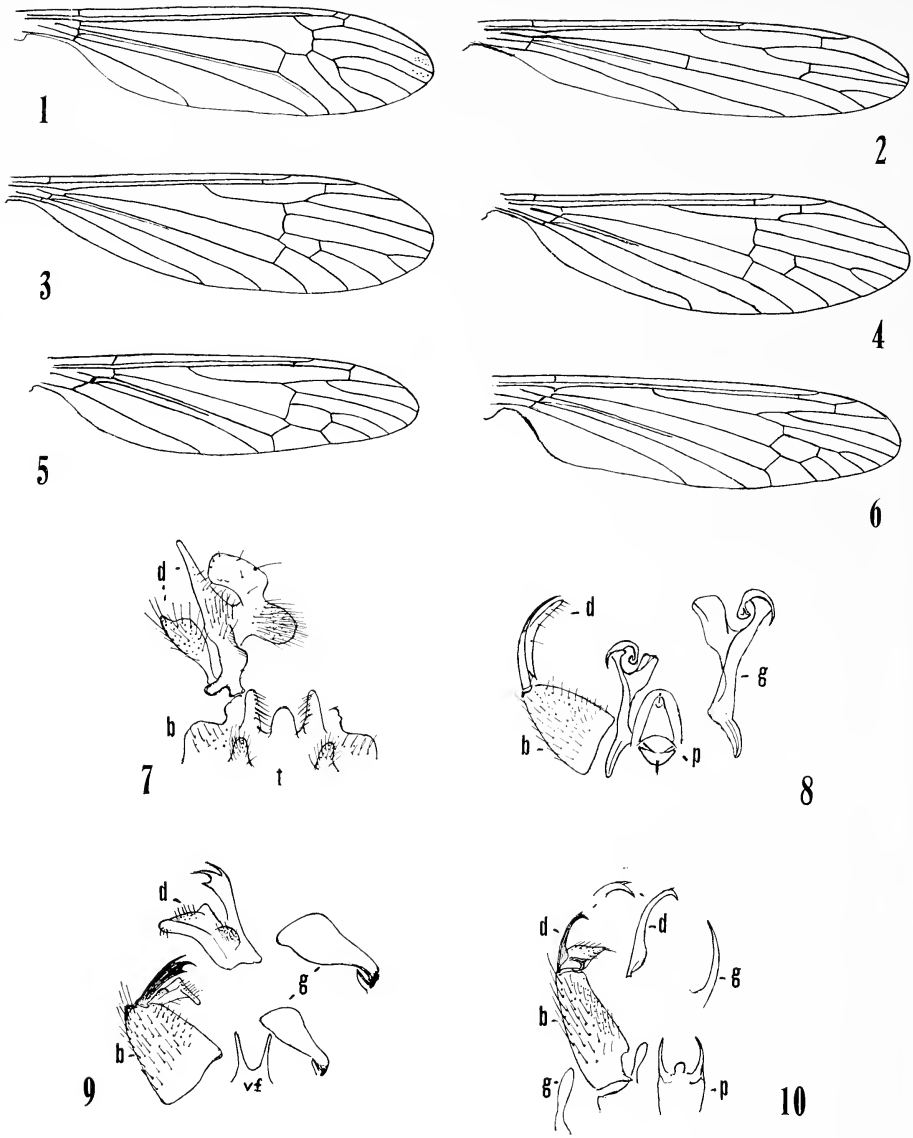
General coloration of thoracic dorsum polished ferruginous, pleura brownish yellow; antennae 13-segmented, about one-third as long as wing, terminal segment microscopic, flagellar segments slightly sinuous, with setae on outer face at base; wings strongly darkened, stigma darker brown; basal section of vein M_3 lacking, the posterior branch of M appearing branched, as in the subgenus; abdomen black, bases of intermediate five segments conspicuously yellow; male hypopygium with posterior border of tergite trilobed, with two more basal lobes on disk; outer dististyle expanded outwardly, the lateral angle more produced, inner style large and complex, with two enlarged flattened lateral lobes, the cephalic one conspicuously hairy, at apex narrowed into a needlelike spine.

Male: Length about 9 mm.; wing 11 mm.; antenna about 4.1 mm. Frontal prolongation of head yellow, palpi dark brown. Antennae 13-segmented, of moderate length, nearly one-half the body or slightly exceeding one-third the length of wing; scape and pedicel yellow, first flagellar segment brownish yellow, outer third darker, remaining segments black; first flagellar segment long-cylindrical, about twice the second, succeeding segments progressively shorter, the terminal one microscopic; each flagellar segment after the first slightly sinuous beyond its base, this with setae on upper side only; *Dolichopeza* (*Sinoropeza*) *postica* has twelve or in cases thirteen antennal segments, the terminal one microscopic, all segments cylindrical throughout, the setae very small and not restricted to base, terminal segment elongate, about two-thirds the penultimate. Head brownish yellow, orbits darker; sides of anterior vertex with a concentration of longer setae.

Pronotum brownish yellow. Mesonotal praescutum with three polished ferruginous stripes, interspaces slightly differentiated, sides uniformly medium brown, with dense virtually contiguous microscopic pits; posterior sclerites brownish yellow. Pleura brownish yellow, dorsopleural membrane brown. Halteres with stem yellowish brown, clearer basally, knob dark brown. Legs with coxae brownish yellow, trochanters yellow; remainder of legs light brown, tips of femora narrowly darker. Wings (Fig. 1) strongly darkened, prearcular and costal fields slightly more yellowed; stigma dark brown, preceded and followed by small pale yellow brightenings; veins before cord brownish yellow, darker brown beyond cord. Sparse microscopic trichia in outer end of cell R_3, with fewer in R_5. Venation: Sc_2 entering

[1] Contribution from the Entomological Laboratory, University of Massachusetts, Amherst, Mass.

[2] Part XX of this series of papers was published in the Journal of the New York Entomological Society, **80**: 7–11, March 1972.



FIGS. 1–6, venation; 7–10, male hypopygium.

FIG. 1. *Dolichopeza* (*Sinoropeza*) *fasciventris*, n.sp.
FIG. 2. *Orimarga* (*Orimarga*) *suspensa*, n.sp.
FIG. 3. *Paradelphomyia* (*Oxyrhiza*) *pugilis*, n.sp.
FIG. 4. *Limnophila* (*Brachylimnophila*) *garhwalensis*, n.sp.
FIG. 5. *Hexatoma* (*Eriocera*) *paragnava*, n.sp.
FIG. 6. *Hexatoma* (*Eriocera*) *perhirsuta*, n.sp.
FIG. 7. *Dolichopeza* (*Sinoropeza*) *fasciventris*, n.sp.

R opposite fork of *Rs*; R_{1+2} entirely pale, erect, nearly in alignment with R_2; outer medial branches as in the subgenus, basal section of M_3 lacking, posterior branch of *M* appearing branched; *m-cu* about two-thirds its length before fork of *M*.

Abdomen with basal tergite brown, remaining segments black, the bases of third through seventh segments conspicuously yellow. Male hypopygium (Fig. 7) with posterior border of tergite, *t*, trilobed, central lobe shorter, glabrous, apex rounded, lateral lobes nearly twice as long, narrowed outwardly, tips blunt, inner margin with a row of long black setae; disk of tergite laterally with a conspicuous lobe with long black setae. Outer dististyle, *d*, relatively small, expanded outwardly, outer angle slightly more produced; inner style large, complex in structure, with three principal lobes, the axial one narrowed into a straight slender rod, laterally produced into two broad flattened lobes, the outer one darkened, nearly glabrous, apex broadly obtuse, cephalic lobe densely setiferous, the apex narrowed into a needlelike spine.

HOLOTYPE: ♂, Chug, Northeast Frontier Agency, Kameng, Assam, India, 6,800–7,300 feet, July 30, 1961 (Fernand Schmid).

The only other regional member of the subgenus is *Dolichopeza* (*Sinoropeza*) *postica* Brunetti, of the eastern Himalayas, which differs in the longer simple antennae, apparently with only twelve segments, with the vestiture small and reduced, and with the abdomen uniformly blackened. I possess a paratype male of this species but the abdomen is lacking. Brunetti's description of the male hypopygium indicates that it is quite distinct from that of the present fly. The two Chinese members of the subgenus are entirely distinct, these being *D.* (*S.*) *multiseta* Alexander, of Fukien, and *D.* (*S.*) *paucisetosa* Alexander, of Kiangsi. Edwards (*Rec. Indian Mus.*, **26:** 304; 1924) mentions a specimen of *postica* from the Brunetti series but not type material that has the male antennae longer and apparently represents a still further species.

Orimarga (*Orimarga*) **suspensa**, n.sp.

General coloration light gray, the thorax slightly patterned with light brown; legs medium brown; wings whitened, unpatterned, veins light brown, trichia of outer medial veins sparse, vein M_{3+4} about one-third longer than M_4; male hypopygium with outer dististyle narrowed into a long slender blackened spine; gonapophysis bifurcate, outer arm at apex bearing a semicircular structure, its outer end a strong curved spine.

Male: Length about 7 mm.; wing 6–6.2 mm.; antenna about 1.5 mm.

Female: Length about 7–7.5 mm.; wing 7–7.5 mm.

Rostrum and palpi dark brown. Antennae black; flagellar segments long-oval, their ends truncate, terminal segment short-oval. Head light gray.

Thorax light gray, praescutum with four slightly darker brownish gray stripes, the intermediate pair narrowly and vaguely separated; centers of scutal lobes less evidently darkened. Pleura light gray, sternopleurite variegated by darker gray, more extensive ventrally. Halteres whitened. Legs with fore coxae light brown, remaining pairs and all trochanters yellow; remainder of legs medium brown. Wings (Fig. 2) whitened, unpatterned, prearcular and

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FIG. 8. *Orimarga* (*Orimarga*) *suspensa*, n.sp.

FIG. 9. *Paradelphomyia* (*Oxyrhiza*) *pugilis*, n.sp.

FIG. 10. *Limnophila* (*Brachylimnophila*) *garhwalensis*, n.sp.

(Hypopygial symbols: *b*, basistyle; *d*, dististyles; *g*, gonapophysis; *p*, phallosome; *vf*, ventral fork).

costal fields slightly more yellowed; veins light brown, yellow in the brightened fields. Macrotrichia of outer medial veins relatively sparse, M_4 with only two or three, in cases lacking. Venation: R_{1+2} about one and one-half to twice R_{2+3}; M_{3+4} about one-third longer than M_4; *m-cu* nearly opposite to shortly beyond the origin of *Rs*.

Abdomen dark brown. Male hypopygium (Fig. 8) with both dististyles, *d*, elongate, outer style very gradually narrowed into a slender blackened spine. Phallosome with gonapophyses, *g*, distinctive, bifurcated at near midlength, the inner arm a broad flattened blade, outer arm slender, at apex with a suspended central semicircular chitinized structure, its outer end narrowed into a strong curved spine, the opposite end with apex obtuse or truncated.

HOLOTYPE: ♂, Chug, Northeast Frontier Agency, Kameng, Assam, India, 6,800–7,300 feet, July 30, 1961 (Fernand Schmid). Allotopotype, ♀, pinned with type. Paratopoytpes: 5 ♂ ♀.

The most similar regional species are *Orimarga* (*Orimarga*) *subbasalis* Alexander and *O.* (*O.*) *tenuistyla* Alexander, both from Assam. The hypopygium, especially the gonapophyses, are quite different in the two species. The male sex of *subbasalis* still is unknown but the details of venation and vein trichiation provide distinctive characters for the separation of the flies.

Paradelphomyia (*Oxyrhiza*) **pugilis**, n.sp.

General coloration of thorax polished orange, head gray; legs obscure yellow; wings brownish yellow, stigma very slightly paler; male hypopygium with outer dististyle terminating in three spines; gonapophyses clavate, basal half narrowed, outer half mitten-shaped; ventral fork with spines variable, in cases apparently lacking.

Male: Length about 5–6 mm.; wing 5–6.5 mm.; antenna about 1.0–1.2 mm.

Female: Length about 5.5 mm.; wing about 6 mm.

Rostrum dark brown, palpi black. Antennae dark brown to brownish black; flagellar segments elongate, subequal to or slightly shorter than their verticils. Head gray.

Thorax almost uniformly polished orange. Halteres with stem whitened, knob more yellowed. Legs with coxae and trochanters yellow; remainder of legs obscure yellow, outer tarsal segments light brown, claws long and slender, gently curved. Wings (Fig. 3) faintly brownish yellow, stigma very faintly darker, entirely distad of vein R_2; veins light brown. Sparse trichia in outer ends of cells R_2 to *1st A*; on veins beyond general level of origin of *Rs*, including nearly the outer two-thirds of both anal veins. Venation: R_{2+3+4} varying in length from shorter than R_{2+3} to nearly twice this length; cell M_1 about one-third its petiole; *m-cu* less than its own length beyond fork of *M*.

Abdominal tergites brownish yellow, sternites paler, in male segments seven and eight darker brown to form a ring. Male hypopygium (Fig. 9) with apex of basistyle, *b*, produced into a microscopic point. Outer dististyle, *d*, expanded outwardly, terminating in three spines, the outer two approximated, lower spine more separated, in the paratypes the intervening margin with three or four small points, lacking in the holotype; inner style with basal half stout, outer end narrowed, apex rounded. Gonapophysis, *g*, of distinctive conformation, appearing clavate, basal half slender, outer end more expanded to appear mitten-shaped, wider across base; ventral fork, *vf*, of aedeagus present in holotype, apparently lacking in the two paratypes studied, the fork including two slender gently divergent spines.

HOLOTYPE: ♂, Dwali, Almora, India, 8,410 feet, September 12, 1958 (Schmid). Allotype: ♀, Khati, Almora, 7,700–8,000 feet, September 10, 1958. Paratypes: 6 ♂ ♀, with the allotype, September 10–11, 1958; one ♂, Rata, Almora, 11,000 feet, September 14, 1958 (all Schmid).

Among the regional species the present fly most resembles *Paradelphomyia* (*Oxyrhiza*) *angustistyla* Alexander, *P.* (*O.*) *bigladia* Alexander, *P.* (*O.*) *distivena* Alexander, *P.* (*O.*) *flavescens* (Brunetti), and *P.* (*O.*) *ruficolor* Alexander, differing evidently in hypopygial structure.

Limnophila (*Brachylimnophila*) **garhwalensis**, n.sp.

Mesonotum brownish gray, praescutum with four very indistinct light brown stripes, pleura yellow; halteres light yellow; wings faintly brownish yellow, prearcular and costal fields clearer yellow, stigma small, pale brown, cell M_1 variable in size, approximately one-half its petiole; abdominal tergites brown, sternites more yellowed, especially in female; male hypopygium with outer dististyle slender, bifid near apex, inner gonapophyses very narrow.

Male: Length about 5–5.5 mm.; wing 7–7.5 mm.; antenna about 1.2–1.3 mm.

Female: Length about 8–8.5 mm.; wing 8–9 mm.

Rostrum and palpi black. Antennae with scape and pedicel yellowed, flagellum slightly darker; proximal flagellar segments large, especially the first, progressively smaller outwardly, outer segments long-cylindrical, somewhat shorter than their longest verticils. Head brownish gray; anterior vertex broad.

Pronotal scutum light brownish gray, scutellum and pretergites yellowed. Mesonotal praescutum light brownish gray, with four very indistinct light brown stripes, tuberculate pits blackened, darker than the pseudosutural foveae; posterior sclerites of notum more yellowed. Pleura chiefly yellowed, ventrally clearer yellow to more reddened. Halteres light yellow. Legs with coxae and trochanters light yellow, remainder of legs slightly darker yellow, outer tarsal segments infuscated to blackened. Wings (Fig. 4) faintly brownish yellow, prearcular and costal fields clearer yellow, including the veins; stigma small, pale brown, inconspicuous; veins pale brown. Longitudinal veins beyond general level of origin of *Rs* with long trichia. Venation: Sc_1 ending shortly beyond fork of R_{2+3+4}. Sc_1 alone longer than the gently arcuated *r-m*; R_{1+2} about three times R_2; cell M_1 variable in size, usually small, about one-half its petiole or less, in cases larger.

Abdominal tergites brown, sternites yellowish brown in male, clear yellow in females. Ovipositor with cerci very long, only slightly upcurved. Male hypopygium (Fig. 10) with outer dististyle, *d*, slender, gently curved to the acute tip, with a smaller subapical spine on outer margin. Phallosome with gonapophyses, *g*, very slender, lateral apophyses (or interbases) paddle-shaped.

HOLOTYPE: ♂, Dakwani, Pauri Garhwal, Kumaon, India, 9,300–11,000 feet, August 5, 1958 (Fernand Schmid). Allotopotype: ♀, with type. Paratopotype: 1 ♂. Paratypes: 2 ♀♀, on one pin, Kulara, Pauri Garhwal, 12,000 feet, August 3, 1958.

The most similar members of the subgenus include *Limnophila* (*Brachylimnophila*) *nemoralis* (Meigen) and *L.* (*B.*) *adjuncta* (Walker), Western Palaearctic; *L.* (*B.*) *inaequalis* Alexander and *L.* (*B.*) *nesonemoralis* Alexander, Eastern Palaearctic, and *L.* (*B.*) *occidens* Alexander, Western Nearctic, all differing among themselves in details of coloration of the body, legs and halteres, in venational details, and in hypopygial structure, especially the outer dististyles and gonapophyses.

Hexatoma (*Eriocera*) **paragnava**, n.sp.

Size large (wing 15 mm.); antennae of male very long, approximately three times the wing, flagellar segments with very sparse small spinoid setae; halteres light yellow; wings whitened, prearcular and costal fields yellowed, including the veins, remaining veins dark brown to

brownish black; cell *1st* M_2 long, M_{3+4} about one-half longer than M_4; abdominal tergites brownish gray, lateral margins yellowed, sternites yellowish orange.

Male: Length about 11 mm.; wing 15 mm.; antenna about 47 mm.

Front and mouthparts very reduced, brown, palpi black. Antennae of male very long, approximately three times the wing; proximal segments brownish yellow, remainder black; scape much enlarged, flagellar segments very long, with dense erect white setae and very sparse black spinoid setae, on first segment these shorter than the normal setae, on second and third segments longer and more erect, microscopic on outer segment. Head light gray, vertical tubercle more brownish gray, very large, bulbous, on posterior aspect with long setae.

Pronotum brownish yellow. Mesonotal praescutum light gray with four darker stripes, intermediate pair nearly confluent, lateral stripes darker, vestiture long and conspicuous on sides, shorter on disk, occurring on both the stripes and the interspaces; scutal lobes more darkened, vestiture sparse to lacking; scutellum gray, with sparse paler setae; postnotum more brownish gray, more yellow laterally, without vestiture. Pleura pale yellowish brown, vaguely patterned with darker, ventrally light gray pruinose. Halteres small, light yellow. Legs with coxae yellowed, vestiture short and sparse; trochanters obscure yellow; femora yellow, tips narrowly blackened; tibiae and tarsi brownish yellow, terminal segment darker. Wings (Fig. 5) whitened, prearcular and costal fields yellowed, including the veins; stigma small, pale brown; narrow inconspicuous pale brown seams over cord and certain longitudinal veins, most evident on R_{1+5} and *Cu* in cell *M*; veins of disk dark brown to brownish black, conspicuous. Veins behind costa nearly glabrous, with sparse scattered trichia on R_1 and distal section of R_5. Venation: R_{1+2} and R_2 short, subequal; *Rs* long, exceeding the anterior branch of *Rs*; cell M_1 lacking; cell *1st* M_2 long, M_{3+4} about one-half longer than M_4; distal section of Cu_1 nearly in transverse alignment with cord, cell M_4 at margin very extensive.

Abdominal tergites brownish gray, posterior borders narrowly darker, lateral margins of intermediate segments more yellowed; sternites yellowish orange, hypopygium dark brown.

HOLOTYPE: ♂, Chug, Northeast Frontier Agency, Kameng, Assam, India, 6,800–7,300 feet, July 30, 1961 (Fernand Schmid).

The most similar regional species include *Hexatoma* (*Eriocera*) *gnava* Alexander and *H.* (*E.*) *neognava* Alexander, which differ from the present fly in their smaller size, vestiture, and in details of coloration of the body and wings.

Hexatoma (*Eriocera*) **perhirsuta**, n.sp.

Belongs to the *spinosa* group; size large (wing about 19 mm.); general coloration of head and thorax light brown, these with abundant very long and conspicuous erect brownish yellow setae; wings pale yellowish brown, veins yellowed, appearing inconspicuous against the ground, cell M_1 present; abdominal tergites and pleural membrane dark brown, sternites more orange, the color clearest midventrally.

Male: Length about 16 mm.; wing 19 mm.; antenna about 46 mm.

Rostrum very short, brownish yellow; palpi obscure yellow, terminal segment blackened. Antennae of male very long, exceeding twice the length of wing, dark brown, the enlarged scape slightly paler; flagellar segments very long, all with scattered small stout setae, more delicate on outer segment. Head light brown, with abundant very long brownish yellow setae, vertical tubercle conspicuous.

Mesonotum chiefly light brown, lateral praescutal borders broadly paler, posterior sclerites more whitened. Thoracic dorsum excepting the postnotum with very long erect brownish

yellow to pale brown setae, V-shaped suture dark brown. Pleura brownish yellow anteriorly, dorsal sternopleurite and posterior sclerites more whitened, with long white setae. Halteres with stem dull orange yellow, knob dark brown. Legs with coxae light gray, with long white setae, trochanters yellow; femora brownish yellow, remainder of legs darker brown. Wings (Fig. 6) very pale yellowish brown, stigma small, slightly darker brown; veins yellowed, very inconspicuous against the ground. Veins behind costa with sparse scattered trichia on R, very few on distal section of R_5. Venation: R_{2+3+4} about two-thirds the basal section of R_5; cell M_1 slightly longer than its petiole; *m-cu* about one-third longer than distal section of Cu_1.

Abdominal tergites and pleural membrane dark brown, sternites more orange, clearest midventrally.

HOLOTYPE: Chug, Northeast Frontier Agency, Kameng, Assam, India, 6,800–7,300 feet, July 30, 1961 (Fernand Schmid).

Generally similar to the Japanese *Hexatoma* (*Eriocera*) *jozana* Alexander and *H.* (*E.*) *stricklandi* (Edwards), differing from these and other regional species by the unusually long vestiture of the head and thorax. There are no closely allied Oriental species known to me.

On a Species of *Simulium* (*Ectemnaspis*) from the Northeastern United States (Diptera)

Pedro Wygodzinsky
The American Museum of Natural History, New York

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Abstract: The capture of two females of a black fly species of the subgenus *Simulium* (*Ectemnaspis*) in the foothills of the Catskill Mountains, in Ulster County, New York, is reported. The females are indistinguishable, in color and structural characters, from *bicoloratum*, the type of *Simulium* (*Ectemnaspis*), and two very closely related species. The subgenus has previously only been reported from South America.

DISCUSSION

On one day early in July of 1971, two female specimens of a black fly species indistinguishable from species of the *Simulium* (*Ectemnaspis*) *bicoloratum* complex, an endemic South American group, were collected in the eastern foothills of the Catskill Mountains of New York. Had the author found these specimens in a collection labeled as from the Catskills, he would have shrugged if off as a rather regrettable error in labeling, and would not have pursued the matter any further. As it happens, it was the author himself who collected the Catskill specimens, by means of a Malaise trap run routinely for a general survey of diurnal flying insects on woodlands northwest of Kerhonkson, Ulster County. These black flies were among a large number of miscellaneous insects contained in one of the two collecting jars of the Malaise trap. The specimens were fresh when found, brightly colored, with normal turgidity of the abdomen, and with flexible appendages. There is thus no chance of doubt about their provenance. The trap had been used for at least two weeks before the specimens were found, and although many other black flies had been encountered in the trap before and also later, the *Ectemnaspis* were found only once. None were observed biting man, although other species were.

During the spring and early summer of 1972, a concentrated search for additional specimens of *Ectemnaspis* was carried out in the area where the specimens had been found. A Malaise trap was run again in the original location, and many streams were explored for the aquatic stages of the species, all with negative results, even though many other black fly species were obtained. Stream collecting, however, was severely hampered during late June and early July (the period when pupae of the enigmatic species would most likely be found) because of extremely heavy rains, with flooding especially of the larger, permanent streams which frequently became torrential.

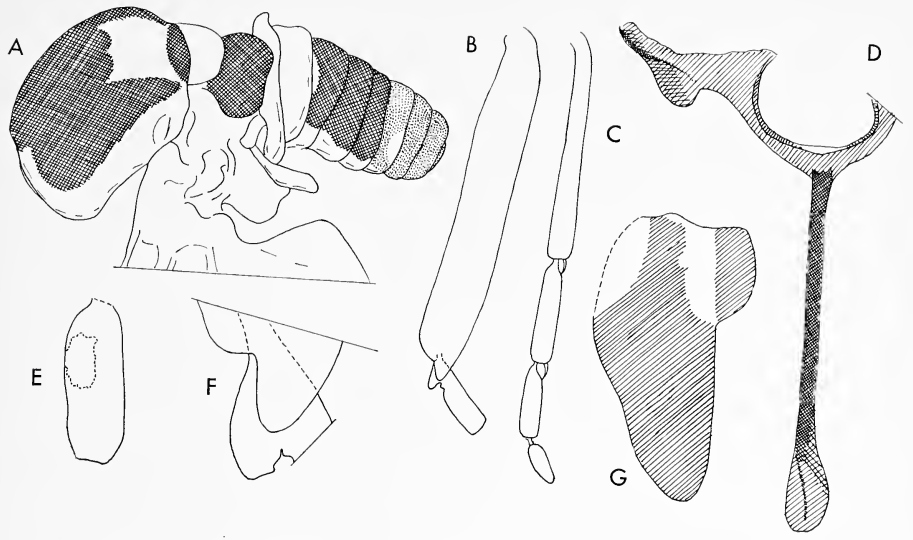

FIG. 1. *Simulium* (*Ectemnaspis*) sp., from Ulster County, New York, female. A. Thorax and abdomen with color pattern, dorsolateral view. B. Fore tarsus, first to fourth tarsomeres. C. Hind basitarsus with second tarsomere. D. Portion of genital fork. E. Second segment of maxillary palp, with outlines of sensory vesicle. F. Calcipala and pedisulcus. G. Cercus and paraproct.

Considering the unusual nature of this find I thought it advisable to publish the available data so as to stimulate others interested in black fly study to make a special search for this species.

The subgenus *Simulium* (*Ectemnaspis*) Enderlein, 1934, has as its type the South American species *Simulium bicoloratum* Malloch, 1913. This species was recently redescribed in great detail (Wygodzinsky, 1971) from abundant material of larvae, pupae, and adults of both sexes. The species occurs along the Andean chain, at elevations from 2000 to 3600 meters, with its range extending from Bolivia to Venezuela. Wygodzinsky (loc. cit.) also described two closely related species, *cormonsi* and *jaimeramirezi*, sympatric with *bicoloratum* although restricted to the Andes of Mérida, in Venezuela. The adults of these three species are very similar and are difficult or impossible to separate, but the pupae are clearly distinct. The highly apomorphic species forming this complex are connected by other species which share some but not all of the complex's characters to superficially quite dissimilar, comparatively plesiomorphic species such as *Simulium perflavum* Roubaud, 1906. Once the much needed subgeneric revision of neotropical *Simulium* is carried out, the species discussed above will probably all be formally included in *Ectemnaspis*. The subgenus is restricted to South America, with a possible center of diversity in northern South America. *S.* (*Ectemnaspis*), or any species that could be considered as belonging to the

subgenus, has never been reported from Central America, Mexico, the United States, or Canada.

I am unable to distinguish the New York material from the females of the *Simulium* (*Ectemnaspis*) *bicoloratum* complex. The importance of a slight difference in the shape of the paraproct (Fig. 1G) as compared to that of the South American species is uncertain, and may well fall within the range of individual variation. The true identity of the species will only be established after the male, pupa and larva, become known. In order to facilitate recognition and comparison of the New York form, a few of its morphological characters and its color pattern (black and yellow) are illustrated here (Fig. 1). Figures illustrating the features of the Andean species to which reference has been made above are found in Wygodzinsky (1971).

MATERIAL EXAMINED: U.S.A.: New York, Ulster County, Cherrytown, southwest of Kerhonkson, July 1–15, 1971, P. and B. Wygodzinsky col. (2 females, in the American Museum of Natural History).

I assume that the two females captured belong to an established population because simultaneous wide-distance dispersal of two specimens from some unknown South American location to the Catskills where the trap was located is an unacceptable hypothesis. Speculations about the age and history of this population are not advisable until additional material comes to hand, and especially until the specific status of the population can be determined.

Literature Cited

WYGODZINSKY, P. 1971. Descriptions and redescriptions of species of the blackfly genus *Simulium* from the northern Andes (Simuliidae, Diptera). American Mus. Novitates, **2447**: 1–38.

Extent of Pesticide Use, Food Supply, and Pollution

David Pimentel
Department of Entomology and Section of Ecology and Systematics,
Cornell University, Ithaca, New York 14850

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Abstract: *Only 5%* of this country's total crop acres receive insecticide treatment, and about half of this is applied to cotton and tobacco acres. Despite the large increases in insecticide use, crop losses due to insect pests are also increasing and are now estimated by the USDA to be nearly 13%. In part, these trends are due to the practice of substituting insecticides for sound bioenvironmental pest controls (e.g., crop rotation and sanitation) and also to higher consumer standards.

If pesticides were not used, crop losses, based on available data, were estimated to increase 7% (representing $2.1 billion). Overall, except for supplies of crops such as apples, peaches, and onions, most food crops would not be seriously affected by discontinuing use of pesticides.

Although pesticides should not be eliminated, a need exists to treat only when necessary, to reduce aircraft spray drift, and to reactivate sound bioenvironmental controls. Also, additional acreages of some crops could be profitably planted to offset crop losses due to pesticide reduction.

Concerning the toxicity of pesticides, the prime danger appears to be to those who apply these poisons. Unfortunately, the available data on long-term, low-level effects of pesticides to public health are inconclusive.

Existing levels of pesticide pollution already have been responsible for kills of some species of beneficial insects, fishes, and birds. This serious pollution has occurred when only *a small percentage* of the crop acres are being treated with pesticides.

A systems approach to pest management, in which the multiple factors of pests, crop culture, costs, benefits, and risks to environment and health are evaluated, is suggested as meeting the needs of agriculture and society as a whole.

INTRODUCTION

Early in the sixties Carson (1961) and others warned the public that continued pesticide use would eventually result in a "silent spring" and exact a high "human price." Conversely, Borlaug (1972) and others have warned that if the "use of pesticides in the USA were completely banned, crop losses would probably soar to 50%." Unfortunately, these statements have been made to the public without adequate scientific evidence.

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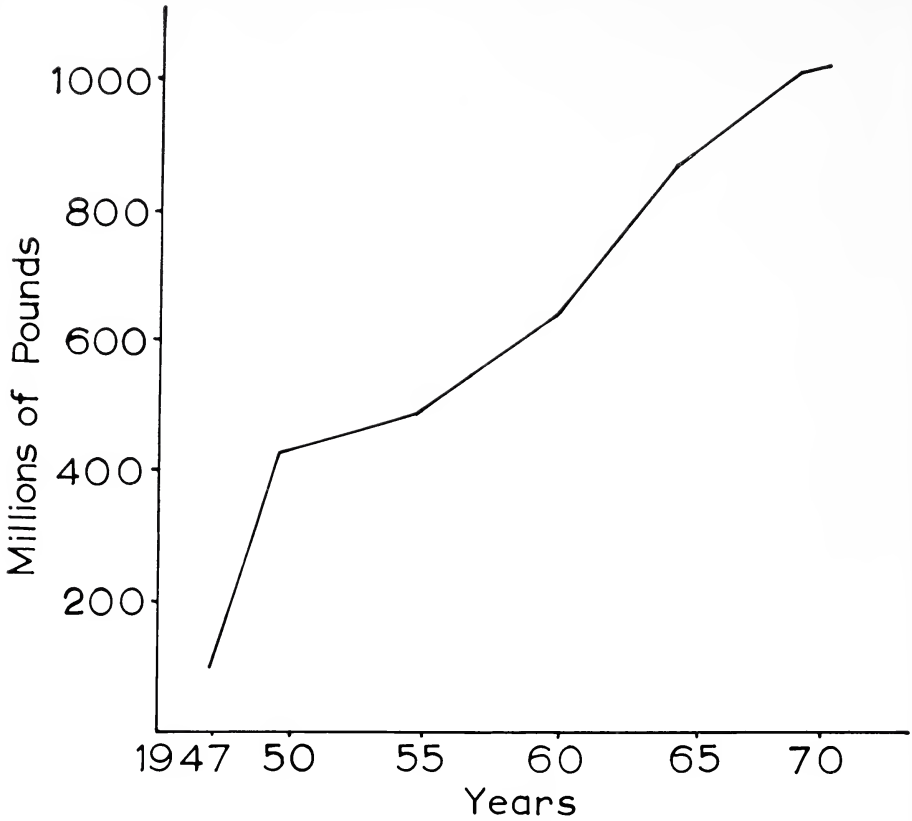

FIG. 1. Quantities of pesticides produced in the United States (USDA, 1971a).

To place the problem in a more balanced perspective, this paper endeavors to evaluate the data concerning use of pesticides in food production and their effects on man's health and his environment. The extent of pesticide applications on various crops and pest losses during the pre- and post-synthetic pesticide eras are compared. In addition, attention is given to the costs and benefits of pesticide use and the risks both to the environment and man's health.

Much of this analysis is based on USDA (U.S. Department of Agriculture) survey data. Some of these data were collected in various studies during the 1960's and unfortunately there are no more recent data available. Furthermore, some of these data are estimates gathered in surveys and so have inherent limitations but again are the most comprehensive available. Despite these reservations, the need remains to conduct an analysis of pesticide use in crop production in order to gain a perspective on pesticide use. Too many claims and counterclaims concerning the risks and benefits of pesticides have been made with little, if any, attention given to available data, however incomplete.

TABLE 1. Some examples of percentages of crop acres treated, of pesticide amounts used on crops, and of acres planted to this crop (USDA, 1968; USDA, 1970*a*).

Crops	Insecticides		Herbicides		Fungicides		% of Total Crop Acres
	% Acres	% Amount	% Acres	% Amount	% Acres	% Amount	
Non-Food	1	50	0.5	NA[a]	< 0.5	NA	1.26
Cotton	54	47	52	6	2	1	1.15
Tobacco	81	3	2	NA	7	NA	0.11
Food	4	NA	11.5	NA	< 0.5	NA	98.74
Field Crops	NA	NA	NA	NA	NA	19	NA
Corn	33	17	57	41	2	NA	7.43
Peanuts	70	NA	63	3	35	4	0.16
Rice	10	NA	52	2	0	NA	0.22
Wheat	2	NA	28	7	0.5	NA	6.11
Soybeans	4	2	37	9	0.5	NA	4.19
Pasture Hay + Range	0.5	3	1	9	0	NA	68.40
Vegetables	NA	8	NA	5	NA	25	NA
Potatoes	89	NA	59	NA	24	12	0.16
Fruit	NA	13	NA	NA	NA	NA	NA
Apples	92	6	16	NA	72	28	0.07
Citrus	97	2	29	NA	73	13	0.08
All Crops	5	54	12	36	0.5	10	NA

[a] Not available

PESTICIDE USE PATTERNS

Nearly a billion pounds of pesticides, or about 5 pounds per person, are used annually in the United States (USDA, 1971*a*) (Fig. 1). Of the one-half billion pounds of pesticide applied to crop and farm lands, 54% is insecticide, 36% herbicide, and 10% fungicide (USDA, 1971*a*). Nearly another half billion pounds of pesticides are used by government agencies, industries, and homeowners.

Pesticides used in agriculture are not evenly distributed (USDA, 1970*a*); for example, 50% of all insecticide used in agriculture is applied to the non-food crops of cotton[1] and tobacco (Table 1). Of the food crops, corn, fruit, and vegetables receive the largest amounts of insecticide. Of the herbicidal material applied, 41% is used on corn with the remaining 59% distributed among the other crops (Table 1). Most of the fungicidal material is applied on fruit and vegetables with only a small amount used on field crops (Table 1).

According to the latest data published by the U.S. Department of Agriculture (USDA, 1968), crop land (including pastures) in 1966 totaled 890.8 million

[1] Cotton is not strictly a non-food crop; the seed is used as livestock food and in producing vegetable oil.

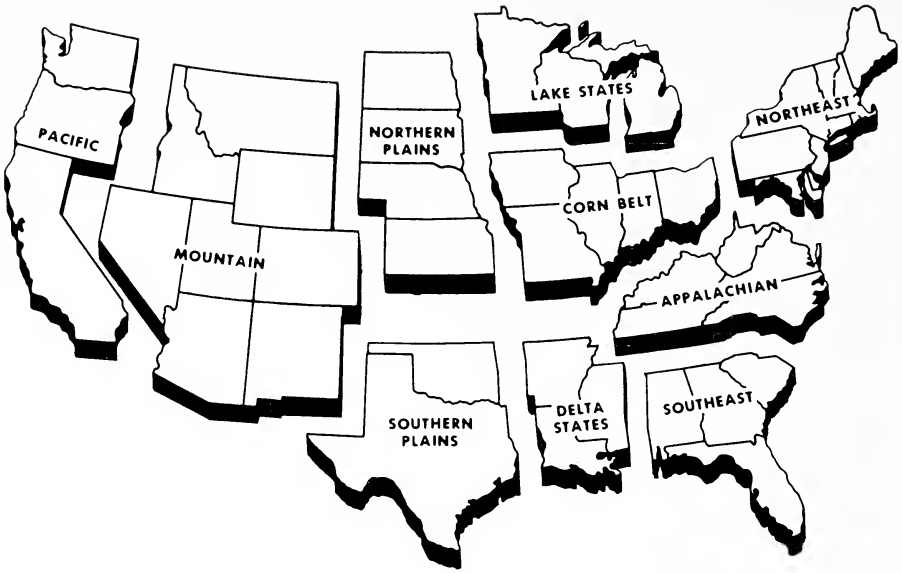

FIG. 2. Farm production regions in the United States (after the USDA Economic Research Service (USDA, 1968)).

acres, of which only 5% was treated with insecticides, 12% with herbicides, and 0.5% with fungicides. If crop land devoted to pastures is removed from the total acreage, then the percentage of crop land (including the non-food crops of cotton and tobacco) treated with insecticides, herbicides, and fungicides is 12%, 27%, and 1.3%, respectively.

Note that although cotton receives nearly 50% of the total insecticide used in agriculture, about half (46%) of the total cotton acreage receives no insecticide treatments at all (Table 1). The largest percentage (79%) of the acres treated is in the Southeast and Delta states; whereas the smallest percentage (37%) treated is in the southern plains (Fig. 2). Of the food crops, only citrus, apples, and potatoes have more than 85% of their acreage treated with insecticides (Table 1). Many acres of small grains and pastures receive little or no treatment with insecticides.

Herbicides are applied for weed control to only 12% of the crop acreage (Table 1). Those crops which have more than half of their acreage treated include peanuts, corn, potatoes, cotton, and rice. Of all pesticides, herbicide use has increased the fastest (USDA, 1971*a*).

Fungicides are used on more than half of the citrus, apple, and other fruit acres (Table 1). Most other crops are grown with little or no fungicide treatment.

In general, the larger growers (annual sales, $40,000 and over) applied more pesticide material to a larger percentage of their acres than did the smaller

growers (sales less than $2,500) (USDA, 1968). The difference (excluding pastures) ranged from 6% for the small producer to 21% for the larger producer. Some individual crops, however, were exceptions to these use trends. For instance, the small potato producers used more insecticides or treated about 78% of their acres, the intermediate-size producers (sales, $10,000 to $20,000) treated 98% of the acres, and the large producers treated only 69% of their acres (USDA, 1968). This trend may be explained by the fact that substantially more of the larger potato producers are located in the northern plains where fewer treatments are necessary.

Average insecticide treatment for all crops equals 1% of the crop acreage in the mountain-states region, 3% in the northern plains, 17% in the Corn Belt, and 19% in the Southeast (Fig. 2) (USDA, 1968). This range of 1 to 19% is relatively wide from the mean of 5%. These differences are, in part, due to differences in crops grown, intensity of insect attack, and cultural practices followed in the different regions.

For any one crop, pesticide treatment may vary according to geographic region. For example, in the northern plains where large quantities of potatoes are grown, 42% of the potato acreage is treated with insecticides; while in the Southeast, where early potatoes are grown, 100% of the potato acreage is treated (USDA, 1968). This difference probably reflects the higher intensity of pest attack occurring in the warmer regions.

PEST LOSSES IN AGRICULTURE

According to the latest USDA estimates (1951–60), crop losses due to all pests were $9.9 billion or 33.6% (includes loss in yield and quality, Table 2). Losses due to insects and plant diseases have increased since the previous decade while losses from weeds have decreased significantly (USDA, 1965).

The usage of DDT and the synthetic insecticides has grown in the decades following their introduction in 1946. Although crop losses due to insects have increased despite the significant use of insecticides, important advances have been made in reducing insect losses from certain pests in some crops. For example, losses in yield and quality from potato insects declined from 22% in 1910–35 (Hyslop, 1938), to 16% in 1942–51 (USDA, 1954), and to 14% in 1951–60 (USDA, 1965). This reduction is expected, considering the effectiveness of insecticides in controlling the major potato insect pests.

In contrast, losses in apples caused primarily by codling moth and apple maggot generally have not declined with increased use of organic insecticides. A 10.4% loss in yield and quality was reported for the period 1910–35 (Hyslop, 1938), a 12.4% loss for 1942–51 (USDA, 1954), and a 13.0% loss for the period 1951–60 (USDA, 1965). This loss pattern probably reflects higher-quality standards for salable fruit as well as the decline in sanitation and other cultural controls formerly practiced in orchards for control of these pests.

TABLE 2. Comparison of annual pest losses in agriculture for the periods 1904, 1910–35, 1942–51, and 1951–60 and an estimate of losses if no pesticides were used.

	Insects		Crop Diseases		Weeds		Total Loss		Potential Production
	$[a]	%	$	%	$	%	$	%	$
No Pesticide	4.8[b]	16.3[b]	4.2[c]	14.2[c]	3.0[d]	10.2[d]	12.0	40.7	29.5[e]
1951–60[f]	3.8	12.9	3.6	12.2	2.5	8.5	9.9	33.6	29.5[e]
1942–51[g]	1.9	7.1	2.8	10.5	3.7	13.8	8.4	31.4	26.7
1910–35[h]	0.6	10.5	NA[i]	NA	NA	NA	NA	NA	5.7[j]
1904[k]	0.4	9.8	NA	NA	NA	NA	NA	NA	4.1

[a] Billion dollars.

[b] Assumes that, in addition to total crop losses of $3.8 billion on both treated and untreated acres due to insect attack (1951–60 data), a $1.0 billion loss would occur if 5% of the crop acres receiving insecticide treatment (USDA, 1968) were left untreated. The $4.8 billion (16.3%) crop loss figure if no insecticide were used for insect control is based on the following: An overall 12.9% crop loss due to insects occurs on both treated (5%) and untreated (95%) acres. On the treated acres, 71% are planted to cotton, corn, fruit, and nuts. If all cotton were untreated, losses were assumed to average 32% (USDA, 1968; USDA, 1965; Parencia and Ewing, 1950; Parencia, 1959; Adkisson, et al., 1962; McGarr and Wolfenbarger, 1969; Black, 1971; Adkisson, 1972); losses on all untreated corn assumed to average 15% (USDA, 1968; USDA, 1965; Lilly, 1954; Apple, 1957; Burkhardt, 1962; Peters, 1964; Whitcomb, et al., 1966) and losses on all untreated fruit and nuts to average 60% (USDA, 1968; USDA, 1965; Oatman and Libby, 1965; Asquith, 1970; Glass and Lienk, 1971). A 12% loss was assumed for all the other untreated acres (USDA, 1968; USDA, 1965). The estimated value of cotton was $2.5 billion; corn, $4.4 billion; fruit and nuts, $1.4 billion; and all other, $21.2 billion (USDA, 1961). Thus crop losses due to insects without insecticides are: $32\%(\$2.5 \times 10^9) + 15\%(\$4.4 \times 10^9) + 60\%(\$1.4 \times 10^9) + 12\%(\$21.2 \times 10^9) = \$4.8$ billion.

[c] Assumes that, in addition to total crop losses of $3.6 billion on both treated and untreated acres due to crop disease (1951–60) data, a $0.6 billion loss would occur if the 0.5% of the crop acres receiving fungicide treatment (USDA, 1968) were left untreated. The $4.2 billion (14.2%) crop loss figure if no fungicide were used for crop disease control is based on the following: An overall 12.2% crop loss due to diseases occurs on both treated (0.5%) and untreated (99.5%) acres. On the treated acres, 51% of the acres are planted to peanuts, potatoes, citrus, and apples. Untreated peanut losses were assumed to average 25% (USDA, 1965; 1968; Jackson, 1967; Horne, 1968), losses on untreated potatoes assumed to average 30% (USDA, 1968; USDA, 1965; Manzer et al., 1965; Harrison and Venette, 1970), losses on untreated citrus assumed to average 60% (USDA, 1968; USDA, 1965; Ruehle and Thompson, 1939; Ruehle and Kuntz, 1940; Mokerek, 1970), losses on apples assumed to average 80% (USDA, 1968; USDA, 1965; Palmiter and Forshley, 1960; Ross, 1964), and losses on all other crops assumed to average 12% (USDA, 1968; USDA, 1965; Chester, 1950). The estimated value of peanuts was $0.18 billion; potatoes, $0.61 billion; citrus, $0.46 billion; apples, $0.25 billion; and all other, $28.0 billion (USDA, 1961). Thus crop losses due to diseases without fungicides are: $25\%(\$0.18 \times 10^9) + 30\%(\$0.61 \times 10^9) + 60\%(\$0.46 \times 10^9) + 80\%(\$0.25 \times 10^9) + 12\%(\$28 \times 10^9) = \$4.2$ billion.

[d] Assumes that, in addition to the $2.5 billion loss (1951–60 data) due to weeds, the 12% of the acres receiving herbicides (USDA, 1968) would require $0.5 billion in cultivation and other weed control practices to provide equally effective crop production. The $3.0 billion (10.2%) loss figure due to weeds if no herbicides were used is based on the following:

According to USDA estimates, corn losses due to insects have been increasing. A 3.5% loss was reported for the period 1942–51 (USDA, 1954) and 12.0% loss for the period 1951–60 (USDA, 1965). Factors contributing to increased corn losses due to insects include the continuous culture of corn on the same land year after year (Tate and Bare, 1946; Hill, et al., 1948; Ortman and Fitzgerald, 1964; Robinson, 1966) and the planting of insect-susceptible types rather than resistant-corn types (Painter, 1951; Sparks, et al., 1967; Starks and McMillian, 1967). This latter factor has been implicated in the greater losses in rice and wheat varieties used in the "green revolution" (Pradhan, 1971).

ESTIMATED LOSSES WITHOUT PESTICIDE USE

Estimated crop losses if no pesticides were employed are presented in Table 2. Without pesticides, crop losses due to insects would increase to $4.8 billion (16.3%), diseases to $4.2 billion (14.2%), and weeds to $3.0 billion (10.2%). Total losses without pesticides are estimated at $12.0 billion or 40.7% of potential crop production, an increased loss of 7.1%.

These estimated crop losses are exaggerated because insect, disease, and weed losses were assessed separately and then added together. For example, both insect and disease attacks on one apple were counted as a loss both for insects and for diseases. This approach yields an estimated total loss for apples from insects, diseases, and weeds of 150% (insects 60% + disease 80% + weeds 10%

←

A $2.5 billion loss due to weeds occurs on the 890.8 million acres of treated and untreated crop lands (pastures included) (USDA, 1968). On the treated acres, 46% are corn, wheat, sorghum, rice, and pasture (USDA, 1968). If substitute practices of weed control (cultivation and other practices) were employed for herbicides, the additional cost per acre is estimated at $5 for corn (USDA, 1968; USDA, 1965; Drew and Van Arsdall, 1966; Armstrong, et al., 1968; Buckholtze and Doersch, 1968; USDA, 1971*b*); $5 for wheat (USDA, 1968; USDA, 1965; USDA, 1971*b*; Friesen, 1965; Stobbe, 1970); $3 for sorghum (USDA, 1968; USDA, 1965; USDA, 1971*b*); $10 for rice (USDA, 1968; USDA, 1965; USDA, 1971*b*; Friesen, 1965; Smith, 1968); $5 for pasture (USDA, 1968; USDA, 1965; USDA, 1971*b*); and $5 for others (USDA, 1968; USDA, 1965). The millions of acres treated with herbicides are corn, 37.8; wheat, 15.3; sorghum, 0.9; rice, 1.0; pasture, 5.4; and other, 39.3 (USDA, 1968). Thus crop losses due to weeds which includes the alternative control costs are: $2.5 \times 10^9 + \$5(37.8 \times 10^6) + \$5(15.3 \times 10^6) + \$3(4.9 \times 10^6) + \$10(1.0 \times 10^6) + \$5(5.4 \times 10^6) + \$5(39.3 \times 10^6) = \$3.0$ billion.

[e] Pest Losses [for 1960] + Actual Crop Production [for 1960 (USDA, 1961)] + Potential Crop Production $9.9 billion + $19.6 billion = $29.5 billion.

[f] USDA, 1965.

[g] USDA, 1954.

[h] Hyslop, 1938.

[i] Not available.

[j] Insect losses and crop production estimates for 1935 (USDA, 1936).

[k] Marlatt, 1904.

= 150%) (Table 2). Obviously, total apple losses cannot be greater than 100% and a more accurate estimate is 90 to 95% without pesticides. Crop losses due to insects, disease, and weeds were estimated separately and exactly how much overlap exists in the loss figures is not known. Recognizing that these loss figures when added together are exaggerated, we can still gain a fair idea about the costs and benefits of pesticide use.

The estimated increased annual dollar loss if no pesticides were used is $2.1 billion ($12.0 billion – $9.9 billion = $2.1 billion). Contrast this estimated $2.1 billion loss with the $3.8 billion spent in 1969 (USDA, 1970*b*) and estimated $4.8 billion spent in 1971 for the farm price support program which also includes diverting nearly 60 million acres from planting crops like cotton, corn, and wheat (USDA, 1970*b*). This analysis is presented to provide a perspective concerning pesticide uses, benefits, and risks. It neither advocates doing without pesticides nor substituting payment to farmers for their losses due to pests if no pesticides were used.

Based on these estimates, overall crop losses would increase from 33.6% to 40.7%, or 7.1 percentage points if no pesticides were used in crop production. In fact, this nation normally produces an estimated surplus of 10% in quantity (USDA, 1970*b*). A 7.1% increased loss without the use of pesticides would not cause starvation. If no pesticides were used, the supply of food for the nation would be ample, but quantities of certain fruits and vegetables such as apples, peaches, plums, oranges, potatoes, and cabbages would be significantly reduced. Because of this, we might have to use substitutes for some of the fruits and vegetables we normally like to eat.

Actually, the loss in some fruits and vegetables would not be quite as large as the estimate if "cosmetic standards" were modified (Southwood and Way, 1970). Although safe and nutritionally sound, some fruits and vegetables are not sold in the market today because of their less-than-perfect outer appearance. For example, oranges with dark blemishes or scales on the peel are not sold, but these skin blemishes do not adversely affect the flesh. Also, cabbages with eaten holes in the outer leaves are not sold, but with these outer leaves removed, the cabbages are perfectly wholesome.

DOLLAR RETURN ON PESTICIDE USE

Using the figure of $2.1 billion (1960) to represent the additional loss incurred without pesticide use, an estimate can be made of the dollar return per dollar invested in pesticides for crop protection. With about $0.56 billion spent (1966) for pesticides in agriculture (USDA, 1970*c*) and assuming application costs for labor and machinery to be ⅓ the cost of the pesticide materials, the return per dollar invested for pesticide control is about $2.82. This estimate is somewhat below previous estimates of $4 to $5 returns, but the latter are based on different methods of calculation (PSAC, 1965; Headley, 1971).

An estimate of the increase in retail food prices due to the additional 7.1% loss of agricultural productivity can be projected. Because farm products have low-level elasticity, for every 1% decrease in quantity of farm products produced there is roughly a corresponding 4% increase in price (Brandow, 1961); therefore, the 7.1% increased loss would result in a possible 28.4% increase in farm product value to the farmer. This would amount to about a 9% increase in retail food prices (Robinson, 1971). If prices did rise, farmers probably would respond with efforts to increase output of the affected crops to establish a new quantity and new equilibrium price. Hence, through farmers' efforts to offset the 9% increase in price, the 7% loss gradually would be reduced.

Headley (1971) has proposed that planting additional acres could compensate for the increased crop losses caused by reduced pesticide use. He suggested that a "12% increase in crop land would reduce insecticide use by 70 to 80% and maintain output." Obviously, to plant and harvest 60 million (diverted acres) additional crop acres would be costly, but additional costs would be more than offset by the economics of the overall changes. For example, an estimated $0.75 billion would be saved by not applying pesticides. Added to this would be the saving of $3 to $4 billion usually spent for diverting acres. Headley did not propose the alternative of increased crop acres planted as the only substitute for pesticide use, but as one sound procedure which could be employed to reduce pesticide use and thereby environmental pollution.

For a few crops like apples, an increase in acres planted would not be a practical substitute for pesticide use because codling moth larvae and apple maggots inside the apples make this fruit unsalable. Oranges also are in the same category as apples, because of the currently high "cosmetic standards" now expected by the consumer. The public could be educated to be concerned more for the quality of their produce and less for the "cosmetic appearance" of the fruits and vegetables.

PESTICIDE POLLUTION

Before 1900 the primary aim in pest control was to eliminate the pest insect by any means short of destroying the crop. Lead arsenate was used in large quantities, and it was common to observe fruits and vegetables for sale which were "powder white" with residues.

Concern for the health of humans consuming these contaminated foods developed during the early 1900s and various regulations emerged. In 1954 tolerances were established for pesticides on raw agricultural commodities and regulated by the Federal Food, Drug, and Cosmetic Act as amended by the Miller Bill of 1954 (Public Law 518). This legislation limited the quantity of pesticide residues found in or on fruits, vegetables, and other agricultural products.

Thus by the mid-fifties, human health became a significant factor in assessing

the risks and benefits of pest control recommendations. At present there is increased concern for human health because recent investigations have indicated that some pesticides are carcinogenic, teratogenic, and mutagenic (HEW, 1969). More stringent standards and tests are now included in new pesticide registration procedures.

In addition, public interest in the 1960s focused on the deterioration of the environment caused by pesticides. Governmental legislation establishing the new Environmental Protection Agency followed in an effort to enforce protection of the environment from all pollutants including pesticides. All pesticides registered today by the EPA are carefully investigated for their potential hazard to the environment, as well as to man himself.

The public has demanded, and rightly so, to see the pesticide use "balance sheet"—to know the risks versus benefits relative to dollar economics, public health, and environmental pollution. A gross estimate was made earlier that the return per dollar invested in pesticidal control is $2.82; but this does not include the costs of pollution.

Pesticides may destroy natural enemies of other pests resulting in other pest outbreaks, thereby requiring additional pesticide sprays. The presence of chemical residues is always a risk. If too much pesticide is found on crops at harvest, the crop may be confiscated and destroyed. In addition, high residues may be caused by drift or by a gradual accumulation of the pesticide in a certain region. DDT in milk is an example, not because of any use associated with dairy cattle but because of a general contamination of the environment with DDT. Farmers following recommended treatment schedules on their own crops rarely have had pesticide residues above legal tolerances in their products (HEW, 1969).

Recommended use of pesticides normally results in tolerable residues, which implies that at present there is little or no direct danger to the health of man. Unfortunately, little is known about the effects of long-term, low-level dosages of pesticides on man (HEW, 1969). Furthermore, the possible interaction of low-level dosages of pesticides either with drugs or with the numerous food additives which the public consumes has not been studied.

Another growing public health problem is the hazard involved in the handling and application of pesticides. During 1968, 72 human lives were lost accidentally through the use of agricultural chemicals (HEW, 1971). This number will probably grow with the increased usage of the more toxic pesticides such as parathion. Both Metcalf (1972) and Smith (1972) asked a valid question when they inquired why the agriculturalists responsible for pesticide recommendations were not recommending safer, less toxic pesticides—such as fenthion, dicapthon, or malathion—rather than parathion and similar highly toxic pesticides as substitutes for the restricted DDT.

In addition to being a danger to human health, pesticides exact high costs

from our environment as pollutants. Economists refer to these pollution costs as part of the "external" costs (Edwards, 1971). While the direct cost of treating crops with pesticides is borne by the farmer, pollution costs are borne by society as a whole. Hence, the grower, in deciding to employ a pesticide for pest control, is concerned mainly with the price of the pesticide and application costs; the external costs are paid by society.

Scientists are concerned that so little is known about the ecological effects of pesticides on the plants and animals making up man's life system. At least an estimated 200,000 species of plants and animals comprise the life system of the United States. Information on the effect of pesticides is available for less than 1% of these species, and at best most of this information is incomplete (HEW, 1969; Pimentel, 1971). This lack of information should be alarming to both the public sector and the government when it is recognized that man's survival depends upon the functioning of his life system. This system provides man with a quality atmosphere; it protects him from deadly solar ultraviolet light (screened out by oxygen and ozone); it functions in degrading pollution wastes; and it plays many roles in the production of man's food and fiber (Allee, et al., 1949; PSAC, 1965).

No one knows *how many* species in the life system can be destroyed before the survival of man himself is endangered. Obviously, some species are more important to man than others. However, any gross tampering with the life system, as is occurring today with the wide release of agricultural and industrial chemicals into the environment, may threaten man's survival.

Pesticides have reduced some populations of beneficial insect parasites, predators, and pollinators in certain regions of our country. This reduction has increased some crop losses (PSAC, 1965; HEW, 1969). For example, when predator populations were inadvertently eliminated on beans and potatoes treated with DDT, chlordane, and other insecticides, outbreaks of mites occurred. At times the densities of these plant pests increased 20-fold above their "natural control" level (Klostermeyer and Rasmussen, 1953). Some pesticides have caused fish kills and sometimes have stopped reproduction in a species, such as lake trout (Burdick, et al., 1964). In addition, several valuable bird species, including eagles, falcons, and pelicans, have declined in part due to pesticides in some habitats in the United States (PSAC, 1965; HEW, 1969; Pimentel, 1971).

Pesticide pollutants are now widespread and occur in the water, soil, air, and most living organisms, including man. In the United States alone, nearly 40,000 pounds of DDT are estimated to be present in a total of nearly 200,000,000 humans (PSAC, 1965). However, no harmful effects are believed to have resulted from this dosage (HEW, 1969).

Even the amount of pesticide measured drifting in the atmosphere is disturbing. Concentrations of DDT, for example, were found to range from below detectable levels to 23 ng/m^3 for rural air samples. In urban communities which

had pest control programs, concentrations ranged from below detectable levels to as much as 8,000 ng/m^3 (Tabor, 1965, in Cohen and Pinkerton, 1966).

Pesticides can enter the atmosphere either during application by volatilization and codistillation, or they can be picked up from soil and plants by the wind. Pesticide application by aircraft spraying is especially effective in polluting the environment. Various studies indicate that as little as 25% of the pesticide applied by aircraft reaches crop level; the other 75% drifts away in the atmosphere (Hindin, et al., 1966; Ware, et al., 1970; Buroyne and Akesson, 1971; Akesson, et al., 1971). With 60% of all insecticides used in agriculture being applied by aircraft (USDA, 1971*a*), the problem of polluting the atmosphere and the environment is significant. Drift can be prevented if suitably large spray droplets are used in application with maximum winds of 7 mph. However, they are not as effective as fine droplets against some insect pests. Large droplets are satisfactory though for most herbicides. Some states such as California and Texas have initiated legislation concerning droplet size as well as other factors in an effort to control the drift problem with aircraft applications.

ALTERNATIVE METHODS OF PEST CONTROL

Pesticide use in some crops could and should be reduced. In others, these economic poisons are valuable tools when employed as one part of a crop systems management program. Let us examine some current alternative methods of pest control which might be immediately employed to reduce pesticide use.

One possible alternative to pesticides already mentioned involves increasing the number of crop acres planted to offset pest losses. This would mean reactivating some of the nearly 60 million acres now diverted from crop production. This alternative might be satisfactory for crops such as corn and cotton, but would not work with crops such as apples and peaches.

A second alternative is to plant some major crops in geographic regions where their pests are generally less numerous, thus decreasing use of pesticides. Implementing such a change would be sociologically difficult, but the environmental significance of such a step warrants further consideration. The importance of geographic regions for production is well illustrated by the codling moth pest in apples. In the South, there are 3 complete generations of the pest per year, whereas in the far northern regions there may be only a single generation (Jenne, 1912; Chapman and Lienk, 1971). Obviously, less insecticide is needed in the northern region for control of the codling moth. Also, it should be pointed out that there are varieties of apples which are significantly resistant to the codling moth (Cutright, 1937). Implementing sanitation and other cultural controls would also contribute to reducing this pest (Metcalf, et al., 1962).

Pest problems with vegetables also vary in severity in different climatic regions. For example in the Southeast, 100% of the potato acreage received insecticidal treatments, whereas in the northern plains only 42% received treat-

ments (USDA, 1968). Similar differences occur with fungicides. In the northern plains, 94% of the potato acres was treated with fungicides; in the mountain region only 19% of the potato acres was treated (USDA, 1968). Although other factors are involved, these figures suggest that some regions have fewer pest problems and thus may be more advantageous for culture of a particular crop than other regions.

Another successful alternative is to rotate crops. For many decades crop rotation proved to be an effective and profitable practice. Unfortunately, in the past few decades, pesticides have been substituted for this practice in some crops. In other cases, employing one pesticide may prevent the rotation of a crop. For example, some herbicides may reduce corn rotations with crops of oats, soybeans, and other non-host crops of corn pests because of the hazards of herbicide residues for these susceptible crops (Knake and Slife, 1962; Wisk and Cole, 1965; USDA, 1968; Swain, 1970; and Burnside, et al., 1971). As a result, in some cases there is a tendency to grow corn on corn and this may increase insect, disease, and weed pest problems. For instance, corn rootworm is a pest problem which may follow repeated corn croppings (Tate and Bare, 1946; Hill, et al., 1948; Metcalf, et al., 1962; Ortman and Fitzgerald, 1964; Robinson, 1966). The resulting rootworm problem may require additional insecticide for its control. This contributes to pollution and also increases the overall costs of pest control.

Another long-time, effective control technique for some pests is crop sanitation. Destroying crop remains eliminates a large portion of the corn borer population (Thompson and Parker, 1928). In the 1930s and 40s, fall plowing of corn stubble and stalks was widely used as a control measure for the corn borer; however, this measure was never economically evaluated.

Resistant varieties of crop plants could replace some of the more susceptible varieties. Although only a few insect resistant varieties are presently available, these have been highly effective in reducing crop damage. For example, the Hessian fly, a serious pest of wheat, is well controlled by resistant wheat varieties (Painter, 1951). The effectiveness of this pest control technique is further substantiated by a comparison of the reproduction of chinch bugs on two varieties of sorghum. On one variety (dwarf yellow milo), the bug produced an average of 99.4 offspring, whereas on a highly resistant variety (Kansas orange sorgo), the production of offspring averaged only 0.3 (Dahms, 1948).

Resistant varieties have been used more extensively for control of plant diseases than for insect damage control. Sometimes years of research are required to find resistant factors in plants and then to incorporate these factors into a variety which has all the desirable yield and quality characteristics (Painter, 1951; Van der Plank, 1968). The use of insect resistant plant varieties is usually assumed to be a long-range alternative, but resistant varieties have been developed in 3 to 5 years. Certainly resistant varieties are an alternative which merits immediate and greater attention.

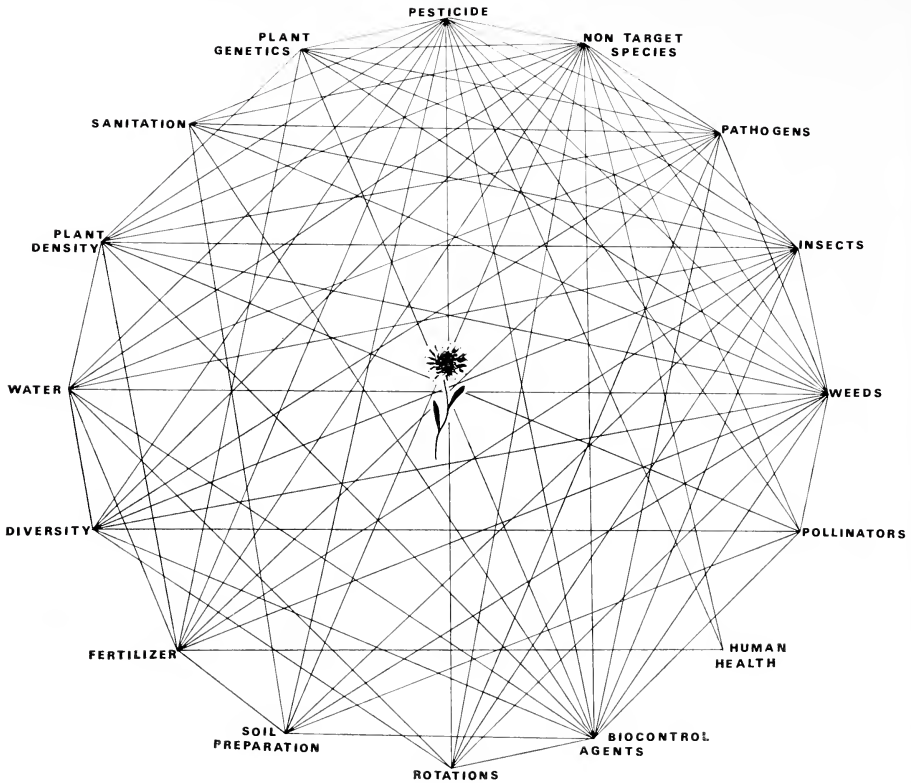

FIG. 3. The inter-relationships of the factors involved in the control of insect, pathogen (crop diseases), and weed pests associated with a particular crop plant.

Other controls which have proven effective for specific pests include such cultural practices as soil preparation, water management, and roguing of diseased hosts.

In addition to those bioenvironmental controls which could be implemented immediately for control of certain pests, new research should be undertaken to develop new bioenvironmental controls. Proven potential exists in other controls such as parasites (including pathogens), predators, attractants (chemical and physical), sterile male, and genetical means (PSAC, 1965).

Insecticide usage, for instance, could be drastically cut if bioenvironmental controls were developed for just a few major crop pests. For example, an estimated 40% of all insecticide applied annually in the United States is employed against only three pests; the cotton boll weevil, the cotton bollworm, and the apple codling moth (ACS, 1969). Development of effective bioenvironmental controls of these three pests would significantly reduce total insecticide use.

Pesticides are valuable pest-management tools and this deserves reemphasis.

The prime difficulty with them lies in man's tendency to completely substitute pesticides for effective bioenvironmental controls. Pesticides should be employed primarily as "stop-gap" or "fire-fighting" tools and sound bioenvironmental controls relied upon as the primary control method (PSAC, 1965).

"systems" approach to pest control

Because there is no simple answer or single technique for pest control, there is need for a "systems" approach to this complex problem. This approach would include the application of ecological principles to all aspects of crop culture and pest management and analysis of costs, benefits, and risks of all factors involved in crop production and pest management.

With the systems approach, pest management becomes an integral part of a total crop-culture program including the other crops grown in the region (Watt, 1964; Pimentel, 1970; Shoemaker, 1971). This type of pest control requires an understanding of the basic mechanisms affecting the crop and the interactions of major factors such as the pest itself, crop plant, water, soil, and fertilizers. Included in the systems analysis, in addition to crop-cultural practices, are the effects of economics as well as the maintenance of public health and the system's environmental quality. Then the total costs, benefits, and risks of the factors in the system can be evaluated and used as a basis for making sound decisions about pest control measures.

Figure 3 illustrates some of the complex interrelationships among different factors involved in pest control in an agro-ecosystem. These relationships are even more intricate than they appear. For example, a group of pests, together with all their enemies, also exists at each point where insect, disease (pathogens), and weed pests are pinpointed (Fig. 4).

The tools of systems analysis and computer technology are invaluable aids in dealing with the many interactions in crop systems. Initially, only the major pests need be included in a pest-management program; then as additional information is gathered, a more complete and sophisticated pest-management program could be developed for the crop and the region.

Unfortunately, at present there is no good, practical example of the systems approach being applied to pest control. However, the advantages of this approach can be understood by analyzing the utilization of crop rotation for corn rootworm control and the herbicide, 2,4-D, for corn weeds. To rotate corn with another non-host crop of corn pests has several associated costs and benefits. A cost consideration is the fact that the second crop may not yield the profit per acre of corn. Specialized equipment is needed to plant and harvest both crops. The benefits include reduced costs for insecticide for the rootworm, reduced danger of poisoning to the farmer and his laborers, and also reduced environmental pollution. If a legume were used in the rotation, other benefits might include reductions in associated insect pests, plant pathogens, and weed

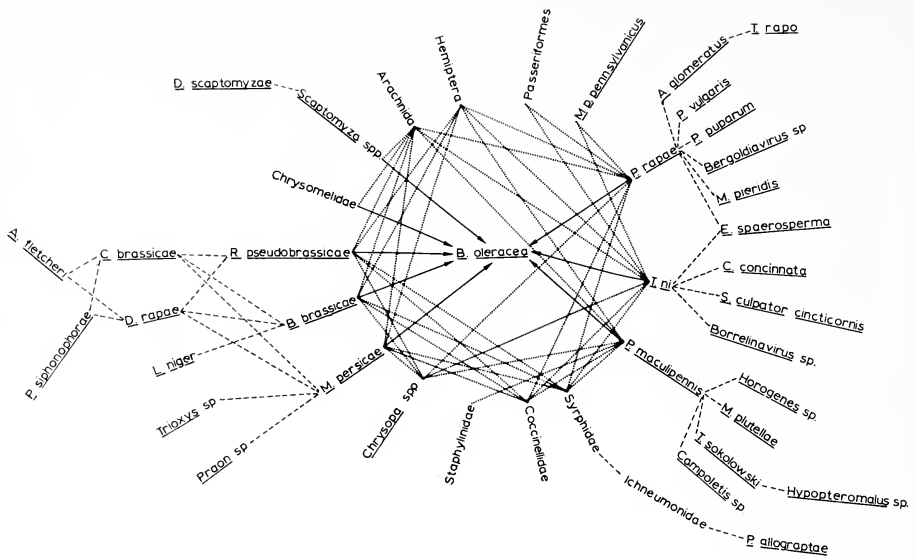

FIG. 4. The relationships between the cole crop-plant (*Brassica oleracea*), the insect pests (————), the parasitic (– – – – –), and predaceous (· · · · ·) enemies of the insect pests (Pimentel, 1961).

pests, plus reduced fertilizer needs for corn. When 2,4-D is used for weed control, the costs include application charges, increased chances of environmental pollution (Pimentel, 1971), and perhaps an increase in insect pests. For example, aphid numbers have been shown to increase several-fold on certain plants exposed to 2,4-D (Maxwell and Harwood, 1960; Adams and Drew, 1969). On the other hand, the benefits of 2,4-D weed control include reduced costs in some instances (Drew and Van Arsdall, 1966; Armstrong, et al., 1968) and more effective control of weeds if conditions are wet. All the factors involved in management of the corn ecosystem could be programmed for a systems analysis to determine the optimal management practices for the total system including the environment surrounding the crop.

The need for a systems approach to pest management and for the development and use of additional bioenvironmental controls is clear. Strong measures for change should be instituted now to halt the increased reliance on pesticides, which, according to USDA figures, has escalated during some years as much as 24% (USDA, 1970*a*).

CHANGES IN PESTICIDE USE

Immediate reductions in pesticide use would be possible by substituting "treat-when-necessary schedules" based on the actual measurements of pest populations for the currently employed "routine spray schedules" which waste

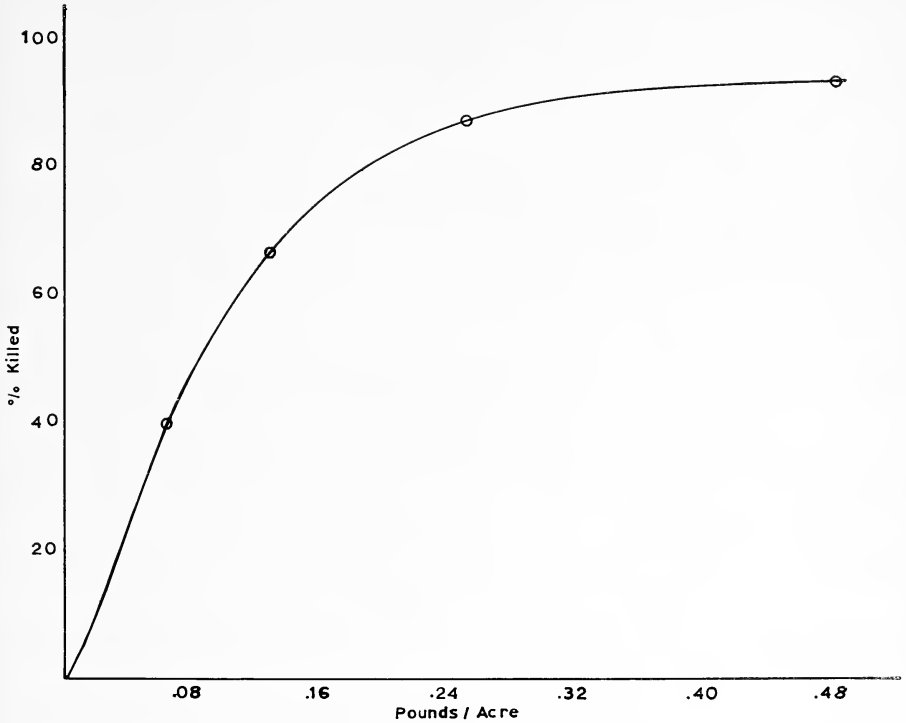

Fig. 5. Amount of dieldrin applied per acre and the percentage kill of boll weevils after 22 hours exposure (Bottger, et al., 1958).

pesticides, contribute to pollution, and increase food costs. Estimates suggest that farmers could reduce insecticide use 35 to 50% with little or no effect on crop production by just "treating-when-necessary" (PSAC, 1965).

A further reduction in pesticide use would also be possible if the current policy favoring 100% pest kills were replaced by lower-level pest kills based on sound economic-threshold densities (Smith, 1969). The increased costs of 100% pest kills can be easily seen in Fig. 5. Note that the top of the "S" curve is flattened; thus increasing the amount of pesticide applied per acre results in smaller and smaller increases in both percentage kills and crop yields. Policies which favor 100% pest kills on crops are wasteful, may be dangerous, and often result in costly "overkills."

In conclusion, pesticide use in the United States could be reduced significantly if:

1. Bioenvironmental pest controls which were replaced with pesticides were again put into full practice wherever possible.
2. Some or all of the 60 million acres currently diverted at a cost of $3 to $4

billion annually were planted to help balance the increased crop loss resulting from a reduction in pesticide use.

3. A "treat-when-necessary" program based on monitoring pest populations were initiated and aircraft spray drift were reduced.
4. The public were educated to be concerned for the safety of their fruits, vegetables, and other produce and attach less importance to "cosmetic appearance."

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Resistance in the Eggplant to Two-Spotted Spider Mites

A. BENEDICT SOANS, DAVID PIMENTEL, AND JOYCE S. SOANS
DEPARTMENT OF ENTOMOLOGY AND SECTION OF ECOLOGY AND SYSTEMATICS,
CORNELL UNIVERSITY, ITHACA, N.Y. 14850

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Abstract: Seven varieties of the eggplant *Solanum melongena* L. were selected for an evaluation of resistance to the two-spotted spider mite *Tetranychus urticae* Koch. The Sinompiro variety which was observed in the field to be highly resistant to mites did not exhibit a high level of resistance when tested in the laboratory. The Black Beauty and Sinompiro varieties exhibited some resistance to the mites. The Dingras #1 and #3 varieties showed a lower level of resistance than the Black Beauty and Sinompiro varieties.

INTRODUCTION

Two-spotted spider mites (*Tetranychus urticae* Koch.) are serious pests of several food crops including eggplant (*Solanum melongena* L.) (Metcalf et al. 1962). Some eggplant varieties exhibit natural resistance to certain insect pests. Poos and Haenseler (1931) reported that in New Jersey, Long Purple was seriously injured by the potato leafhopper (*Empoasca fabae* Harris), whereas other common varieties (Black Beauty, New York Improved, and Florida High Bush) were only slightly affected.

Dharmaraju and Chowdary (1960) in Ceylon tested 38 varieties of eggplant for resistance to the stem borer (*Euzophera perticella* Ragonet) and found that the incidence of infestation ranged from 91% for Chodavaram to 67% for Sattenapalli variety. Srinivasan and Basheer (1961) reported that the percentage of infested fruits was only 10.8% for the variety Coimbatore, but 48.0% for the variety Surtigote.

Nowhere in the literature did we find a report of an investigation of potential resistance to mites in eggplant. However, Professor H. M. Munger (1970, personal communication), of Cornell University, while in the Philippines, observed that certain eggplant varieties (Sinompiro, Karume Long, Dingras #1 and #3) had few mites, whereas others (Millionaire) had many mites. The aim of this investigation was to evaluate these five varieties of eggplant, plus two others, for resistance to the two-spotted mite.

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MATERIALS AND METHODS

In this study, the following seven varieties of the eggplant were tested in the laboratory for their relative degree of resistance to spider mites:

1. Black Beauty
2. Karume Long
3. Sinompiro
4. Dumaguete Long Purple
5. Millionaire
6. Dingras #3
7. Dingras #1

Earlier we mentioned that Professor Munger indicated that varieties Sinompiro, Karume Long, Dingras #1 and #3 showed some resistance, whereas variety Millionaire was susceptible to mites. No information was available on Dumaguete Long Purple and Black Beauty.

The eggplants were grown in an environmental chamber under controlled conditions. Illumination with a daily photoperiod of 16 hr and at about 500 ft-candle at the plant level was provided by fluorescent lights (VHO Powertube, Cool White™ F72T12CW, 72 in., Sylvania Electric Products, Inc., Danvers, Mass. 01923, USA). The temperature was maintained at 80 ± 2° F and relative humidity at 70 ± 5%. Each plant was grown in a 15 cm. diameter plastic pot in a mixture of loam, sand, peat, and fertilizer. The pots were watered on alternate days and the soil was fertilized once in two weeks with a standard dilution of fertilizer (Stern's Miracle-Gro,™ 15-30-15). The test plants were randomly arranged in the environmental chamber.

The eggplants were tested eight weeks after germination. When leaves or leaf discs were used for the tests, the third leaf from the base was selected for uniformity. In tests requiring confinement of mites to a part of the leaf during the test period, the following leaf-disc technique [a slight modification of the method devised by Rodriguez (1953)] was used.

For this test, leaf discs 2.5 cm. in diameter were cut with a sharp cork borer (#15). A streak of pure lanolin (Botany™) was applied to the cut edge of the leaf disc to prevent the escape of mites. A circular piece of cellucotton, about 5 cm. in diameter and moistened with tap water, was placed in a plastic petri dish about 6 cm. in diameter. One leaf disc was placed, ventral side facing upward, on the moist cellucotton in a petri dish. The cover of the petri dish was kept slightly open to prevent the condensation of water on its inner side and subsequent drip onto the leaf disc. The cellucotton was moistened every 48 hr. During the tests, petri dishes containing the leaf discs were marked and randomly placed in the growth chamber.

Spider mites for all tests were reared under similar conditions on Fordhook lima bean plants (selecton 242). The bean plants were replaced every two weeks.

TABLE 1. A comparison of spider mite responses on seven varieties of the eggplant, by Duncan's multiple-range test. Means underscored by the same line differ significantly; * p = 0.05 and ** p = 0.01.

Varieties: 1 = Black Beauty; 2 = Karume Long; 3 = Sinompiro; 4 = Dumaguete Long Purple; 5 = Millionaire; 6 = Dingras #3; 7 = Dingras #1							
Test Explanation[a]							
Mean preference of 20 mites for varieties	1	6	3	7	4	5	2
	1.7	2.3	2.15	2.6	3.7	3.9	4.8 **
Mean number of mites leaving the leaf disc during four days	5	1	4	2	6	3	7
	0.2	0.5	0.7	0.9	0.9	1.3	1.3 *
Mean number of progeny produced/pair after 12 days	6	5	1	3	7	4	2
	77.6	86.6	90.4	103.0	117.8	120.4	123.6 **
Index of mite damage for varieties	1	3	6	7	4	2	5
	3.2	3.2	3.2	3.4	3.6	4.2	4.2 **

[a] See text for methods.

The data on susceptibility or resistance were tested by the analysis of variance. When the treatment differences were found to be significant, the means were compared by Duncan's new multiple-range test (Duncan, 1955). The specific methods for each of seven different experiments are described in the results section.

RESULTS

Feeding Preference. The feeding preference of the mites was tested using the following multiple-choice design. Seven leaf discs, one from each variety, were placed in a circle close to the margin of an open plastic petri dish, 10 cm. in diameter. The leaf discs were not lined with lanolin. A thin film of tanglefoot was applied to the vertical wall of the dish to prevent the escape of mites. The petri dishes were placed in a dark humid chamber with a relative humidity of about 100%. Twenty mites which had been starved for 12 hours were released at the center of the petri dish. After 12 hours, the number of mites on and under each leaf disc was noted. Ten replications were run.

The Black Beauty variety was least preferred ($p = 0.01$) and Karume Long was the most preferred variety (Table 1).

Repellency Test. One leaf disc from each variety was placed on moist cellucotton in a plastic petri dish. The disc was not ringed with lanolin. Ten mites were released on the disc. After four days, the number of mites that had wandered off the leaf disc and drowned in moist cellucotton was recorded. There were ten replicates.

The mites were repelled most ($p = 0.05$) by Sinompiro and Dingras #1 varieties and least by the Millionaire variety (Table 1).

Oviposition Response. One leaf disc of each variety was placed on moist cellucotton in a plastic petri dish and one young female mite was placed on the disc. The petri dishes were placed inside the environmental chamber and the number of eggs laid on each disc was counted after 72 hr. Ten replicates were run.

The smallest number of eggs (2.9/female) was laid by the mites on the Sinompiro variety and the largest (5.0/female) number on Karume long variety, but the differences were *not* significant.

Longevity and Fecundity. Leaf discs of the various varieties, ringed with lanolin, were placed individually on moist cellucotton in petri dishes. One young female mite was placed on each disc. There were ten replicates. The mites were observed daily and their longevity was recorded. The leaf discs were replaced every 72 hours. The number of eggs laid by each mite was recorded daily. The eggs were then removed with a moist camel-hair brush. There were no differences in longevity, but the number of eggs laid by a female was lowest (4.3) on Black Beauty and highest (12.8) on the Millionaire variety.

Mite Reproduction. To determine whether there were any differences in the rate of multiplication of the mites on the various varieties, a test was run with mites caged directly on the plants. The mites were confined to a leaf by drawing a narrow ring of lanolin around the petiole. Three young female mites and three males were released on each test leaf. Ten replicates were made. After 12 days, the number of adult mites on each test leaf was counted.

The mean number of adult progeny per pair of mites was lowest (77.6) on the Dingras #3 variety and highest (123.6) on the Karume Long variety ($p = 0.01$) (Table 1).

Index of Damage. Five plants of each variety were randomly placed inside the growth chamber and were uniformly infested with mites by placing on each plant a heavily infested bean leaf. After three weeks, the extent of damage suffered by each plant was given a visual rating according to the following scale.

Rating	*Observed Damage*
0	No apparent damage
1	Less than 10% damage
2	About 25% damage
3	About 50% damage

4	About 75% damage
5	100% damage

The varieties Black Beauty, Sinompiro, and Dingras #3 showed the least damage ($p = 0.01$), while the Karume Long and Millionaire varieties showed the greatest damage (Table 1).

DISCUSSION

The responses of the seven eggplant varieties to mites based on seven different tests are not consistent. In general, however, varieties Black Beauty and Sinompiro exhibit some degree of resistance to mites. These results were not totally in agreement with Professor Munger's observations in the Philippines, which indicated that the Sinompiro variety was highly resistant to mites.

That resistance responses of plants to insects vary from field conditions to laboratory conditions is not surprising and has been observed by other workers (Kindler and Kher, 1970; Curry and Pimentel, 1971). Conditions in the laboratory are never exactly the same as in the field relative to light, soil nutrients, water, temperature, and wind; hence, it is not surprising that plants respond differently. Any one or a combination of these factors may alter the physiology of the plant, and in turn, its resistance factors.

Furthermore, much depends upon what test(s) is being used to measure resistance. Mite resistance in eggplant varieties is quite complex and is illustrated by the results with the Sinompiro variety. On this variety, mites had an intermediate level of preference but once present, they were seldom repelled by the variety compared to the other varieties. Mite reproduction was also intermediate; however, heavy mite infestations did little damage to this variety. Certainly an examination of the results in Table 1 indicates other differences in response, suggesting that several factors are involved in eggplant resistance to mites. Again, these results support the principle that most resistance in plants to insects is due to polygenic characteristics (Painter, 1951).

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Northern Distribution Records for *Tachysphex terminatus* (Smith) (Hymenoptera: Sphecidae, Larrinae)

Nancy B. Elliott and William M. Elliott
Biology Department, Hartwick College, Oneonta, New York 13820

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Abstract: Specimens of *Tachysphex terminatus* (Smith) were collected from localities in Alberta and Alaska during June, 1971; these localities are considerably north of the previously known range of the species.

Tachysphex terminatus (Smith) is a small black digger wasp, common in sandy habitats throughout much of North America. G. E. Bohart in Muesebeck, *et al.*, 1951 listed the range of the species from Ontario and British Columbia extending south to Arizona and Georgia.

As part of a study of morphological variation in this species (Elliott, 1971), specimens of *T. terminatus* from 61 museum collections in the United States and Canada were examined. Northern records found among these specimens are as follows:

1 ♂ Hull, Quebec, 21 July, 1947 (W. R. Mason); Lakeside, Quebec (J. W. Buckle): 1 ♂ 24 June, 1931; 2 ♀ 11 July, 1931; 5 ♀ 16 July, 1931; 5 ♀ 19 July, 1931; 1 ♀ 22 July, 1931; 2 ♀ 23 July, 1931; 1 ♀ 24 July, 1931; 4 ♀, 5 ♂ 27 July, 1931; 3 ♀ 28 July, 1931; 1 ♀ 30 July, 1931; 2 ♀, 1 ♂ 1 August, 1931; 1 ♀ 2 August, 1931; 2 ♀ 3 August, 1931; 1 ♂ 8 August, 1931; 1 ♂ Lanoraie, Quebec, 24 June, 1924 (J. W. Buckle); 1 ♂ St. Hilaire, Quebec, 30 July, 1927 (J. W. Buckle); 1 ♀ Ottawa, Ontario 24 July, 1947 (W. R. Mason); 1 ♀ Ottawa, Ontario, 31 August, 1947 (W. R. Mason); 1 ♂ Cape Breton National Park, Nova Scotia, 5 August, 1954 (A. & H. Dietrich); 1 ♀ Prince Edward Island National Park, Prince Edward Island, 25 August, 1953 (E. L. Kessel); 1 ♀ Vernon, British Columbia, 5 August, 1947 (Hugh B. Leech).

The northernmost extension of the recorded collection localities is approximately 50.5° north latitude for Vernon, British Columbia. In the summer of 1971, we collected samples of *T. terminatus* which greatly extend the northern limit of its range. Collection data for these samples along with approximate latitude of each locality are as follows:

4 ♀, 3 ♂ Whitecourt, Alberta, 20 June, 1971 (54° N); 3 ♀, 42 ♂ Mile 1246 Alaska Highway, Alaska, 23 June, 1971 (60° N).

Specimens from both these populations exhibited normal abdominal color patterns for members of this species found west of the Rockies; males were all-black, while females had red-tipped abdomens, unlike individuals from eastern populations in which individuals of both sexes are generally red-tipped.

Acknowledgments: We wish to thank Dr. F. E. Kurczewski, Department of Forest Entomology, State University of New York, College of Environmental Science and Forestry, Syracuse, N.Y., for corroborating our identification of the wasps. A list of museums from which specimens of *T. terminatus* have been examined is found in Elliott, 1971.

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Geographic Distribution of the Genus *Parargyractis* Lange (Lepidoptera: Pyralidae) Throughout the Lake Erie and Lake Ontario Watersheds (U.S.A.)[1]

MICHAEL A. LAVERY AND ROBERT R. COSTA
DEPARTMENT OF BIOLOGICAL SCIENCES, STATE UNIVERSITY OF NEW YORK, COLLEGE AT BROCKPORT, BROCKPORT, NEW YORK 14420

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Abstract: The geographic distribution of the immature stages of aquatic lepidopterans (genus *Parargyractis*) was studied in 43 streams throughout the American section of the Lake Erie and Lake Ontario watersheds. *Parargyractis* populations were commonly distributed throughout the watersheds, but the distribution was somewhat localized. In 64% of the streams where *Parargyractis* were found, larvae and/or pupae were relatively abundant. The immature stages were frequently encountered within the same community of insects that usually require clean stream conditions for survival (Plecoptera, Ephemeroptera, Trichoptera).

INTRODUCTION

Most insects of the large order Lepidoptera are terrestrial throughout their entire life history. However, some members of a few families of moths are capable of a true aquatic existence. Members of the pyralid genus *Parargyractis* are especially well adapted to an aquatic life in their immature forms.

Parargyractis larvae live in rapid streams on the surfaces of submerged rocks. Each larva is protected from the current by a case consisting of an irregular sheet of silk cemented around most of its periphery to the rock. The larvae move about under these silken cases feeding on diatoms and other debris of rock surfaces. Pupation occurs in oval, dome-shaped cocoons into which holes have been cut at each end to allow for passage of water. The pupa is suspended from the ceiling of the felt-like outer covering of the cocoon within a finely woven, silken, waterproof lining. Just before pupation the last instar larva cuts a crescent-shaped slit in the cocoon through which the adult will emerge. When gravid, the adult female enters the water, using its hind legs as oars, and glues groups of eggs onto rocks (Lange, 1956, 1971).

Little information exists relative to the geographic distribution of the genus *Parargyractis*. Lloyd (1914), the first investigator to describe the immature stages of *Elophila fulicalis* (now in *Parargyractis*), found larvae and pupae in only a limited area of Fall Creek, Ithaca, New York. However, in a similar stream nearby, it was absent. This led him to conclude that the distribution of

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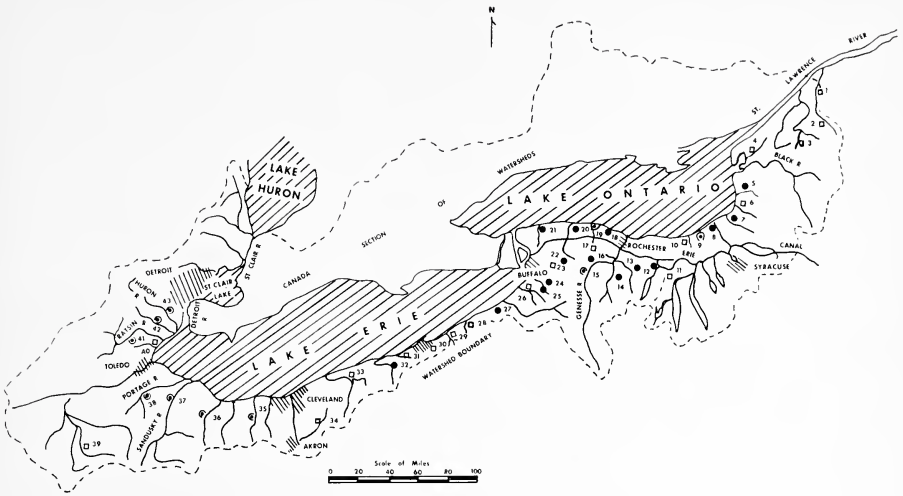

Fig. 1. Geographic distribution of *Parargyractis* throughout the American section of the Lake Erie and Lake Ontario watersheds. (● = present; ⊙ = present and very abundant; □ = not found. Number beside symbol refers to stream name and exact location of sampling area found in Table 1.)

P. julicalis was extremely local. Forbes (1923), in his studies of the Lepidoptera of New York and neighboring states, found that *P. julicalis* distribution was common and general. Pennak (1953) noted that although the geographic distribution of *P. julicalis* was not completely known, it probably was common in the eastern United States. Welch (1959) noted that *Cataclysta* (now *Parargyractis*) was widely, but often only locally, distributed over the eastern half of the United States and northeastern Canada. Lange (1971) described four species of *Parargyractis* from California, and found members to be well represented in western United States.

Despite this common distribution, few stream studies have reported the presence of the immature stages of *Parargyractis*. Lavery and Costa (1972) have recently shown that a reason for this may be the selective nature of sampling methods commonly used in stream studies. They demonstrated that the Surber square-foot sampler, which is extensively used in North American stream surveys to sample benthic macroinvertebrates, was totally unreliable in estimating *Parargyractis* populations. They concluded that the behavior of *Parargyractis* larvae in constructing silken canopy-like cases that adhere tightly to rocks and their habit of lodging in crevices or depressions over which the case is built account for much of the unreliability. This apparent inaccuracy of the Surber sampler was also noted by Culley (1967) who took two samples in a stream densely populated with *Parargyractis* larvae and pupae (34 per

square foot) but found only one larva in the Surber net. It is quite apparent that the selective nature of sampling methods used in stream studies accounts partially for the paucity of information on the biology and distribution of the immature forms of *Parargyractis*.

Hence, the genus *Parargyractis*, although thought to be widely distributed and common in the eastern United States, is often only encountered locally. However, almost no information exists on how extensive its distribution is within a definite geographic area. If members of this genus are common, there appears to be virtually no information available on the abundance of the immature stages in streams.

The objectives of this study, therefore, were: 1) to determine the extent of distribution of *Parargyractis* throughout a definite area, the American section of the Lake Erie and Lake Ontario watersheds, and 2) to estimate the numerical importance of *Parargyractis* larvae and pupae in streams within this defined area. It was hoped that in so doing the importance of this group in the ecology of benthic stream communities would be clarified.

METHODS

Streams within the Lake Erie and Lake Ontario watersheds having accessible riffle areas were chosen for sampling. Since it was temporally not feasible to sample all streams, an attempt was made to evenly allocate sampling areas throughout the two watersheds. When possible, the major streams (usually between 10 and 20 meters in width) were sampled.

Rocks were removed from riffle areas and carefully examined for the cases of *Parargyractis* larvae and pupae. The cases, when found, were ruptured with forceps and the immature forms were removed and preserved in 70% ethanol.

Duration of actual sampling was recorded in an attempt to quantify the sampling effort. A minimum of 30 minutes was spent sampling streams where few or no lepidopterans were observed. If many were encountered, sampling was often limited to less than 30 minutes. The total number found at each area was then determined and expressed as numbers found per thirty minutes of sampling. A numerical comparison between areas could then be made and the relative numerical importance assessed.

At each area, other invertebrates observed in the same habitat with *Parargyractis* were recorded. Usually these invertebrates were classified to family and then returned to the stream. In some instances, animals were classified only to order. These observations yielded general information on invertebrate populations commonly associated with *Parargyractis* populations.

RESULTS AND DISCUSSION

A total of 43 streams were sampled throughout the Lake Erie and Lake Ontario watersheds (Table 1). Members of *Parargyractis* were found in 58%

Table 1. Name and exact location of area sampled

Number[1]	Name	Location
	Lake Ontario Watershed	
1	Grasse River	St. Lawrence Co., N.Y. at bridge on SUNY A.T.C. Campus; Canton, N.Y.
2	Elm Creek	St. Lawrence Co., N.Y. on Rt. 87, just north of Hermon, N.Y.
3	Matoon Creek	St. Lawrence Co., N.Y. at bridge on Rt. 58 south of Guveneur, N.Y.
4	Perch River	Jefferson Co., N.Y. bridge on Rt. 180 south of Limerick, N.Y.
5	South Sandy Creek	Jefferson Co., N.Y. upstream from bridge on Rt. 11
6	Salmon River	Jefferson Co., N.Y. In town of Pulaski, N.Y.
7	Little Salmon River	Oswego Co., N.Y. at bridge on Rt. 69 just east of Colosse, N.Y.
8	Rice Creek	Oswego Co., N.Y. at bridge on Rt. 104
9	Sterling Creek	Cayuga Co., N.Y. downstream from bridge on Rt. 104A on west edge of town of Sterling, N.Y.
10	Wolcott Creek	Wayne Co., N.Y. downstream from Wolcott Falls in Wolcott, N.Y.
11	Flint Creek	Ontario Co., N.Y. south of Rt. 96 on west edge of town of Phelps, N.Y.
12	Canandaigua Outlet	Ontario Co., N.Y. downstream from bridge on Rt. 96
13	Mud Creek	Ontario Co., N.Y. upstream from bridge on Rt. 20
14	Honeoye Creek	Ontario Co., N.Y. upstream from bridge on Rt. 20
15	Oatka Creek	Genesee Co., N.Y. downstream from bridge on Rt. 63, 0.5 miles north of Pavilion, N.Y.
16	Black Creek	Genesee Co., N.Y. bridge on Rt. 237, 0.3 miles north of Byron, N.Y.
17	Spring Creek	Genesee Co., N.Y. bridge on Rt. 237
18	Salmon Creek	Monroe Co., N.Y. bridge on Rt. 31
19	Sandy Creek	Monroe Co., N.Y. north Hamlin, N.Y.
20	Marsh Creek	Orleans Co., N.Y. bridge on Sawyer Rd., 0.5 miles north of Rt. 18
21	Eighteenmile Creek	Niagara Co., N.Y. bridge on Rt. 104, 0.9 miles west of Wright's Corners, N.Y.
	Lake Erie Watershed	
22	Little Tonawanda Creek	Genesee Co., N.Y. downstream from bridge on Rt. 20
23	Cayuga Creek	Erie Co., N.Y. bridge on Rt. 358
24	Little Buffalo Creek	Erie Co., N.Y. bridge on Rt. 358 in village of Marilla, N.Y.
25	Buffalo Creek	Erie Co., N.Y. downstream from bridge on Rt. 20A in Wales Center, N.Y.
26	Eighteenmile Creek	Erie Co., N.Y. downstream from bridge on Rt. 5, west of Lakeview, N.Y.

TABLE 1. (*Continued*)

Number[1]	Name	Location
	Lake Erie Watershed Continued	
27	Walnut Creek	Chautauqua Co., N.Y. upstream from bridge on Rt. 20, 0.25 miles west of Silver Creek, N.Y.
28	Chatauqua Creek	Chautauqua Co., N.Y. bridge at Hawley St. in Westfall, N.Y.
29	Twentymile Creek	Erie Co., Pa. bridge on Rt. 5
30	Mill Creek	Erie Co., Pa. Bridge on Rt. 97 in southern part of Erie, Pa.
31	Elk Creek	Erie Co., Pa. south of Rt. 20, west of Girard, Pa.
32	Conneaut Creek	Erie Co., Pa. downstream from bridge on Rt. 6n, 1 mile north of Cherry Hill, Pa.
33	Grand River	Ashtabula Co., Ohio, under bridge on Rt. 6
34	Cuyahuga River	Portage Co., Ohio, 0.25 miles west of Rt. 700, near town of Welshfield, Ohio
35	Black River (East Branch)	Lorain Co., Ohio, 0.2 miles east of Rt. 301
36	Vermilion River	Huron Co., Ohio upstream from bridge on Rt. 250 in Fitchville, Ohio
37	Sandusky River	Seneca Co., Ohio, 0.6 miles east of Rt. 53, bridge on Darr Rd., 4 miles north of Fort Seneca
38	Portage River	Wood Co., Ohio, bridge on Water St., Pemberville, Ohio
39	Ottawa River	Putnam Co., Ohio, upstream from bridge on Rt. 224 in Kalida, Ohio
40	South Otter Creek	Monroe Co., Mich. bridge on Rt. 25 in Casalle, Mich.
41	Raisin River	Monroe Co., Mich., bridge 2 miles north of Rt. 50; 4 miles south of Maybee, Mich.
42	Stony Creek	Monroe Co., Mich. east of bridge on Rt. 25 about 3 miles north of Monroe, Mich.
43	Huron River	Wayne Co., Mich. bridge on Rt. 24 in Flat Rock, Mich.

[1] Number corresponds to that found on Fig. 1.

of the 43 streams sampled. Immature stages were found to be widely distributed and common throughout the watersheds (Fig. 1). Distribution, however, was somewhat localized, for, in some cases, members were found in one stream but not in a very similar nearby stream. The conclusions of Pennak (1953) and Welch (1959) that members of *Parargyractis* are common and widely distributed throughout the eastern United States are supported by these findings. In addition, this study shows the extent of distribution in a given geographic area.

The quantitative estimates at each area where *Parargyractis* was found appear in Table 2. To facilitate evaluation, these estimates were classified into three categories: 1) very abundant; 26 to 87 specimens collected per 30 minutes;

Table 2. Abundance of *Parargyractis* immature stages at each area sampled; 18 May–17 September 1972

Number[1]	Date Sampled	Abundance, (no. per 30 min.)	Classification[2]
1	27 August	none	
2	26 August	none	
3	26 August	none	
4	26 August	none	
5	25 August	8	scarce
6	25 August	none	
7	25 August	16	abundant
8	1 August 1972	5	scarce
9	1 August	38	very abundant
10	1 August	none	
11	24 August	none	
12	4 August	1	scarce
13	26 August	16	abundant
14	26 August	2	scarce
15	26 July	28	very abundant
16	25 July	15	abundant
17	25 July	none	
18	20 May	16	abundant
19	18 May	70	very abundant
20	24 May	1	scarce
21	22 July	3	scarce
22	28 July	1	scarce
23	28 July	none	
24	28 July	1	scarce
25	28 July	20	abundant
26	10 August	none	
27	10 August	8	scarce
28	10 August	none	
29	17 September	none	
30	17 September	none	
31	17 September	none	
32	17 September	22	abundant
33	18 August	none	
34	18 August	none	
35	17 August	75	very abundant
36	17 August	48	very abundant
37	17 August	87	very abundant
38	17 August	26	very abundant
39	16 August	none	
40	16 August	none	
41	16 August	48	very abundant
42	16 August	45	very abundant
43	16 August	34	very abundant

[1] Number refers to exact sampling location found in Table 1.
[2] Classification; see text for explanation.

TABLE 3. Taxonomic list of other invertebrates found in same community with larvae and pupae of *Parargyractis*

Taxon		% of total streams	% of streams containing *Parargyractis*
Tricladida	Planariidae	57	48
Annelida	Hirudinea	7	9
Isopoda	Asellidae	10	9
Amphipoda	Gammaridae	22	17
Trichoptera	Hydropsychidae	100	100
	Hydroptilidae	35	35
	Helicopsychidae	20	30
Ephemeroptera	Baetidae	98	87
	Heptageniidae	75	70
Diptera	Chironomidae	98	98
	Simuliidae	52	48
	Tipulidae	22	26
Plecoptera	Perlidae	38	22
Coleoptera	Psephenidae	68	74
	Elmidae	32	35
	Dryopidae	7	9
Megaloptera	Corydalidae	2	4
Gastropoda	Ancylidae	20	26
	Various snails	29	20
Pelecypoda	Spaeriidae	22	30
Hydracarina		2	0

densely populated areas where larvae and/or pupae could be picked at will; 2) abundant; 15 to 25 specimens collected per 30 minutes; immature forms not densely populated yet easily found; and 3) scarce; 1 to 14 specimens collected per 30 minutes.

In streams containing *Parargyractis*, 40% had very abundant populations, 24% had abundant populations, while 36% contained scarce populations. Thus in 64% of the streams, immature stages of *Parargyractis* were abundant to very abundant. This appears to indicate that in many cases *Parargyractis* populations constitute important components of the stream biota. It further supports the belief that their quantitative importance as a group has apparently been underestimated (Lavery and Costa, 1972).

Other invertebrates commonly observed in the same benthic community with *Parargyractis* larvae and pupae are listed in Table 3. The five groups encountered in over 70% of the streams were: Hydropsychidae (Trichoptera); Baetidae and Heptageniidae (Ephemeroptera); Chironomidae (Diptera) and Psephenidae (Coleoptera). The Simuliidae (Diptera) and Planariidae (Tricladida) were found in about 50% of the streams. Hydroptilidae and Helico-

psychidae (Trichoptera); Tipulidae (Diptera); Perlidae (Plecoptera); Elmidae (Coleoptera); Ancylidae (Gastropoda), various snails (Gastropoda); Spaeriidae (Pelecypoda); and Gammaridae (Amphipoda) were present in 20–30% of the streams. Of all these invertebrate groups (Table 3), many are usually associated with well-aereated, nonpolluted streams. Therefore, one can expect the immature stages of *Parargyractis* to be most often associated with clean stream environments, a finding which could be of considerable interest to stream-water-quality investigators.

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Susceptibility of Sixteen Species of Muscoid Flies to the Microsporidian Parasite *Octosporea muscaedomesticae*[1]

JOHN PAUL KRAMER
DEPARTMENT OF ENTOMOLOGY, CORNELL UNIVERSITY, ITHACA, NEW YORK 14850

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Abstract: *Cochliomyia macellaria, Phormia regina,* and *Drosophila melanogaster* were highly susceptible to *Octosporea muscaedomesticae. Hylemya antiqua, Phaenicia sericata, Musca autumnalis,* and *Muscina stabulans* were slightly susceptible. *Calliphora terraenovae, C. vicina, C. vomitoria, Lucilia illustris, Fannia scalaris, Haematobia irritans, Myospila meditabunda,* and *Stomoxys calcitrans* were not susceptible. The significance of these findings is discussed.

INTRODUCTION

In a previous report concerned primarily with the morphology and tissue specificity of *Octosporea muscaedomesticae*, I briefly noted that several species of muscoid flies were susceptible to infection by this microsporidian under laboratory conditions (Kramer, 1964). The present study is an elaboration on these observations with considerations of quantitative as well as qualitative aspects of the problem. The results of this study extend our knowledge of the potential host range of *O. muscaedomesticae* in nature. They also provide us with some insight into the character of host specificity among the dipterophilic microsporidians.

MATERIALS AND METHODS

The flies used in this study were one-day-old adults derived from disease-free laboratory cultures. All flies with the exception of the *Drosophila melanogaster*, *Hylemya antiqua*, and the blood-feeding *Haematobia irritans* and *Stomoxys calcitrans* were fed a 10 percent sucrose solution containing 2×10^8 spores per ml by a method described previously (Kramer, 1964). The *D. melanogaster* were permitted to feed on bits of corn-meal-molasses agar containing spores of the microsporidian. Liquid Diet 116 E.C. prepared by General Biochemicals of Chagrin Falls, Ohio, was used as the vehicle for spore ingestion by the *H. antiqua*. The *H. irritans* and *S. calcitrans* were fed spore-containing defibrinated bovine blood. Flies of all species were held in cages for ten days following a spore-contaminated meal. During this post-inoculation period all flies were provided with an ample supply of appropriate food. The *Octosporea muscaedomesticae* spores fed to all sixteen species of flies were taken from the alimen-

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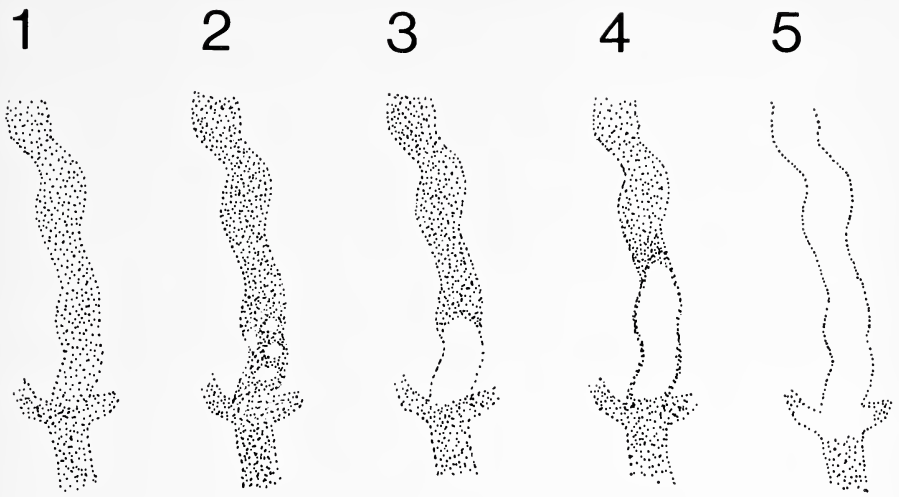

Figs. 1–5. Diagrammatic depictions of uncoiled proximal intestines of adult muscoid flies. Fig. 1. Normal condition. Fig. 2–5. Intestines infected with *Octosporea muscae-domesticae*. Fig. 2. Scattered infection. Fig. 3. Light infection. Fig. 4. Medium infection. Fig. 5. Heavy infection.

tary tracts of *Phormia regina* reared and infected in the laboratory. On post-inoculation day ten the alimentary tract of each fly was examined for gross lesions. Smears prepared from tracts lacking definite signs of infection were also examined. Both fresh wet mounts and stained smears were studied.

RESULTS AND DISCUSSION

The proximal intestines of many flies remained flexible and translucent and microscopical examinations of tissue fragments revealed no signs of infection or parasite proliferation (see Fig. 1). The changes wrought by the parasite in susceptible flies varied in degree from inapparent to severe. Smears prepared from some intestines that appeared normal on gross inspection revealed minute scattered pockets of infection. In other intestines small but distinct milkwhite spots were found (see Fig. 2). These blemishes contained numerous heavily parasitized cells. In some flies sizable portions of the proximal intestine were milkwhite, distended, rigid, and crammed with the parasite. The extent of derangement and discoloration varied. About one-fourth of the proximal intestine adjacent to the collecting arms of the malpighian tubes was afflicted in some cases (see Fig. 3). In others one-half of this organ was occupied by the parasite (see Fig. 4). In still others the entire proximal intestine was heavily infected (see Fig. 5).

Eight species of flies were susceptible to infection by *Octosporea muscae-*

TABLE 1. The *Octosporea muscaedomesticae* burden in eight species of susceptible muscoid flies on post-inoculation day ten.

Species	Parasite Burden					Percentage Heavily Infected
	Negative	Inapparent	Light[1]	Medium	Heavy	
(Anthomyiidae)						
Hylemya antiqua	16	0	1	2	0	0
(Calliphoridae)						
Cochliomyia macellaria	0	0	0	2	18	90%
Phaenicia sericata	17	1	2	0	0	0
Phormia regina	0	0	0	0	20	100%
(Drosophilidae)						
Drosophila melanogaster	0	0	2	2	16	80%
(Muscidae)						
Musca autumnalis	9	2	0	0	0	0
Muscina stabulans	17	1	0	0	0	0
(Sarcophagidae)						
Sarcophaga bullata	12	3	0	0	0	0

[1] Includes scattered infections.

domesticae. The extent to which the parasite flourished and spread within the proximal intestines of these susceptible hosts was quite variable (see Table 1). Heavy parasite burdens were found in *P. regina, C. macellaria,* and *D. melanogaster* with some regularity. While most *H. antiqua, P. sericata, M. autumnalis, M. stabulans,* and *S. bullata* were not infected, a few *H. antiqua* and *P. sericata* did harbor light or medium burdens. Inapparent burdens were found in a few *M. autumnalis, M. stabulans,* and *S. bullata.* No sign of infection at any level was found in eight other species of flies (see Table 2).

The foregoing results reveal no sharply defined correlation between susceptibility to infection and the taxonomic affinities or bionomics of the flies considered. Three species of Calliphoridae were susceptible in varying degrees whilst four species belonging to this family were not susceptible at all. While two species of Muscidae were slightly susceptible, four were not. The susceptible species do not share a common life style. As Greenberg and Povolný (1971)

TABLE 2. Species of muscoid flies which were not susceptible to infection by *Octosporea muscaedomesticae*.

(Calliphoridae)	(Muscidae)
Calliphora terraenovae (27)*	*Fannia scalaris* (12)
C. vicina (16)	*Haematobia irritans* (31)
C. vomitoria (13)	*Myospila meditabunda* (9)
Lucilia illustris (11)	*Stomoxys calcitrans* (28)

* = number of flies examined on post-inoculation day ten.

note, *C. macellaria, P. sericata, P. regina,* and *S. bullata* are attracted to carrion whilst *D. melanogaster* is generally found on decaying fruit; *M. stabulans* is most often found in association with feces or decaying plant material. *M. autumnalis* frequents cattle droppings and females feed on secretions around the heads of cattle and other mammals (James and Harwood, 1969). *Hylemya antiqua* is found in association with the onion plant almost exclusively (Metcalf et al., 1962). In all probability the factors that separate the susceptible from the nonsusceptible species will be found on the biochemical level, e.g., differences in pH values of intestinal secretions or differences in the activities of gastric enzymes.

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Biology Notes on the Bee *Andrena accepta* Viereck (Hymenoptera, Andrenidae)

JEROME G. ROZEN, JR.[1]
THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK, N.Y. 10024

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Abstract: This paper describes the nest and other aspects of the biology of *Andrena* (*Pterandrena*) *accepta* Viereck and provides a taxonomic description of its postdefecating larva. This species is the first North American representative of the genus known to nest communally. Details of the nest structure are discussed, the provisions are described, and a fly larva (Conopidae) is recorded from the metasoma of an adult female. Characters of the mature larvae of *Andrena* are presented that tentatively permit the larvae to be distinguished from those of the andrenid subfamily Panurginae.

The holarctic genus *Andrena* contains approximately 2,000 species. Though common, their biology has been comparatively little studied, in part because these species have been difficult to identify, and in part because investigators mistakenly assume that there is little diversity in the biology of the species. This paper describes the nest and other aspects of the biology of *Andrena* (*Pterandrena*) *accepta* Viereck[2] and provides a taxonomic description of its postdefecating larva. This species, which ranges widely from the East Coast to Utah and south into Mexico, is unusual because it is the first North American species in the genus known to have communal nests.[3] Several British species, *A. bucephala* Stephens and *ferox* Smith, nest communally (Yarrow and Guichard, 1941; Perkins, 1917).

Mrs. Marjorie Statham Favreau assisted in locating nests and in excavating them. Specimens associated with this study are in the collection of the American Museum of Natural History.

BIOLOGY

Description of Nest Area: This species was found nesting at Apache, Cochise County, Arizona on August 29, 1972, and a nest was excavated the following day. The surrounding area (Fig. 1) is desert scrub and includes such plants as mesquite, *Yucca, Lepidium*, and *Mentzelia*. The host plant *Helianthus* grew within several meters of the nest area and was abundant in the general vicinity.

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[1] Deputy Director for Research and Curator of Hymenoptera, the American Museum of Natural History. Research leading to this report was supported by NSF grant GB-32193

[2] Kindly identified by Dr. Wallace E. LaBerge, Illinois Natural History Survey.

[3] The North American *Andrena erythronii* Robertson normally nests with a single female to a burrow, but occasionally several females are found in a nest (Michener and Rettenmeyer, 1956).

FIG. 1. Site of *Andrena accepta*. Most nests were concentrated near person.

Four active burrows were initially discovered in an area of three square meters and a number of other burrows were found close by during the next week. The four burrows found first were in a low area which accumulated standing water during rain and which cracked when the water evaporated. The surface of the nest site was nearly flat and the soil, which included some pebbles and stones below the surface, was moderately soft because of recent rain. Most burrows were unshaded, but several were situated near, and at times shaded by, plants. No other species of *Andrena* was found nesting in the area but a number of species of *Perdita, Pseudopanurgus aethiops* (Cresson) and *Nomadopsis helianthi* (Swenk and Cockerell) nested in the general area.

Nesting Activity: None of the nest entrances seemed to be associated with objects on the ground. All entrances were open, although in the morning the yellow-marked faces of adults could often be seen in burrows just below the ground surface. A tumulus was usually absent but a copius tumulus, 2 cm. high and about 8 cm. in diameter, surrounded the entrance of one nest that had probably been recently begun.

The following information is based on the excavation of a single nest (Fig. 2). Neither the main burrow nor its rami were filled with soil. The burrow, 7.0 mm. in diameter, descended in a meandering fashion, and ramified a number of times (see Fig. 2) starting at a depth of about 18 cm. Tunnel walls,

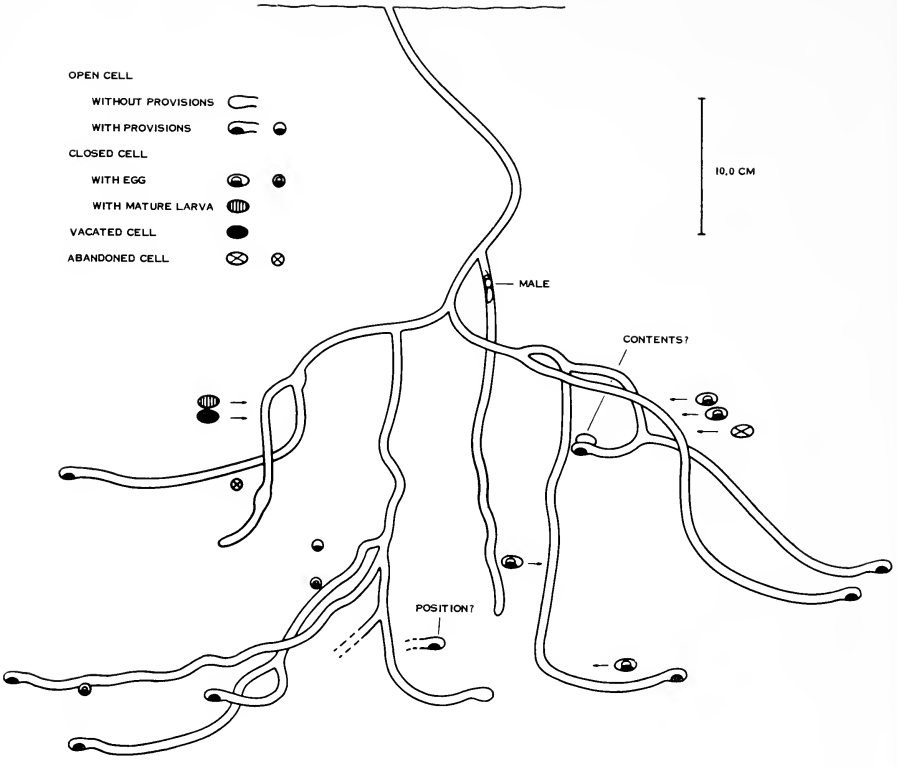


FIG. 2. Two-dimensional diagram of nest of *Andrena accepta*, side view, showing contents of cells.

as well as the walls of the laterals, were not specially worked or lined. In a few places the tunnels swelled but the significance of these enlargements is not known.

Laterals of about the same diameter as the burrows varied considerably in length, the shortest being about 3 cm. The laterals generally extended horizontally and each seemed to dip slightly before rising again to the cell. After cell provisioning, egg laying and cell closure, the laterals were filled with soil so that they were indistinguishable from the surrounding earth. Laterals still open contained a plug of loose earth one centimeter or more from the cell opening. This plug may serve as a barrier to the entrance of parasites; its presence is an unusual feature, not seen by the author in other bees.

A total of 23 cells, mostly from the present generation, were uncovered. Essentially horizontal, they had a length that varied from 13.0 to 15.0 mm. (four measurements) and a maximum diameter of 7.0 to 8.0 mm. (eight measurements)

and were symmetrical around their long axis. They were lined with a conspicuous, waterproof, shiny lining and the soil around the cells was impregnated with a substance that caused the earth there to be harder than the surrounding soil. The cell closest to the surface was at a depth of 31 cm. and the deepest, at 56 cm. The cell closure was a distinct spiral with five rows to the radius and was concave on the inside.

Eleven females were associated with this nest and a single male was discovered near the highest ramification of the burrows (Fig. 2). The male, though large, seemed to be completely normal; it was capable of flight and the head was not enlarged nor were the eyes reduced as has been found in some males in the communal nests of some bees. The ovaries of all females, except one, contained well developed oöcytes, indicating that the females were able to oviposit. The female with only very small oöcytes was parasitized by a young conopid larva.

Eleven cells, most provisioned, were open and eleven females were captured in association with the nest. The correlation of the number of open cells and the number of females suggests that each female was responsible for her own cell and therefore that there is no division of labor among the females in the nest. The large number of open cells and cells containing eggs indicate that the adults had just started their seasonal nesting activity. The single post-defecating larva, described below, almost certainly was from the previous generation and had failed to develop when others pupated. One cell, freshly constructed and containing some pollen, had been abandoned, and the female had packed it with soil, a behavior pattern that suggests that the cell might have been parasitized.

Provisioning: Adults were common on the flowers of *Helianthus*, adjacent to the site. No incompletely provisioned cells were encountered; all pollen masses found in the cells were fully formed whether they were in closed or open cells. Pollen masses were flattened spheres ranging from 7.0 to 8.0 mm. (three measurements) in maximum diameter and with a height of 5.0 mm. (two measurements). Orange in color, the pollen was homogeneously moist. The mass was placed fairly close to the rear of the cell and was not coated with a special waterproof coating.

Development: Each egg, white, with a shiny chorion, 2.5 mm. in length and 0.6 mm. in maximum diameter (one measurement), was situated on top of the pollen mass parallel to the long axis of the cell. The blunt anterior end was closest to the cell closure and touched the provision. The posterior end was also attached to the pollen mass but the middle part of the egg curved upward. Except for a single larva, no other immature stages were uncovered.

Feces were applied to the upper rear of the cell as a single smooth sheet as is characteristic of most panurgines.

Daily Cycle: Males and females of this bee were active on the flowers at 9:30 A.M. and continued to be active during the rest of the morning and perhaps into the afternoon. Females spent the night in the ground.

Seasonal Cycle: The abundance of fresh cells clearly indicated that this species was just starting its adult activity at the end of August. The presence of a postdefecating larva in the ground suggests that the bee diapauses as a postdefecating larva.

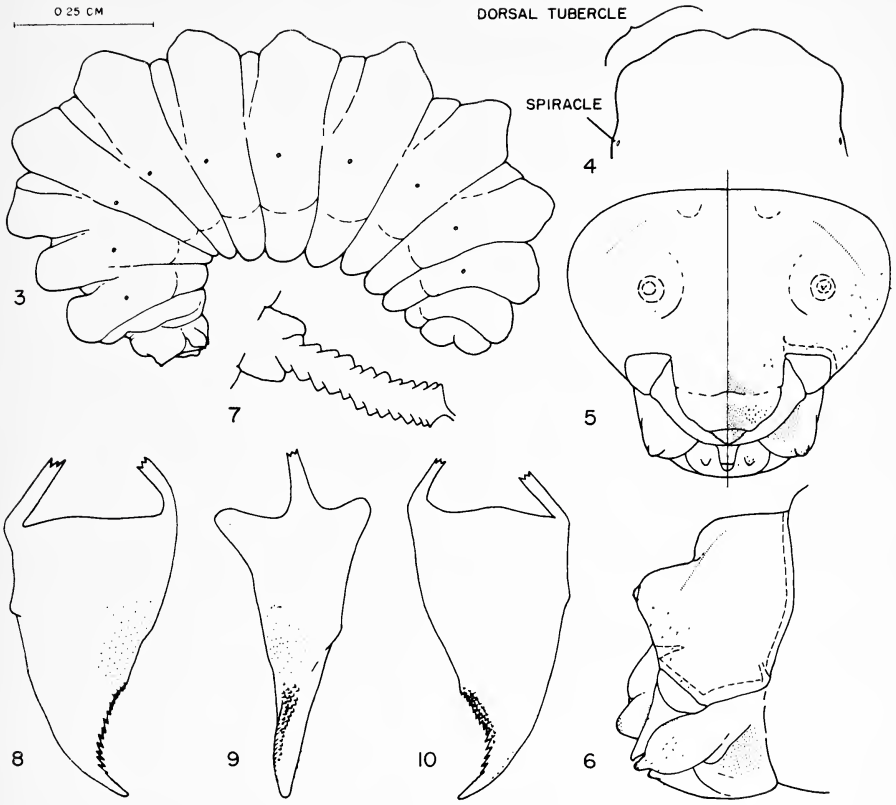
Parasitism: No parasitic bees were found entering nests of *Andrena accepta*.

The identity of the small conopid larva (approximate length, 2 mm.) from the metasoma of the adult female is uncertain; the specimen may belong to either *Zodion* or *Myopa*. It keys to *Zodion* in Smith (1966) and closely resembles the first, or perhaps second, instar of *Zodion obliquefasciatum* (Macquart) (Howell, 1967) because of general body configuration and large anal papillae; its posterior end seems identical to that of *Z. obliquefasciatum* except the posterior spiracles are somewhat differently shaped. However, according to Freeman (1966) *Zodion* has not been recorded from *Andrena* (although it has been associated with the andrenid genus *Panurginus*), whereas *Myopa* is a known parasite of a number of species of *Andrena* and its larva is apparently still undescribed.

MATURE LARVA (Figures 3–10)

The main purpose of the following description is to place on record the anatomical details of the mature larva of *Andrena accepta*. A careful comparison of the larva with those of other *Andrena* has not been attempted. However, the gross external features of this larva are compared with those of the following larvae which are on hand: *Andrena* (*Thysandrena*) *bisalicis* Viereck, *A.* (*Ptilandrena*) *complexa* (Viereck), *A.* (*Leucandrena*) *erythronii* Robertson, *A.* (*Mimandrena*) *imitatrix* Cresson and *A.* (*Trachandrena*) *morresonella* Viereck. Although spiculation, distribution of sensilla, mandibular dentition and shape, internal structures of the head and spiracles were not examined, other structures presented in the description below were identical. Furthermore, accounts of *Andrena* larvae in the literature indicate that the gross features hold for all known *Andrena* larvae and that some of the finer features presented below also apply. The following are the references to these descriptions: *A. complexa* (Michener, 1953), *A. erythronii* (Michener, 1953), *A.* (*Leucandrena*) *placida* Smith (Thorpe and Stage, 1968), and *A.* (*Bythandrena*) *viburnella* Graenicher (Stephen, 1966). The works of these authors and the following description suggest that details of mandibular shape and dentition and of spiracular anatomy may serve as a source of characters for species identification.

So far as can be determined from present limited knowledge, larvae of *Andrena* are distinguishable from those of the Panurginae (Rozen, 1966, 1968, 1970, and 1971) by the fact that *Andrena* possesses only low paired mounds on the labrum and the dorsal abdominal tubercles are transverse, extending laterally from near the midline of the segment, halfway around to the spiracle on each side. In contrast, the labra of all panurgines have two small to large, sharp-pointed, well-defined tubercles. Furthermore, the dorsal abdominal tubercles tend to be conical, often sharply so, on mature panurgine larvae. In *Meliturgula* (Rozen,



FIGS. 3–10. Postdefecating larva of *Andrena accepta*. 3. Entire larva, lateral view. 4. Dorsal part of second abdominal segment, frontal view. 5. Head, frontal view. 6. Head, lateral view. 7. Spiracle, side view. 8–10. Right mandible, dorsal, inner and ventral views, respectively.

1968) the dorsal tubercles are poorly differentiated from the surrounding area and appear somewhat transverse, but the labral tubercles are distinctly panurgine in shape. The mature larvae of other Andreninae are unknown.

Head (Figs. 5, 6): Integument without setae but with scattered sensilla; integument unpigmented except for apex of labrum, mandibles, palpi, and area enclosed by salivary slit. Vertex with pair of paramedian projections; antennae arising from pronounced prominences; clypeus of moderate length compared with other Andrenidae (i.e., most Panurginae). Tentorium complete and well developed; each posterior pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule well developed; hypostomal ridge well developed; pleurostomal ridge well developed; epistomal ridge well developed below anterior tentorial pits, mesiad of pits absent; parietal bands distinct. Each antenna a low convexity bearing three sensilla. Labrum produced on each side into a low mound but distinct, well-defined labral tubercles absent; each mound bearing a cluster of sensilla; epipharynx spiculate. Mandible (Figs. 8–10) slender, tapering

to simple apex; upper apical margin strongly and evenly serrate; lower margin with a few small denticles; cusp weakly produced but with numerous teeth as shown in Fig. 10; dorsal surface spiculate. Maxilla as seen in lateral view projecting only slightly beyond apex of labium; maxilla well defined, with cardo somewhat defined; and with dorsal surface of maxilla spiculate; palpus large, well defined and much more distinct than labral prominences; palpus directed anteriorly. Hypopharynx spiculate except for small median section; hypopharyngeal groove deeply incised and complete. Labium indistinctly divided into prementum and postmentum; palpus large but not projecting so far as maxillary palpus. Salivary opening a U-shaped slit, the ends of which extend to hypopharyngeal groove; area enclosed by salivary slit nonspiculate.

Body (Figs. 3, 4): Color of preserved larva whitish. Most of integument nonspiculate but some ventral regions spiculate; tenth abdominal venter nonspiculate; some areas with few widely scattered, inconspicuous, very fine, minute setae. Most abdominal segments divided into cephalic and caudal annulets with dorsal tubercles being restricted to caudal annulets; paired dorsal tubercles moderate in size, present on thorax and most abdominal segments; abdominal tubercles transverse, i.e., extending laterally as shown in Fig. 4; tubercles not present on ninth and tenth abdominal segments; pleural region not strongly produced; intersegmental lines rather deeply incised; intrasegmental lines distinct on most segments. Spiracles (Fig. 7) with atrium projecting above body wall; atrial wall without teeth but faintly corrugated; peritreme present; primary tracheal opening with collar; subatrium moderately long. Sexual characteristics not evident.

Material Studied: One postdefecating larva, Apache, Cochise County, Arizona, August 30, 1972, from nest 1 (J. G. Rozen).

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Proceedings of the New York Entomological Society

(Meetings held in Room 129 of the American Museum of Natural History unless otherwise indicated.)

Meeting of January 2, 1973—The Annual Meeting

The meeting was held in Room 129, and Dr. Howard Topoff, President, presided; 10 members and 6 guests were present. The Report of the Nominating Committee, composed of Dr. David Miller, Dr. James Forbes, and Dr. John A. L. Cooke, proposed the following candidates for offices for 1973:

President—Dr. Howard Topoff
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Assistant Secretary—Dr. Charles C. Porter
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There were no further nominations and the slate of candidates was unanimously elected. Ms. Barbara Paparesta was elected to Active Membership, Mr. Kevin J. McGrath to Student Membership. Dr. Peter Moller was proposed for Active Membership and Mr. James M. Silverman proposed for Student Membership.

PROGRAM. "Cockroach Control by Spray, Dust and Bait Combinations," by Dr. Ayo Gupta of Rutgers University. Dr. Gupta described a team experiment conducted in actual homes, testing comparative effectiveness of control methods in relation to varying sanitary conditions.

JOAN DEWIND, *Ex. Sec.*

Meeting of February 6, 1973

President Howard Topoff presided; 11 members and 3 guests were present. James Silverman, graduate student at City University of New York, whose interest is in the behavior of cockroaches was elected to Student Membership. Dr. Peter Moller, of Hunter College, whose interest is in orientation in spiders and underlying sensory mechanisms, was elected to Active Membership. Joseph Cerreta, of Fordham University, was proposed for Student Membership.

PROGRAM. "Disease and Insect Problems in the Metropolitan New York Area." Dr. P. Pirone, Senior Plant Pathologist, New York Botanical Gardens, discussed the devastating effect of pollution and insect pests upon New York's plant life.

PETER MOLLER, *Sec.*

Meeting of February 20, 1973

President Howard Topoff presided; 12 members and 12 guests were present. Mr. Joseph M. Cerreta, of Fordham University, whose interest is in insect ultrastructure, was elected to

Student Membership. Ms. Iris L. Goldfarb and Ms. Katharine Lawson of City College of New York and Hunter College, respectively, were proposed for Student Membership.

PROGRAM. "The Cyclops Eye of the Dragon Fly" was discussed by Dr. Richard Chappell, Assistant Professor of Biology at Hunter College.

PETER MOLLER, *Sec.*

NEUROPHYSIOLOGY AND DEVELOPMENT OF THE DRAGONFLY MEDIAN OCELLUS

The role and development of the dragonfly median ocellus are discussed in light of recent neurophysiological evidence obtained from intracellular recordings of receptors and post-synaptic units and from electron micrographs of synaptic organization. Behaviorally, dragonflies whose ocelli were occluded in the field flew up to a branch and remained there as long as they were observed (one hour) while those whose compound eyes were occluded flew skyward until they disappeared from sight, indicating possible roles in diurnal behavior and phototaxis. On the basis of neurophysiological recordings and feedback synaptic organization, an additional role as a shadow or motion detector was suggested. A study of the development of a population of 32 nymphs of *Aeschna tuberculifera* revealed that while the presumptive lateral and median ocelli could not be identified prior to the fourth day of the final instar, they could always be found after the eighth day of the final instar. The mean duration of the final instar was 30.4 days (standard deviation of 6.6 days) for a population of 245 dragonflies of the species *Aeschna tuberculifera* and *Anax junius*. The preceding instar (instar –1) had a mean duration of 16.8 days (standard deviation of 3.6 days) for a population of 100 dragonflies. For ten dragonflies reared through instar –2, the mean duration of that instar was 15.1 days. Developmental study suggests the possibility of severing the ocellar nerve prior to emergence in order to obtain denervated adult ocelli for neurophysiological study.

RICHARD L. CHAPPELL, ARLENE D. KLINGMAN, AND MAUREEN M. BELL
DEPARTMENT OF BIOLOGICAL SCIENCES, HUNTER COLLEGE

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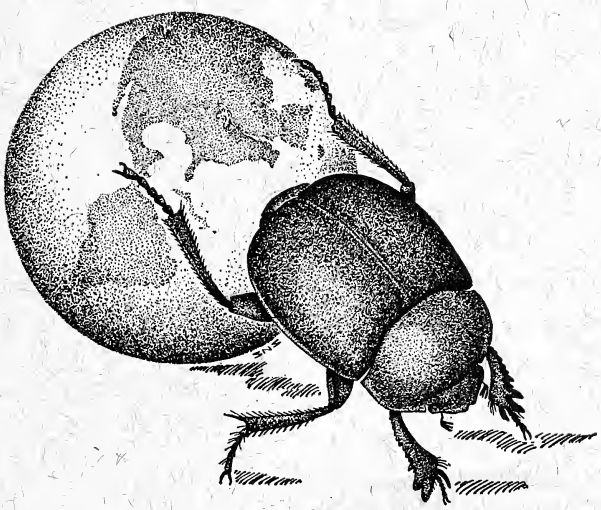

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Mailed August 20, 1973

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CONTENTS

Second Addition to the Supplemental List of Macrolepidoptera of New Jersey

JOSEPH MULLER
R.D. 1, LEBANON, NEW JERSEY 08833

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Abstract: Fifty-six more species, subspecies, and named aberrations with given foodplant, where known, are here added to the Supplemental List of Lepidoptera of New Jersey (1965).

DISCUSSION

Since "Additions to the Supplemental List of New Jersey Macrolepidoptera" (Muller, 1968), I am fortunate to add fifty-six more species as new records for the state list. All specimens collected by myself were attracted by blacklight or bait. Some of the records are from the old collections of O. Bucholz, Frederick Lemmer, and J. W. Cadbury. A few of the species listed have been only recently described.

I find that Lepidoptera are getting scarcer every year, especially Saturnids and the larger Sphingids. Besides air pollution, loss of habitat, and spraying of insecticides against *Liparis dispar* (Linn.), another factor, the mercury vapor lamp, has appeared. These lamps can be found along highways and near shopping centers and gas stations. They are probably responsible for killing millions of moths. They may also interfere with normal mating activity (Ferguson, 1971). On the other hand, injurious insects are still with us. Aerial spraying against gypsy moths, which has gone on for many years, did not reduce their numbers. These pests multiplied to such an extent that they have defoliated trees over the entire state. *Catocala* and other species, whose eggs hatch at the same time as the eggs of gypsy moths, are almost wiped out.

Checklist numbers of moths are taken from McDunnough (1938). Checklist numbers of butterflies follow dos Passos (1964, 1970). Specimens not followed by the name of a collector were caught by the author.

BUTTERFLIES

Hesperiidae

Calpodes Hubner

27 *ethlius* Stoll

Monmouth Beach, Oct. 26. Adams.

Visiting cultivated *Canna.*

Acknowledgment: I thank Dr. A. E. Brower, Dr. C. F. dos Passos, and Dr. F. H. Rindge for some of the determinations.

Staphylus Godman & Salvin
188 *hayhurstii* Edwards
Cape May, Aug. 28. Schweitzer.
Thorybes Seudder
204 *confusis* (Bell?)
Fort Dix area, May 16. Sanford.

Lycaenidae

Satyrium Scudder
363–1 *calanus boreale* Lafontaine
Newton, June 26. dos Passos.
Callophrys Scudder
388b *niphon clarki* Freeman
High Point State Park, June 10. dos Passos.

MOTHS

Nolidae

Celama Walker
889 *sorghiella* Riley
Lakehurst, Oct. 10.
Grasses.

Arctiidae

Apantesis Walker
1036 *oithona* Strecker
New Lisbon, June 17. Cadbury. Lakehurst, Oct. 16. Schweitzer.
Dandelion (*Taraxacum officinale*).
Haploa Hubner
1104 *confusa* Lyman
form *lymani* Dyar.
Newark, June 24. Bucholz.
General feeder.

Phalaenidae

Acronicta Ochsenheimer
1162 *falcula* Grote
Woodglen, May 16. Prostak.
Hazel.
1186 *exilis* Grote
Batsto, June 31, Aug. 10. Schweitzer. New Lisbon, June 24. Cadbury.
Oak.
Loxagrotis McDunnough
1395 *acclivis* Morrison
Hunterdon Co., Sept. 15.
Orthosia Ochsenheimer
1941 *alurina* Smith
Lebanon, Apr. 5–10.
General feeder.
Leucania Ochsenheimer
1986–1 *Linda*. 1952 Franclemont
Lakehurst, Sept. 17. Lemmer.

Cucullinae

Psaphida Walker
2192 *thaxteriana* Grote
Lakehurst, April 19, May 1.
Oak, *Quercus* sp.
Graptolitha Hubner
2219–1 *niviacosta* Franclemont
Batsto, Oct. 21.
Chokecherry, *Prunus virginiana.*
2220–1 *luteocosta* Franclemont
Batsto, Oct. 21.
Chokecherry, *Prunus virginiana.*
Graptolitha Hubner
2226 *hemina* Grote
Lebanon, Oct. 11.
Chokecherry, *Prunus virginiana.*
2228 *signosa* Walker
form *pallidicosta* Franclemont
Lakehurst, Nov. 3. Cadbury.
Metaxaglaea Franclemont
2297–1 *semitaria* Franclemont
Lakehurst Oct. 3–9. Cadbury. Lakehurst, Oct. 1–16. Lemmer.
Eupsilia Hubner
2304–2 *cirripalea* Franclemont
Lebanon, Oct. 15.
Ommatostola Grote
2445 *lintneri* Grote
Cape May, Oct. 23.

Amphipyrinae

Perigea Guenée
2610–1 *apameoides* Guenée
Lakehurst, July 10. Cadbury. Oct. 29.
Monodes Guenée
2650–1 *georgei* Moore & Rawson
New Lisbon, May 2. Schweitzer. Batsto, May 11. Schweitzer.
Laphygma Guenée
2683 *exigua* Hubner
Batsto, Oct. 25. Schweitzer.
Enargia Hubner
2685 *decolor* Walker
form *infumata* Grote
Woodglen, July 2. Prostak.
Erythroecia Hampson
2718 *hebardi* Skinner
Johnsonburg, Aug. 12. Morris Co., Aug. 19. Bucholz.

Heliothiinae

Schinia Hubner
3005 *saturata* Grote
Cape May, May 3. Rutkowski.

Euteliinae

Paectes Hubner

3226 *flabella* Grote

Lakehurst, May 26. July 28. Lemmer.

Sarrothripinae

Characoma Walker

3234 *proteela* Dyar

Halltown, Sept. 1. Prostak. New Market, Sept. 8. Prostak.

Willow, *Salix* sp.

3234–1 *nigrimacula* Warren

New Market, Sept. 8. Prostak.

3234–2 *cadburyi* Franclemont

Cape May, May 17. Rutkowski.

Plusiinae

Autographa Hubner

3257 *alias* Ottolengui

Batsto, June 21. Schweitzer.

White and Black Spruce, *Picea glauca* and *P. mariana.*

Catocalinae

Catocala Schrank

3396 *crataegi* Saunders

form *pretiosa* Lintner

Cape May, June 28.

Crataegus.

Zale Hubner

3482 *coracias* Guenée

Lakehurst, May 21. Lemmer.

Oak (doubtful).

3499 *cingulifera* Walker

race *woodi* Grote

Lakehurst, May 18.

Black Cherry, *Prunus serotina.*

Thysania Dalman

3526 *zenobia* Cramer

Manolapan, Aug. 30, 1972. Dr. J. P. Reed. Vagrant.

Cissusa Walker

3539 *spadix* Cramer

Lebanon, May 8.

Anomis Hubner

3617–1 *commoda* Franclemont

Moorestown, April–May. Cadbury.

Herminiinae

Zanclognatha Lederer

3758 *obscuripennis* Grote

Hunterdon Co., Aug. 15.

Dead leaves. In Smith's *List* without data or locality.

Camptylochila Stephens

3739 *julia* Barnes & McDunnough
Lebanon, July 9.
Dead leaves, lichens.

Notodontidae

Heterocampa Doubleday

3899 *subrotata* Harris
Cape May, Aug. 19.

Liparidae

Gluphisia Boisduval

3940 *lintneri* Grote
form *avimacula* Hudson
Woodglen, Apr. 22. Prostak.

Liparis Ochsenheimer

3965 *dispar* Linnaeus
Over the entire state, Aug. 6–10.

GEOMETRIDAE

Geometrinae

Racheospila Guenée

4039 *rubrolinearia* Packard
Lebanon, Aug. 6.
Oak, *Quercus* sp.; Bayberry, *Myrica* sp.

Sterrhinae

Sterrha Hubner

4181–1 *flavescens* Hulst
Batsto, July 12. Schweitzer.

Cosymbia Hubner

4211–1 *packardaria* Prout
Lebanon, Oct. 7.

Larentiinae

Eupithecia Curtis

4366 *albicapitata* Packard
Lebanon, June 12.
Bores in Chermes galls on spruce and fir.

Itame Hubner

4793 *gausaparia* Grote
Cape May, Aug. 19. Rutkowski. Lebanon, July 20.

Melanolophia Hulst

4856–1 *crama* Rindge
Lebanon, July 17.

Protoboarmia McDunnough

4875 *porcellaria* Guenée
Lebanon, May 28.

Lytrosis Hulst

4993 *sinuosa* Rindge 1971

Smithville, June 22. L. J. Sanford. Ocean Co., June 15. Bucholz. Lakehurst, June 15. Pin Oak, *Quercus palustris*, Sugar Maple, *Acer saccharum*.

Metarranthis Warren

5046 *hypocharia* Herrich-Schaeffer

race *homuraria* Grote

New Lisbon, April–July. Cadbury.

Pero Herrich-Schaeffer

5080 *morrisonarius* Henry Edwards

Batsto, June. Schweitzer.

5082–1 *barnesi* Cassino & Swett

Lakehurst, June 3. Lebanon, May 24.

Nepytia Hulst

5109 *canosaria* Walker

form *fuscaria* Barnes & Benjamin

Lakehurst, July 27. Lemmer.

Pine, *Pinus* sp., Spruce, *Picea* sp., Hemlock, *Tsuga canadensis*.

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Erratum: in "Additional List . . ." (1968), p. 64, no. 375 (*ontario* Edw.), the date should read June 26–28 instead of April.

Mouthpart Morphology of the African Ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae)

WILLIAM H. GOTWALD, JR.
DEPARTMENT OF BIOLOGY,
UTICA COLLEGE OF SYRACUSE UNIVERSITY, UTICA, NEW YORK 13502

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Abstract: The mouthparts of the African ant *Oecophylla longinoda* Latreille are generalized structurally and closely resemble the mouthparts of other species in the subfamily Formicinae. They are essentially identical to those of *O. smaragdina* (Fabricius). Mandibular dentition and midline overlap contribute to the efficiency of predatory attack.

INTRODUCTION

The ant genus *Oecophylla* (subfamily Formicinae) is represented by two living species and several fossil forms. One extant species, *O. smaragdina* (Fabricius), is Oriental and Australian in distribution, while the other, *O. longinoda* Latreille, ranges throughout tropical Africa. One fossil species, *O. leakeyi* Wilson and Taylor, is also Ethiopian in distribution (Wilson and Taylor, 1964). Although Wheeler (1922) recognized *longinoda* and *smaragdina* as distinct species, the differences between the two are based almost solely on the allopatric nature of their distribution (Vanderplank, 1960).

Ants of the genus *Oecophylla* build arboreal nests of leaves bound together by larval silk. Nest-building behavior is extraordinary, for the larvae that supply the silk are carried about by the worker ants and are utilized as "animated shuttles" (Wheeler, 1922). The biology of *O. longinoda* has been studied in detail by Ledoux (1950), Way (1954), and Vanderplank (1960).

O. longinoda is aggressive and territorial, a single colony vigorously defending its tree or trees against intruders. Workers can inflict a painful bite on human skin (Weber, 1943, 1949), although the pain is due in part to the effects of "poison" sprayed on the wound from the tip of the gaster (Vanderplank, 1960). Thus, in East Africa, its reputation as a painful biter is implied in its Kiswahili name, "maji ya moto" or hot water ant (Vanderplank, 1960). *O. longinoda* is an efficient predator and effectively attacks notoriously aggressive ants such as the *Anomma* driver ants (Gotwald, 1972). Vanderplank (1960) noted that the efficiency of *Oecophylla* as a predator is positively correlated with colony size.

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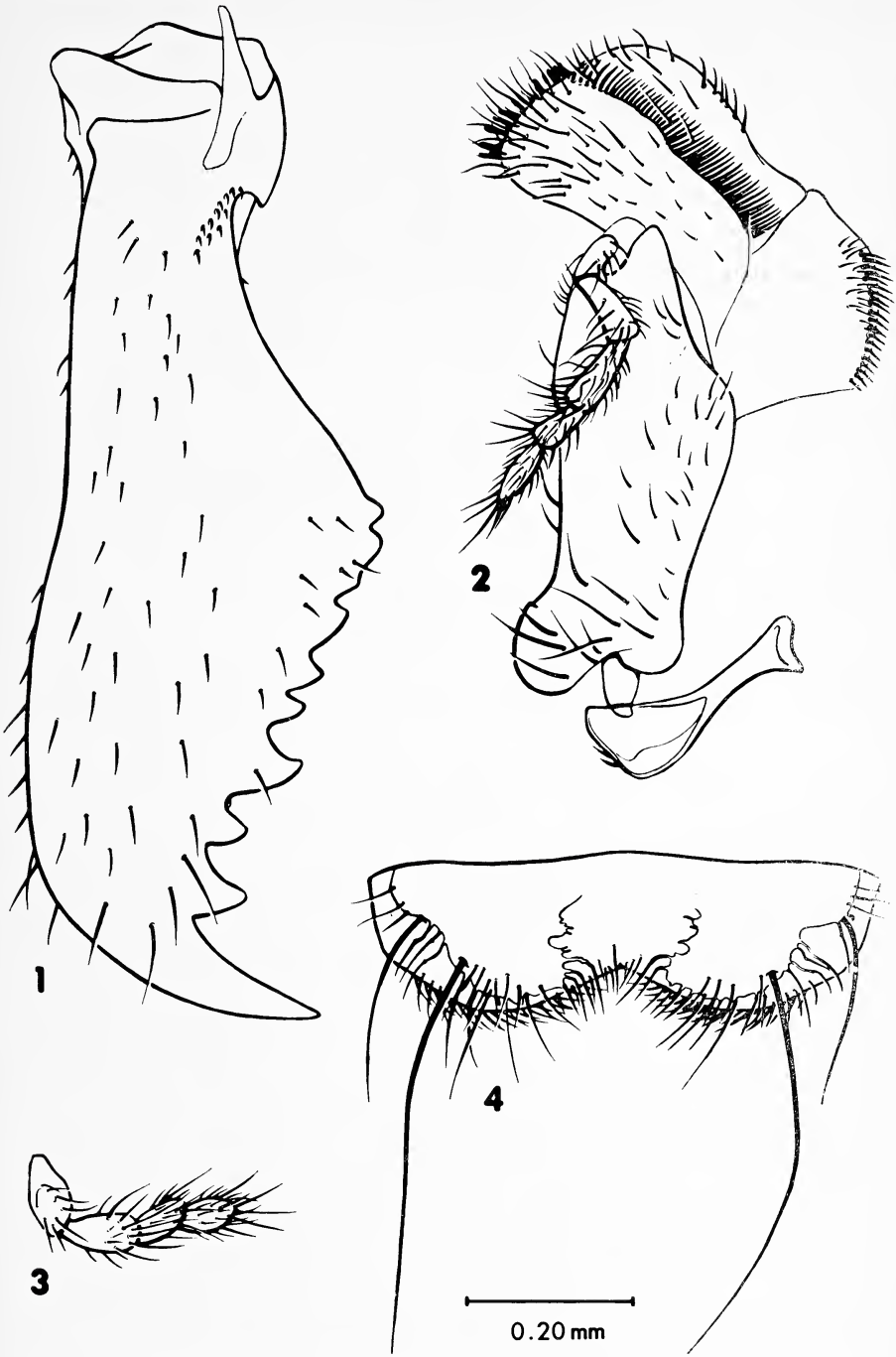

FIGS. 1–4. Mouthparts of *Oecophylla longinoda*, major worker. 1, right mandible, dorsal view; 2, left maxilla, external view, the maxillary comb is drawn as seen through the transparent galea; 3, right labial palpus, lateral view; 4, labrum, extensor surface.

While the predatory success of *O. longinoda* is due in large part to behavioral adaptations, the ant is also morphologically adapted to its role. Since the species lacks a sting, it relies almost completely on its strongly dentated mandibles for prey capture and transport. The mandibles are used during foraging to grasp and pull at the prey until it is immobilized (Gotwald, 1972). Workers are dimorphic with maxima and minima forms. In a related division of labor, the maxima workers forage as predators, while the minima workers remain in the nest (Weber, 1946, 1949).

The morphology of *O. longinoda* has been neglected in most investigations. This paper compares the mouthparts of *O. longinoda* with those of other species of Formicinae and particularly with those of *O. smaragdina*. Because the mandibles play a role in the predatory success of *O. longinoda*, their morphology is evaluated relative to function in prey capture, immobilization, and transport.

METHODS

Specimens of *O. longinoda* examined in this study were collected by the author in the coastal scrub and grassland region of Ghana at Legon on 5 June 1971. These workers were attacking (Gotwald, 1972) a column of the driver ant *Dorylus* (*Anomma*) *nigricans* Illiger. The specimens of *O. smaragdina* examined were collected by Dr. Rossiter Crozier (University of Georgia) at Kuala Lumpur, Malaysia on 25 August 1967.

Mouthparts of major workers of both species were removed from the head capsule, dissected into component parts, stained, and mounted in Canada balsam on microscope slides. The descriptive terminology is that previously used by the author (Gotwald, 1969). Drawings were made with the aid of a microprojector.

DESCRIPTION OF THE MOUTHPARTS OF *Oecophylla longinoda*

Mandible (Fig. 1): Mandible linear and triangular with distinct masticatory and basal margins; masticatory margin provided with large apical tooth and up to eight subapicals; transitional denticles present at juncture of masticatory and basal margins; in dorsal view, basal margin recurved proximally to form a sharp ridge.

Maxilla (Fig. 2): Maxillary palpus five-segmented. Stipes subrectangular; lateral margin forming a smoothly rounded lateral shoulder; distal margin drawn to a point; medial margin with convex expansion proximally; numerous setae inserted on external face, particularly on proximal third and lateral half. Galea with well-developed maxillary comb; galeal crown not conspicuously developed; distal margin of galea with ten or more broad setae; several setae inserted so as to approximate a galeal comb, but lacking characteristic shape of comb setae (Gotwald, 1969). Lacinia subquadrate with well-defined gonia; apex poorly developed; lacinial comb conspicuous, continuous, and occupying two-thirds of lateral margin; a second series of setae inserted laterad of lacinial comb.

Labium: Labial palpus four-segmented (Fig. 3). Premental shield lightly sclerotized and bearing numerous, scattered setae; subglossal brushes composed of densely packed setae of moderate length; epimental sclerites fairly well defined; paraglossae absent.

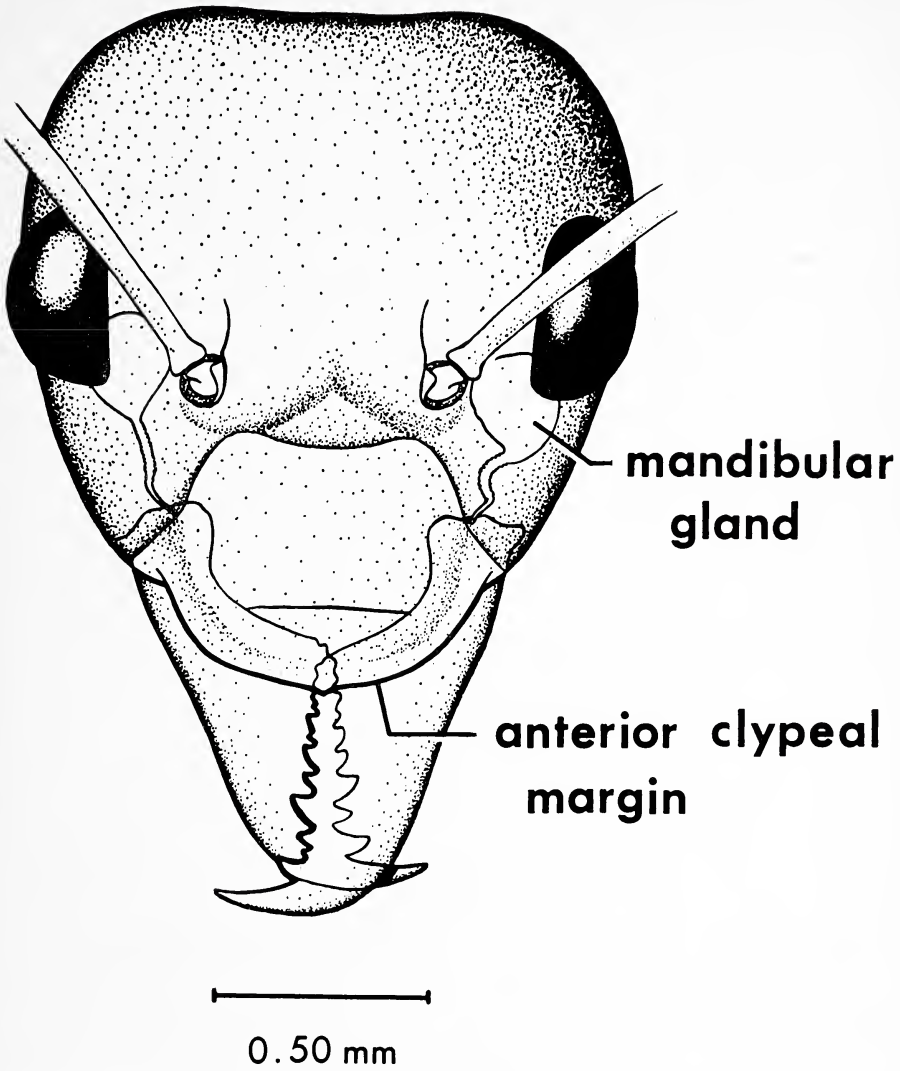

Fig. 5. Head of an *Oecophylla longinoda* major worker, frontal aspect. The head is drawn as rendered transparent in the laboratory preparation. Note the mandibular midline overlap.

Labrum (Fig. 4): Distal margin emarginate but not cleft medially, forming two smoothly rounded lobes; hemocoel extending into each lobe; numerous small setae inserted along the distal margin, several long setae inserted along or close to the lateral and distal margins of hemocoel; of these setae, four are conspicuously longer than all others; most of extensor surface posterior to margins of hemocoel devoid of setae; labral tubercles absent.

DISCUSSION

The mouthparts of the subfamily Formicinae, with few exceptions, are generalized structures (Gotwald, 1969), and palpal segmentation is usually primitive (i.e., maxillary palpus is six-segmented and labial palpus four-segmented). In these characteristics, the subfamily closely resembles the dolichoderines and myrmeciines (Gotwald, 1969). The mouthparts of *O. longinoda* differ little from other species in the Formicinae. The triangular mandible, with distinct basal and masticatory margins is typically formicine, although in being more linear, it resembles the dolichoderine ant, *Dolichoderus attelaboides* (F.) (Gotwald, 1969). The sharp ridge at the proximal termination of the basal margin is unique to *Oecophylla* and has not been observed in any of the 107 ant species from all subfamilies (from 61 genera) previously examined in detail by the author (Gotwald 1969, 1970; Brown et al., 1970; Gotwald and Lévieux, 1972).

The maxilla of *O. longinoda* is also typically formicine, although the maxillary palpus is five- and not six-segmented as in *Prenolepis*, *Camponotus*, and *Formica*. The stipes closely resembles that of some *Camponotus* species. The conspicuous lacinial comb of *O. longinoda* sets it apart from many of the formicines where the comb tends to be composed of relatively thin, short setae. The presence of wide, conspicuous setae on the galeal crown is characteristic of many formicines. The maxillary palpus, on the other hand, is unusually short in *O. longinoda*, even when considering the fact that it has one segment fewer than most formicines.

The labrum of *O. longinoda* lacks the cleft or deep emargination observed in the Formicinae and Dolichoderinae but is not otherwise unusual. The primitive labial papal segmentation is retained in *O. longinoda* in spite of reduction in the maxillary palpus.

Bugnion (1930) described the mouthparts of *O. smaragdina*, including the worker, queen, and male in his study. His lengthy descriptions are sometimes ambiguous and the drawings often inaccurate. Although shapes of the stipes and lacinia of *O. smaragdina* as illustrated by Bugnion, for instance, differ considerably from those of *longinoda*, my reexamination of *O. smaragdina* mouthparts revealed that they are essentially the same as those described here.

The mandibles of *O. longinoda* and *O. smaragdina* are identical, even to the presence of the transitional denticles at the juncture of the basal and masticatory margins and the sharp ridge at the proximal end of the basal margin. The labrum in each species is the same and both possess the four prominent setae of the extensor surface. Palpal segmentation is the same for each species. The only divergence noted was in the setal pattern of the lacinia. In *O. smaragdina* a larger number of setae are inserted laterad of the lacinial comb and the comb itself is inserted farther laterad of the lacinial margin than it is in *longinoda*.

The relationship of mandible morphology to predatory behavior patterns

must ultimately focus on the fact that the mandibles maintain a vise-like grip on prey individuals under conditions of stress created by prey escape movements and by tugging actions of the immobilization phase of predatory attack [the prey individual is pulled at from opposing directions, "spread-eagle" fashion, by cooperating foragers (Gotwald, 1972)]. One morphological condition is primarily responsible for this gripping efficiency: The closed mandibles exhibit considerable midline overlap (Fig. 5). Because of this overlap, teeth of the masticatory margin trap and prevent prey structures (particularly legs and antennae) from sliding proximally or distally along the masticatory border. Field observations support this conclusion and are corroborated by laboratory examination of numerous *Oecophylla* workers preserved while grasping prey. Additionally, contraction of the powerful mandibular adductor muscles [the adductors are voluminous and are the most prominent muscles in the head capsule (Gotwald, 1969)] could exert great force on any structure wedged between the mandibles at the points of overlap. The large, sharply pointed apical teeth may effectively pierce some prey structures, and Weber (1949) reported that after biting human skin, *O. longinoda* mandibles were difficult to dislodge. These same morphological features make *Oecophylla* mandibles useful manipulative organs. For instance, worker ants make extensive use of their mandibles in handling the living leaves that are incorporated into the nest (Ledoux, 1950).

Of parenthetical note are the mandibular glands of *O. longinoda* (Fig. 5). These glands are placed within the head capsule partly behind the compound eyes. As in other Formicinae, the mandibular glands of *O. longinoda* discharge chemicals that presumably function in the alarm-defense system of the species (Wilson and Regnier, 1971). Although conspicuous in the head cleared with clove oil, the relatively small size of the glands indicates their primitive condition (Wilson and Regnier, 1971).

CONCLUSIONS

1. The mouthparts of *O. longinoda* are generalized structures that do not depart significantly in morphology from those of other formicine ants.
2. The mouthparts of *O. longinoda* are essentially identical to those of *O. smaragdina*, further supporting, although not proving, the hypothesis that the two are conspecific.
3. Mandibular dentition in combination with midline overlap contribute to the effectiveness of *O. longinoda* mandibles as instruments of prey capture, immobilization, and transport.

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Northern Distribution Records for Several Sphecidae and Pompilidae (Hymenoptera)

Nancy B. Elliott and Frank E. Kurczewski
Department of Forest Entomology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York 13210

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Abstract: Collection records for a number of Sphecidae and Pompilidae from western Canada and Alaska are presented. These records represent northward and westward extensions of the known ranges of these species.

DISCUSSION

During June and July 1971, collections of Hymenoptera were made in western Canada and Alaska. For many of the species collected, these records represent northward extensions of the known ranges reported in the synoptic catalog of Hymenoptera of America north of Mexico and its supplements (Muesebeck et al., 1951; Krombein, 1958; Krombein and Burks, 1967). Notably a large series of the sphecid *Tachysphex terminatus* (Smith) was collected in Alaska considerably north of its previously known range (Elliott and Elliott, 1973). Collection records for additional Sphecidae and one pompilid are presented in this paper with notes on range extensions. All specimens were collected by W. M. and N. B. Elliott. Specimens were determined by F. E. Kurczewski and R. C. Miller.

Pompilidae

Pompilus (*Ammosphex*) *dakota* (Dreisbach). 1 ♀. Alaska. Alaska Hwy. mi. 1246. 23 June 1971. Krombein (1958) defines the range of this species as from Montana and North Dakota south to Arizona and New Mexico. Thus this specimen represents a northern record for the species.

Sphecidae

Plenoculus davisi Fox. 1 ♂. Alaska. Mt. McKinley National Park nr. entrance. 5 July 1971. This species is listed as occurring from Connecticut and New Jersey west to Montana, Arizona, and California (Muesebeck et al., 1951;

Acknowledgments: We wish to thank the U.S. National Park Service for permission to collect in Mt. McKinley National Park. Dr. William M. Elliott, Biology Department, Hartwick College, Oneonta, New York 13820, was of great assistance in making field collections. Richard C. Miller, S.U.N.Y. College of Environmental Science and Forestry, determined *Crabro monticola.*

Krombein, 1958; Krombein and Burks, 1967). Our record of this species from Alaska represents a northward extension of its known range.

Tachysphex aethiops (Cresson). 2 ♂. Alberta nr. Whitecourt. 20 June 1971. This species had previously been recorded from the western states in the mountains (Muesebeck et al., 1951). This locality thus represents a northward range extension.

Tachysphex quebecensis (Provancher). 3 ♂. Alberta nr. Whitecourt. 20 June 1971. This locality is north of the previously known range of the species—Quebec and Maine to North Dakota and California (Muesebeck et al., 1951; Krombein and Burks, 1967).

Crabro (*Crabro*) *monticola* (Packard). 1 ♀. Alaska. Alaska Hwy. mi. 1246. 23 June 1971. This record represents a northward and westward extension of the range of this species which has been recorded from Canada and from Maine to Georgia (Muesebeck et al., 1951).

Oxybelus uniglumis quadrinotatus (Say). 1 ♀. Alaska. Alaska Hwy. mi. 1246. 23 June 1971. This Holarctic species has been recorded from the United States and southern Canada. Its presence in Alaska represents a northward extension of its range in the western hemisphere.

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Undescribed Species of Crane Flies from the Himalaya Mountains (Diptera: Tipulidae), XXII[1]

Charles P. Alexander
Amherst, Massachusetts 01002[2]

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Abstract: Five new species of crane flies from Iran, Sikkim, and India are described, these being *Limonia* (*Sivalimnobia*) **pererratica**, *Limnophila* (*Dicranophragma*) **recurvata**, *Gonomyia* (*Idiocera*) **nigroterminalis**, *Erioptera* (*Psiloconopa*) **iranica**, and *Ormosia* (*Ormosia*) **neidioneura**. Three further previously described Himalayan species of *Ormosia* are illustrated.

Limonia (*Sivalimnobia*) **pererratica**, n. sp.

General coloration of thorax uniformly light yellow, head brown; male antennae long, about one-half the body; legs yellow, femoral tips vaguely darkened; wings yellowed, stigma pale brown, Sc_1 ending opposite three-fifths the length of *Rs*; abdominal tergites bicolored, bases brown, apices yellowed, sternites uniformly light yellow; male hypopygium with a single dististyle, the dorsal style lacking; apex of rostral prolongation of style with a small sclerotized flange margined with about five small points.

Male. Length about 7 mm.; wing 8.5 mm.; antenna about 3.5 mm.

Rostrum and palpi brown. Antennae of male (Fig. 8) unusually long, as shown; brown, bases of flagellar segments slightly paler; flagellar segments long and cylindrical, bases slightly enlarged, verticils subequal to the segments; terminal segment very long, about one-half longer than the penultimate. Head dark brown.

Thorax uniformly light yellow. Halteres with stem light yellow, knob small, light brown. Legs with coxae and trochanters light yellow; femora yellow, tips vaguely darkened; tibiae yellowed, tarsi slightly darker; claw long and slender, with a long spine at near one-fourth the length, with microscopic more basal roughenings. Wings (Fig. 1) faintly yellowed, stigma short-oval, pale brown; veins brown. Longitudinal veins beyond level of origin of *Rs* with trichia, including outer end of *2nd A*. Venation: *Sc* relatively long, Sc_1 ending about opposite three-fifths *Rs*; cell *1st* M_2 subequal in length to distal section of M_{1+2}; *m-cu* shortly beyond fork of *M*.

Abdominal tergites bicolored, proximal segments with basal half light brown, apices yellow, outer segments more uniformly brown; sternites and eighth tergite uniformly light yellow. Male hypopygium (Fig. 7) with tergite, *t*, relatively long and narrow, posterior border with a deep V-shaped emargination, lobes conspicuous, with long black marginal setae. Basistyle, *b*, with ventromesal lobe large, central portion with long setae, those at apex smaller. Dorsal dististyle lacking; ventral style, *d*, generally as in other members of the subgenus, outer half

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[1] Contribution from the Entomological Laboratory, University of Massachusetts.

[2] Part XXI of this series of papers was published in the *Journal of the New York Entomological Society*, **81**: 3–9, March 1973. Five further species are described, from Iran, India, and Sikkim, all collected by Dr. Fernand Schmid to whom I again express my deep thanks and appreciation.

of body of style with abundant very long setae, inner face and prolongation glabrous; rostral prolongation narrow on basal half, angularly bent into the subequal beak, the latter at apex with a conspicuous sclerotized flange having five small marginal points, as shown in the subfigures; prolongation at near midlength with a single long seta from a very small tubercle; second rostral spine placed on body of style, as in the subgenus, slender on more than basal half, terminating in a shorter straight black spine. Phallosome with mesal-apical lobe of gonapophysis, *g*, long, apex obtuse; aedeagus, *a*, long and narrow, lateral flanges greatly reduced.

HOLOTYPE. ♂, Jhum La, Northeast Frontier Agency, Kameng, Assam, India, 7,200–8,000 feet, September 12, 1961 (Schmid).

In the present paper and others the words Northeast Frontier Agency (NEFA) are retained since they are on all specimen labels where concerned. In 1972 this area was changed officially to Arunachal Pradesh.

This species differs from all other previously defined members of the subgenus *Sivalimnobia* Alexander (1963) in the elongate male antennae and especially in hypopygial structure, including the loss of the dorsal dististyle. Other generally similar regional species include *Limonia* (*Sivalimnobia*) *approximata* (Brunetti), *L.* (*S.*) *fortis* (Brunetti), *L.* (*S.*) *kali* Alexander, *L.* (*S.*) *rahula* Alexander, and *L.* (*S.*) *uma* Alexander.

Limnophila (*Dicranophragma*) **recurvata**, n. sp.

General coloration of mesonotum orange yellow, patterned with pale brown; legs brownish yellow; wings whitened, with a conspicuous brown pattern that includes six costal bands, some crossing the wing, others more interrupted, cell *2nd A* relatively narrow; male hypopygium with inner gonapophysis long, apex strongly recurved into a pale spine.

Male. Length about 4.8–5 mm.; wing 5.6–6.2 mm.; antenna about 1–1.2 mm.

Rostrum and palpi black. Antennae with proximal three segments yellow, remainder of flagellum brown; proximal flagellar segments oval, outer ones more elongate, with very long verticils. Head light gray, especially the very broad anterior vertex.

Prothorax brownish yellow. Mesonotal praescutum obscure orange yellow with four vaguely indicated stripes that chiefly are evident by capillary brown lines on the interspaces and midregion, pseudosutural foveae large, orange; posterior sclerites of notum orange yellow, postnotum vaguely more pruinose. Pleura obscure yellow below, above with a narrow darker brown stripe, dorsopleural region more buffy. Halteres with stem pale yellow, knob slightly darker. Legs with coxae and trochanters yellow; remainder of legs pale brownish yellow, tips of femora very narrowly paler; claws yellow, long and slender. Wings (Fig. 2) with ground whitened, with a conspicuous brown pattern that appears as crossbands and extensive suffusions in cells *M* and *Cu*; darkened costal areas six in number, the first postarcular, extending from *C* to *Cu*; second band at origin of *Rs*, from *C* almost to *M*; third band relatively narrow, at fork of *Sc*, crossing the wing at cord to tip of *1st A*; fourth and fifth bands united at costal border to form the stigma, the third and fourth united over the fork of *Rs*, thence virtually continuous to posterior margin, narrowest at outer end of cell *1st* M_2; fifth costal area very short, reaching vein R_1 behind; sixth band subterminal, extending from vein R_3, including the supernumerary crossvein, ending in margin of medial field; other darkenings include large marginal spots on all longitudinal veins excepting R_5, smallest in medial field, the largest at *2nd A*; a narrow continuous seam on vein R_5; cells *M*, *Cu*, and *2nd A* suffused; veins yellow in the ground, darker in the patterned areas. Macrotrichia on veins beyond cord, including also the outer end of *Rs*, outer two-thirds of

M and less extensive on basal section of *Cu* and *1st A*, lacking on *2nd A*. Venation: Vein *2nd A* simple, the cell relatively narrow.

Abdomen dark brown, hypopygium yellow. Male hypopygium (Fig. 9) with outer dististyle, *d*, narrowed on outer half, apex bispinous, axial spine slightly larger, curved; inner style very stout. Phallosome, *p*, with inner gonapophysis, *g*, longer than the outer pair, apex strongly recurved into a pale spine.

HOLOTYPE. ♂, Talung Dzong, Northeast Frontier Agency, Kameng, Assam, India, 7,000–7,800 feet, September 13, 1961 (Schmid).
PARATOPOTYPES: 7 ♂♂, on three pins.

The most similar regional species include *Limnophila* (*Dicranophragma*) *analosuffusa* Alexander, Manipur, and *L.* (*D.*) *kamengensis* Alexander, Assam, differing in details of coloration of the body and wings and in hypopygial characters, especially the phallosome.

Gonomyia (*Idiocera*) **nigroterminalis**, n. sp.

Mesonotum brownish gray, praescutal stripes slightly darker brownish gray; pleura, pleurotergite and dorsopleural membrane clear light yellow; wings brownish yellow, prearcular and costal fields clear light yellow, including the veins; Sc_1 ending shortly beyond origin of *Rs*; vein R_3 nearly erect, about twice the distance on costa between veins R_2 and R_3.

FEMALE. Length about 4.5 mm.; wing 5.5 mm.

Rostrum and palpi black. Antennae dark brown; flagellar segments elongate, subequal in length to the verticils. Head brownish gray, the broad anterior vertex clearer gray.

Pronotum and pretergites brown, sparsely gray pruinose. Mesonotum gray, praescutal stripes only slightly darker brownish gray; remainder of dorsum brownish gray. Pleura, pleurotergite and dorsopleural region uniformly clear light yellow. Halteres brown, base of stem narrowly yellow. Legs with coxae and trochanters clear yellow; femora yellow, tips abruptly brownish black, including about the outer tenth of segment; tibiae yellow, more narrowly brownish black; tarsi brown. Wings (Fig. 3) faintly tinged with brownish yellow, prearcular and costal fields clear light yellow, the latter extended distally to the wing tip, including the veins, remaining veins brown, cord still darker. Venation: Sc_1 ending shortly beyond origin of *Rs*; vein R_3 nearly erect, about twice the distance on costa between veins R_2 and R_3; *m-cu* about one and one-half times its length before the fork of *M*.

Abdominal tergites dark brown, sternites yellow; terminal segments broken.

HOLOTYPE. ♀, Gwaldam, Pauri Garhwal, Kumaon, Uttar Pradesh, India, 6,000–6,400 feet, August 29, 1958 (Schmid).

Among the various regional members of the subgenus that have the wing pattern generally as in the present fly, the distinctive pattern of the legs provides a strong specific character. The most similar such species appears to be *Gonomyia* (*Idiocera*) *proxima* Brunetti, which differs in leg coloration and in details of body and wing pattern, and in the venation.

Erioptera (*Psiloconopa*) **iranica**, n. sp.

Belongs to the *areolata* group; general coloration gray, praescutum scarcely patterned; antennae brown; knobs of halteres weakly darkened; femora obscure yellow, slightly darker shortly before the tips; wings brownish yellow, veins comprising the cord darker; male hypopygium with outer dististyle bifid, inner style simple, produced into a long terminal spine; phallosome with two blackened rods on either side, the outer one scabrous; tergite terminating in a pair of acute black spines.

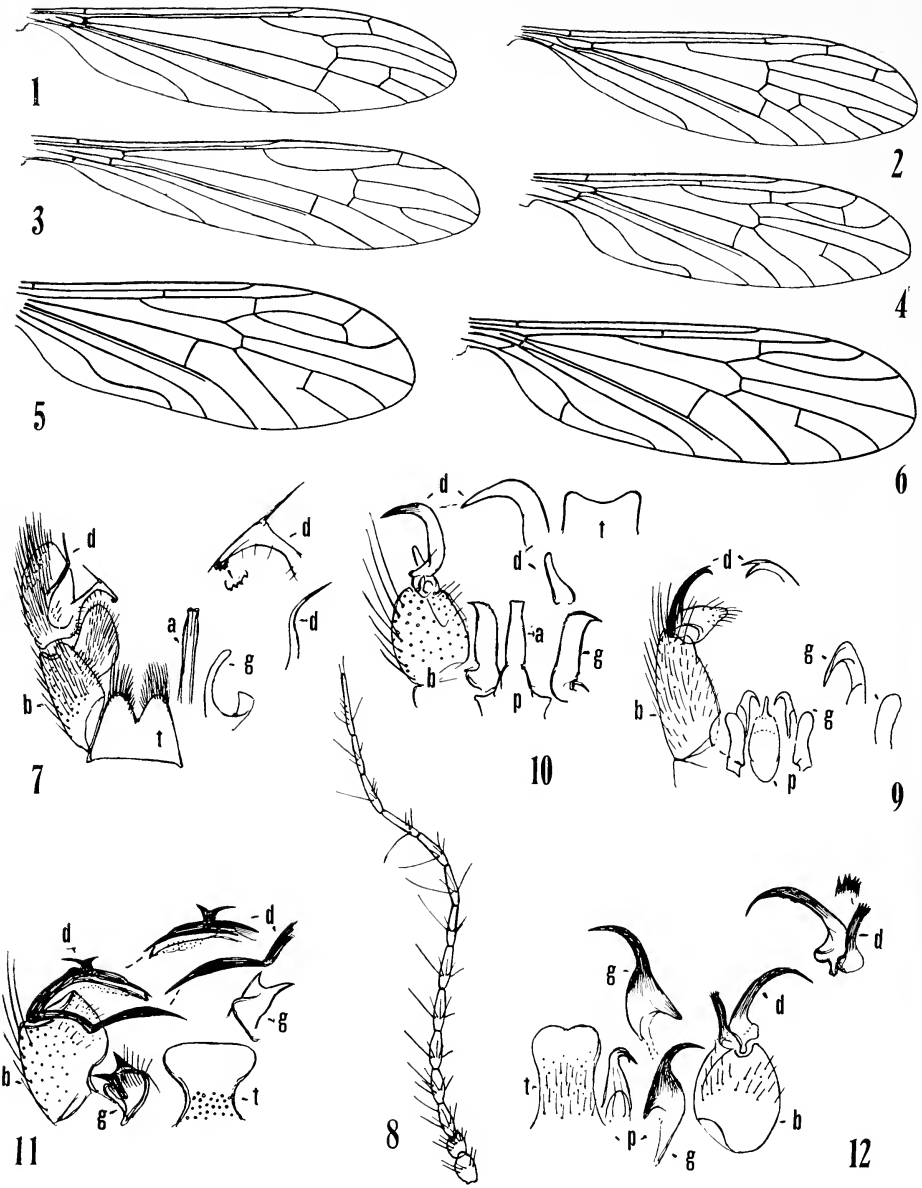

FIG. 1. *Limonia* (*Sivalimnobia*) **pererratica**, n. sp.; venation.
FIG. 2. *Limnophila* (*Dicranophragma*) **recurvata**, n. sp.; venation.
FIG. 3. *Gonomyia* (*Idiocera*) **nigroterminalis**, n. sp.; venation.
FIG. 4. *Ormosia* (*Ormosia*) **neidioneura**, n. sp.; venation
FIG. 5. *Ormosia* (*Ormosia*) *idioneurodes* Alexander; venation.
FIG. 6. *Ormosia* (*Ormosia*) *furcivena* Alexander; venation.
FIG. 7. *Limonia* (*Sivalimnobia*) **pererratica**, n. sp.; male hypopygium.
FIG. 8. *Limonia* (*Sivalimnobia*) **pererratica**, n. sp.; male antenna.

Male. Length about 4.5 mm.; wing 5.3 mm.

Female. Length about 5.5 mm.; wing 6 mm.

Rostrum brown, palpi black. Antennae brown; flagellar segments oval, shorter than the verticils. Head gray.

Pronotum gray. Mesonotal praescutum and scutum gray, humeral region more yellowed, without distinct darker pattern; praescutal interspaces indicated by a linear row of darkened setigerous punctures; scutellum more yellowed, postnotum gray. Pleura with dorsal mesepisternum light brown, mesepimeron and ventral pleurites more yellowed. Halteres with stem pale yellow, knob weakly darkened. Legs with coxae and trochanters light yellow; femora obscure yellow, slightly darker just before tips; tibiae brownish yellow; tarsi dark brown or black. Wings brownish yellow, prearcular and costal fields clearer yellow; a vague darkened pattern along the cord, indicated by a deepening in color of the veins; veins yellowish brown to pale brown. Venation: R_2 slightly oblique; cell *1st* M_2 small; M_{3+4} about one-third as long as the gently arcuated M_4.

Abdominal tergites brown, posterior borders very narrowly pale; sternites yellow, hypopygium brownish yellow. Male hypopygium with posterior border of the tergite bearing two acute black spines, at midline separated by a U-shaped notch. Basistyle at apex produced into a slender lobe, the dististyles thus subterminal; outer style bifid, including a long gently curved outer arm that narrows into a long acute point and a shorter flattened black blade that has an appressed black spine on outer margin beyond base; inner style elongate, yellow basally, outer third blackened, curved, narrowed into a long black spine. Phallosome including two blackened rods on either side, the outer apophysis scabrous by appressed spinules, the subequal inner element smooth, tips narrowly acute, decussate across the midline.

HOLOTYPE. ♂, Zanus, Mazanderan, Iran, 2,000 meters, September 21, 1955 (Schmid).

ALLOTOPOTYPE. ♀, pinned with the type.

The present fly belongs to the group of species having the inner dististyle of the male hypopygium elongate and terminating in a long black spine. Other members of the group having this character include *Erioptera* (*Psiloconopa*) *margarita* Alexander, of the western Nearctic region and *E.* (*P.*) *complicata* (Bangerter), of the Swiss Alps, all such species differing among themselves in the details of hypopygial structure, particularly the tergite, outer dististyle and the phallosome.

Ormosia (*Ormosia*) **neidioneura**, n. sp.

Allied to *idioneurodes*; size small (wing of male 4.5 mm.); general coloration of thorax dark brownish gray, abdomen dark brown; halteres light yellow; wings whitened, restrictedly clouded with brown, chiefly at and beyond the cord; vein R_2 far before the outer

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Fig. 9. *Limnophila* (*Dicranophragma*) **recurvata**, n. sp.; male hypopygium.

Fig. 10. *Ormosia* (*Ormosia*) *idioneurodes* Alexander; male hypopygium.

Fig. 11. *Ormosia* (*Ormosia*) *idiostyla* Alexander; male hypopygium.

Fig. 12. *Ormosia* (*Ormosia*) **neidioneura**, n. sp.; male hypopygium.

(Symbols: Male hypopygium—*a*, aedeagus; *b*, basistyle; *d*, dististyle; *g*, gonapophysis; *p*, phallosome; *t*, 9th tergite).

radial fork; male hypopygium with the outer dististyles and gonapophyses blackened, spinelike, inner dististyles very small, terminating in six small blackened points.

Male. Length about 4 mm.; wing 4.5 mm.; antenna about 0.7 mm.

Head broken. Thorax almost uniformly dark brownish gray, pretergites inconspicuously yellow; praescutal stripes differentiated chiefly by abundant light yellow setae on the interspaces. Halteres light yellow. Legs with coxae grayish brown; trochanters obscure yellow; remainder of legs yellowish brown, the dark color produced by abundant long setae. Wings (Fig. 4) whitened, with restricted brown clouds over various veins, chiefly at and beyond the cord, basal cells almost clear, their trichia reduced in number and very inconspicuous; veins yellow in the clear parts, pale brown in the darkened pattern. Venation: R_2 far before outer radial fork, R_2 and R_{3+4} subequal; a supernumerary crossvein in cell R_3 partially atrophied on one wing of type; veins R_3 and R_4 very strongly upcurved, at margin cells R_2, R_3, R_4 and R_5 subequal in extent; cell M_2 open by atrophy of basal section of M_3, *m* perpendicular; *m-cu* about one-third its length before fork of M; vein *2nd A* very strongly sinuous, as shown.

Abdomen dark brown. Male hypopygium (Fig. 12) with tergal plate, *t*, gently expanded outwardly, sides nearly parallel, apex very insensibly emarginate medially. Dististyles, *d*, with outer style a long blackened rod from a dilated base, curved very gently into a long spine; inner style very small, beyond the expanded base straight, apex terminating in six small acute crowded points. Gonapophyses, *g*, blackened, in shape generally similar to the outer dististyle, base more expanded, the length subequal to the outer style.

HOLOTYPE. ♂, Zomphuk, Sikkim, 6,500–8,000 feet, April 11, 1959 (Schmid).

The most similar regional species include *Ormosia* (*Ormosia*) *idioneura* Alexander, of Northeast Burma, and *O.* (*O.*) *idioneurodes* Alexander, of Manipur, Assam, which have the venation generally as in the present fly, differing in details, as the position of vein R_2 in relation to the outer radial fork (compare Figs. 4 and 5).

Ormosia (*Ormosia*) *furcivena* Alexander

Ormosia (*Ormosia*) *furcivena* Alexander; *Jour. N.Y. Ent. Soc.*, **76:** 67–68; 1968.

Type, ♀, Hkayam Boum, Manipur, Assam [Fig. 6 (venation)].

Ormosia (*Ormosia*) *idioneurodes* Alexander

Ormosia (*Ormosia*) *idioneurodes* Alexander; *Jour. N.Y. Ent. Soc.*, **76:** 68–69; 1968.

Type, ♂, Sirhoi Kashong, Manipur, Assam [Fig. 5 (venation); Fig. 10 (male hypopygium)].

Ormosia (*Ormosia*) *idiostyla* Alexander

Ormosia (*Ormosia*) *idiostyla* Alexander; *Jour. N.Y. Ent. Soc.*, **76:** 69–70; 1968.

Type, ♂, Rumkhang, Khasi-Jaintia, Assam [Fig. 11 (male hypopygium)].

Notes on the Biology of *Phyciodes* (*Eresia*) *eutropia* (Lepidoptera: Nymphalidae) in a Costa Rican Mountain Forest

Allen M. Young
Department of Biology, Lawrence University, Appleton, Wisconsin 54911

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Abstract: This paper discusses various aspects of life cycle and natural history for the neotropical butterfly, *Phyciodes* (*Eresia*) *eutropia* (Lepidoptera: Nymphalidae) as studied in the field at a mountain wet forest locality in central Costa Rica, and in the laboratory. Emphasis is placed on a description of life stages, larval food plant record, habitat selection by adults for egg laying, courtship, and mimetic interaction with other butterflies. The behavior of larvae associated with feeding and defense was also observed under field conditions. It was found that the early stages are very cryptic in coloration and this morphological crypsis is accompanied by various forms of cryptic behavior in the larvae (concealment, curling-up movement, etc.). The egg-adult developmental time in the laboratory is about 46 days when larvae are reared on cuttings of the natural food plant, *Pilea pittieri* (Urticaceae). Eggs are laid in large clusters on the ventral sides of leaves of this food plant, and although this plant occurs in both dark red and light green forms, females exhibit strong preference for laying eggs on dark plants. Oviposition is generally confined to heavily shaded river bottom forest where the food plant is abundant, but other aspects of reproductive behavior occur in sunlit alleys and corridors of secondary growth. There may also be mimetic association with *Ithomia heraldica* (Ithomiidae) here. If this is the case, then it is likely that *P. eutropia* is a Batesian mimic of *I. heraldica* since observations on the appearance and behavior of immatures in the former butterfly suggest palatability.

INTRODUCTION

This paper gives a description of the life cycle for the neotropical butterfly, *Phyciodes* (*Eresia*) *eutropia* Hewitson (Lepidoptera: Nymphalidae), and incorporates a variety of information regarding the natural history and behavior of adults and immature stages. Thus, this report comprises a preliminary and fresh survey of the general biology of this interesting, widespread, and geographically complex Central American species, as recorded for individuals studied from a single population in the central highlands of Costa Rica. The impetus

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for this sort of study takes its origin primarily from the need for more critical examinations of the local biology of many neotropical butterflies and places particular emphasis on accurate records of oviposition and larval food plants (Remington, 1952; Brower, 1958).

At the very outset, a word of caution is given concerning the species name of the butterfly used in this paper. The precise identity of this butterfly remains dubious until a complete revision of the genus in Central America is conducted, and the species designation used here must be regarded as provisional. Specimens reared in this study match up very well with individuals of *P. eutropia* collected elsewhere in Costa Rica (Turrialba) and from the Canal Zone (Gordon B. Small, Jr., pers. comm.). But males of presumably the same species from other Costa Rican localities and also from western Panama are very different, and these individuals may represent a sex-related polymorphic race. The problem here is essentially that of lumping together different morphs (apperently there are several in males) of a single highly polymorphic species (where different morphs displace one another geographically) under a single species name, and distinguishing these instances from other true species in the genus.

DESCRIPTION OF STUDIES

The following major studies were conducted at a single locality in Costa Rica at various times during the period 24 June through 5 September 1971. But the butterfly was not studied continuously during this period, but rather at intermittent times. These studies are: (1) adult habitat preference and larval food plant, (2) features of the life cycle, (3) behavior of adults and immatures, and (4) mimetic associations. The locality is Cuesta Angel, a mountain and ravine-studded region (900 to 1000 meters elev.) in the Heredia Province, and more specifically situated along the road connecting Puerto Viejo with the cities of Alajuela and Heredia. The site is about 9 km before the town of Cariblanco. The actual study area was eventually confined to a strip of relatively undisturbed forest understory bordering one side of the Rio Sarapiqui at the bottom of the 300-meter-deep ravine that constitutes Cuesta Angel. This study area is the same one used to study the biology of *Victorina epaphus* (Young, 1972a), *Itaballia caesia* (Young, 1972b), and *Hymenitis nero* (Young, 1972c). The butterfly is unusually abundant during the study period in this area of the forest, and this facilitated the initiation of the various studies stated above and described below.

The habitat preferences of adult butterflies were studied by walking through various types of vegetation associated with the river edge, and noting the general abundance of individuals, feeding spots, courtship interactions, and oviposition. A total of four days was spent doing this. The larval food plants were located by tracking ovipositing females through the understory and observing several different oviposition sequences; these observations were conducted for a total

Fig. 1. Overall view of the forest ravine, Cuesta Angel, in the central highlands (Heredia Province) of Costa Rica.

of five days. Both adult habitat preferences and larval food plants were usually examined between 8:30 A.M. and 3:00 P.M., but the actual number of hours spent doing this daily was very irregular.

Additional searches for adult activity were conducted from time to time at points higher up on one side of the ravine. A narrow winding gravel road connects the river bottom area with the ridge-top road which goes to Puerto Viejo, and it is easy to look for the butterfly at strategic points along the road. Other searches were made along the ridge-top which is accessible by the Puerto Viejo road and a small network of foot paths leading to more interior places.

Features of the life cycle examined included (1) description of the gross external morphology of immatures, (2) the sizes (body lengths) of immatures, and (3) the developmental time of several individuals from egg to adulthood. All of these were observed essentially simultaneously under laboratory conditions. The "laboratory" was an abandoned toolshed on the premises of the office of the Associated Colleges of the Midwest in San Jose. Here, cultures of the butterfly were maintained in 60 × 25 cm clear plastic bags kept very tightly closed and placed on a wooden table away from direct sunlight. A total of

FIG. 2. Habitat selection for oviposition in *Phyciodes* (*Eresia*) *eutropia* at Cuesta Angel. (A) Herbaceous understory of the river-bottom forest where the larval food plant is found. (B) Vine growth form of the larval food plant, *Pilea pittieri* Killip (Urticaceae) at base of canopy tree (the dark red form of the plant is shown).

four different clusters (each containing several eggs—see below) was transported from Cuesta Angel to the San Jose laboratory within a few hours after being laid in the wild; two of the clusters were brought in very early in the study period (first week of July) and an additional two were retrieved from the wild during mid-August. Each cluster was placed in a separate clean plastic bag, along with additional cuttings of the food plant. The four bags were then examined intermittently, usually every two or three days, for egg hatching, differentiation of instars, etc. Bags were periodically wiped clean of larval frass and old food plant. The temperature in the toolshed was usually about 23°C during the midmorning hours; it is slightly cooler at Cuesta Angel at these hours (during the same months), being 19 to 21°C in the shaded understory where the eggs are typically found. For the first two groups of eggs studied, rearing continued successfully until the late fifth instar (for most of the larvae) when the cultures were neglected for several days and virtually every larva died. Thus the first two egg clusters provided life cycle data only through the first four instars. In the second group of two egg clusters studied later, all individuals successfully pupated but the pupae eclosed en route on a jet flight from Miami, Florida to Chicago, Illinois, with the result that many (virtually all) adults emerged with badly crumpled and damaged wings. Only five pupae (all females) were spared and emerged a few days later at the final destination (Appleton, Wisconsin).

Observations on adult behavior were limited to feeding site selection, oviposition, and courtship site selection. Again, the data here are essentially qualitative. Behavior of immatures refers to observations on the dispersal tendencies of larvae on the food plant in the wild. This was studied for eight days. Initially, the location of an egg cluster in the wild was noted and the number of larvae and their distribution on the plant was observed on later dates. This was done for a single egg cluster discovered on the morning of 30 July 1971. Larval dispersion associated with the onset of pupation was also observed. Finally, the defense behavior of individual larvae was studied both in the field and laboratory. This was done by suddenly prodding larvae with blunt forceps and observing their responses on the food plant.

Mimetic association was observed only in a very preliminary way. Attempts were made to observe other butterflies that resembled adult *P. eutropia* males and/or females both in appearance and habitat selection. These observations were done simultaneously with the observations of adult habitat preference outlined earlier.

RESULTS

HABITAT PREFERENCES AND FOOD PLANT

Both young males and females are most frequently seen on the borders of early secondary growth vegetation where there is a large amount of unobstructed

sunlight and very low (0.5 to 1.5 m) herbaceous canopy cover. These individuals are judged to be "young" by the teneral or near-teneral condition of the wings; they are very fresh with very little or no loss of scales from the wings and minimal tattering. It is interesting to note that adults of any age category are only seen at the bottom of the Cuesta Angel ravine (Fig. 1) and virtually no individuals are seen flying at intermediate levels or ridge-top area of this pronounced local topographic gradient. Adult activity is thus very much confined to the "river-bottom" area of the ravine, and typically within a few meters of the river edge. Here, in sunlit patches of low secondary growth, there is much play activity between young adults of both sexes; males frequently chase after females and this may be a form of courtship activity (although copulation and the immediate sequence of behavioral acts leading to it have not yet been observed in *P. eutropia*).

While courtship and feeding in adult *P. eutropia* are confined primarily to sunlit corridors of young secondary growth, oviposition is clearly associated with very dark and damp forest understory in river-bottom forest. It is relatively easy to spot females searching for oviposition sites since (1) this is a sexually dimorphic species, and (2) these females are often frayed and tattered and thus easily distinguished from the young females which tend to remain in sunlit areas near the forest. Young (and presumably unmated) females are seldom seen in the forest interior, although occasionally teneral adults of both sexes are seen there early in the day. Presumably these individuals emerged from their pupae only a few hours before and have not yet moved out of the forest.

The plant used for oviposition and larval feeding is the herbaceous understory member, *Pilea pittieri* Killip (Urticaceae). At Cuesta Angel, this plant is most commonly encountered in the damp river-bottom forest (Fig. 2-A), where it thrives either as a small sprawling vine around the bases of large trees (Fig. 2-B) or as a small upright plant on the forest floor. Standley (1937) mentions that the genus *Pilea* is represented by more than 30 species in Central America, and that *P. pittieri* is found primarily at mountain elevations and generally in the central region of Costa Rica. While it has been noted that *Pilea microphylla* forms a major component of the herbaceous layer in the mountain valleys of St. Andrew in Jamaica (Robertson and Gooding, 1963), *P. pittieri* in the river-bottom forest at Cuesta Angel is distributed in a very patchy manner, and with considerable variation in patch sizes along the river edge. I have also found this species along stream beds near San Miguel (400-m elev.) and on the Caribbean slopes of the central highlands; the species in general appears to be endemic to the wet Caribbean slopes at elevations between 500 and 1500 meters (William C. Burger, pers. comm.). At Cuesta Angel, the plant is very frequently seen growing out of crevices between large boulders whose surfaces are continually wet from water dripping from places higher up

on the side of the ravine. The plant very conspicuously drops out as one walks up the ravine, and probably does not occur higher than 50 meters above the river bottom. While most individuals of this succulent plant are very dark red, there is a small fraction that are bright green; the origin and biological significance of this color dimorphism in *P. pittieri* is probably unknown. No other larval food plants were found at Cuesta Angel, and ovipositing females are very much confined to those areas of river-bottom forest where patches of *P. pittieri* occur.

Oviposition is very clearly limited to the dark red form of *Pilea pittieri* at Cuesta Angel. In addition to looking for oviposition acts in progress, searches of leaves of the green form revealed no eggs. I interpret this as indicative of strong selection for leaves of the dark red form for oviposition.

FEATURES OF THE LIFE CYCLE

Very soon after being laid, the egg of *P. eutropia* is uniformly creamy-yellow and pear-shaped (Fig. 3-A); there are no visible signs of grooves or ridges on the surface. The egg is about 1.0 mm tall, and just before hatching it turns light orange, which is the basic body color of the first instar larva prior to feeding. The first instar is yellow to light orange and covered with sparse hairs. Upon feeding on plant tissue, the larva immediately becomes dark reddish-green owing to the ingestion and presence of plant pigments in the digestive tract. The head remains light orange. By the end of the first instar, the larva measures about 4 mm in length.

The second instar (Fig. 3-B) is generally very dark green with the head becoming darker brown. The body is now adorned with three rows of highly branched yellow spines that are semi-translucent. The larva attains a body length of about 6 mm during this instar.

The third and fourth instars are essentially very similar in appearance to the second instar; the third instar is about 9 mm long by molting, and the fourth instar 16 mm long. The first four instars of this species are very difficult to photograph owing to their dark coloration and the almost perfect matching with the dark color of the food plant.

The body of the fifth instar is also dark green, but has become lightly speckled in white spots (Fig. 3-C). The head is orange but reflects a gold tinge in sunlight. As with earlier instars, the prolegs are also orange. The spines have become darker orange but with the same distributional pattern (three pairs per segment) as seen in earlier instars. The fifth instar possesses slight reflective properties owing to the cuticular nature of the spine, pigmentation of the head, and pattern of tiny white spots on the body surface. At the end of the active feeding period of the fifth instar, the larva is 29 mm long.

The pupa (Fig. 3-D) is generally dark greenish-brown and, after a few days, the wing pads develop lighter patches of brown. There are very few noticeable

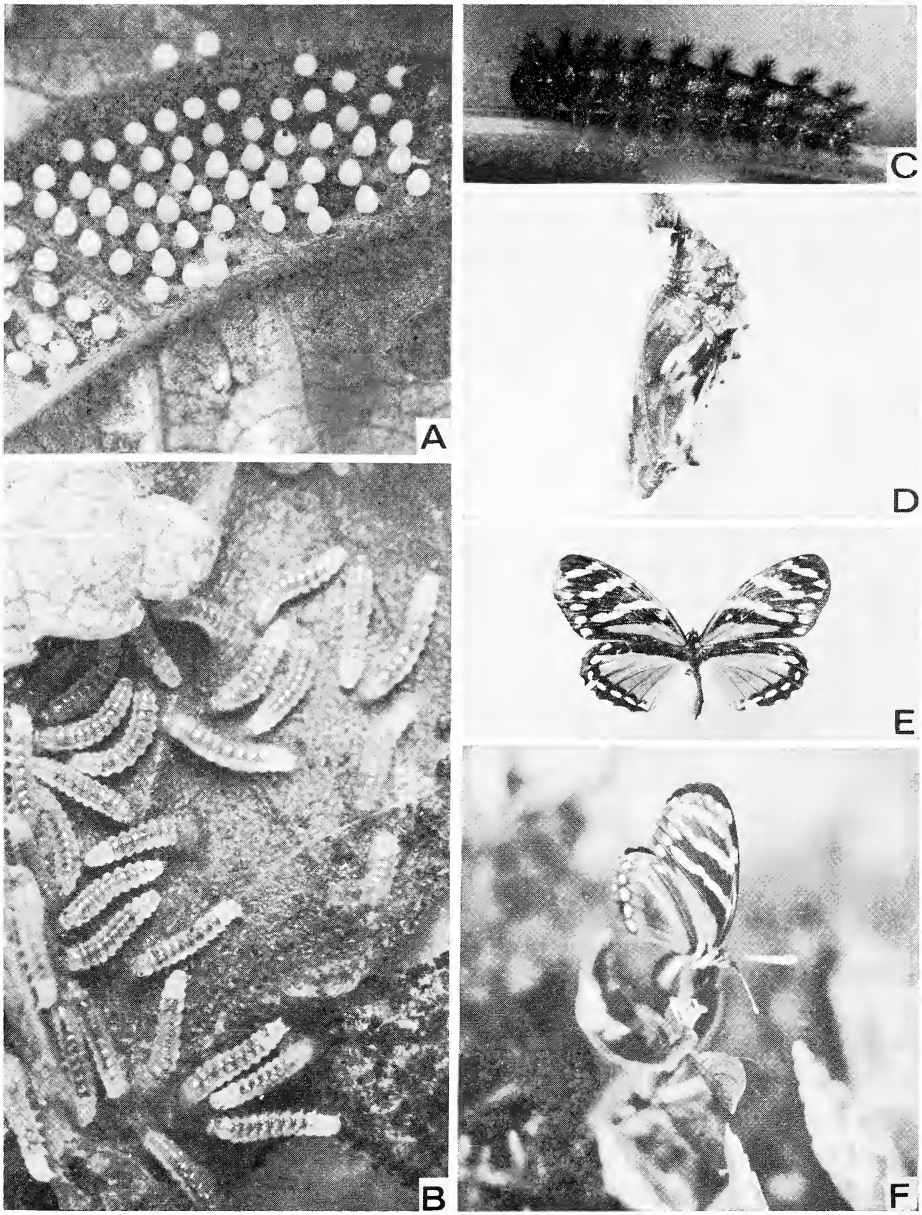

FIG. 3. Life cycle of *Phyciodes eutropia*. (A) Egg cluster, (B) second instar larvae, (C) fifth instar larvae, (D) pupa, (E) adult female, dorsal side, and (F) female ovipositing on *Pilea pittieri*.

Table 1. The developmental time* of *Phyciodes* (*Eresia*) *eutropia* on *Pilea pittieri* as determined in the laboratory**

Statistic	Egg	*Instars* 1	2	3	4	5	Pupa	Total, egg to adult
Duration (in days)	10	4	4	6	6	6	10	46
± S.E.	1.0	1.3	2.4	2.0	3.0	4.4	1.1	
N	228	225	225	225	220	114	108	

* As determined for individuals measured in four different egg clusters through the fourth instar, but for only two egg clusters through the pupa.

** Laboratory conditions, in San Jose, are 20 to 26°C and about 50 percent relative humidity.

markings and the pupa is generally shiny in a manner similar to the fifth instar. The pupa is about 15 mm long.

The dorsal aspects of the adult female are shown in Fig. 3-E, and both sexes are shown together in Fig. 4. Good general accounts of the wing color patterns for this and other species of *Phyciodes* (*Eresia*) are given in Seitz (1924) as the adults have been known for some time. The sexual dimorphism (Fig. 4) is very pronounced, including the shape of the wings, and only one morph of each sex has been found in the population at Cuesta Angel. There is no evidence from rearing studies and wild-caught individuals that the population is polymorphic locally for either sex.

Female adults are larger than males and the egg-adult developmental time of the former is greater by about two days in the laboratory (Table 1). The discrepancy in developmental time between the sexes occurs in the duration of the fifth instar (Table 1). Under field conditions, the developmental time for both sexes may be extended slightly since air temperature there is slightly lower than in the laboratory.

In the laboratory, egg hatchability is very high and there is very low physiological death of eggs under these conditions. The sex ratio of adults which eventually arise from an egg cluster is very close to unity. This was determined from examination of genitalia of individuals emerging from the last two egg clusters studied.

BEHAVIOR OF ADULTS AND IMMATURES

It has already been mentioned that adults, especially young ones, feed and undergo courtship activity in exposed secondary growth vegetation near forests. Undoubtedly there is a limited amount of feeding that also occurs in the forest interior soon after adults eclose. Courtship may truly be limited to sunlit areas if aerial visual cues at distances between the sexes play a major role in mate encounter strategy in this butterfly.

By far the single most noticeable adult activity in the forest in oviposition

(Fig. 3-F). The eggs are laid in orderly clusters (Fig. 3-A) on the ventral surfaces of *Pilea pittieri* and the deposition of a single cluster of 60 to 70 eggs may take between twenty and thirty min. Cluster size apparently varies considerably in the wild. Of a total of six clusters found, the egg number per cluster was: 41, 55, 60, 64, 72, and 76 eggs. It is not known if a female will lay more than a single cluster. A cluster is typically laid only on a single leaf, and during the oviposition, the female remains exceedingly immobile, only shifting slightly the position of her curled abdomen (Fig. 3-F) from her position on the dorsal edge of the leaf. The time of day for oviposition is variable and the process has been witnessed between 11:00 A.M. and 1:45 P.M., usually under conditions of very heavy overcast. Females oviposit on both vines and upright herbs of the food plant and show no preference for either growth form. Owing to the manner in which the leaves droop slightly on either growth form, the eggs remain well hidden to the human eye and perhaps also to cruising predators and parasites. For the cluster observed closely in the wild for several days, there was no loss of eggs prior to hatching.

The larvae of *P. eutropia* must provide one of the best examples of crypsis among the larvae of neotropical butterflies in general. Because of their coloration and reflectance, both of which match beautifully the leaves of the food plant, the larvae are difficult to detect visually during all of their instars. The larvae during all instars remain highly gregarious (Fig. 3-B) both in the laboratory and wild, but this behavior, in the context of predator-avoidance activities, is counteracted by the highly cryptic appearance of these insects. There is relatively little dispersal of larvae from one another until the time of pupation. Feeding occurs both day and night in the laboratory. When prodded just slightly with forceps, a larva will drop off the leaf and curl up into a very tight ball and remain in this position motionless for a few minutes. In the wild, most larvae are found only within a few centimeters of the ground (since *Pilea* is a low herb) and when they drop off the plant, they invariably crawl back up within several minutes. The curling-up behavior results in the highly branched spines being directed in several directions and this may represent an effective deterrent to predator attack. It has not yet been determined if the larvae possess odoriferous defensive chemical secretions against their predators. However, this would appear to be an unnecessary precaution owing to the excellent crypsis and added curling-up and dropping escape behavior of these larvae.

MIMETIC ASSOCIATION

The very familiar "tiger stripe" dorsal wing pattern of orange, black (brown), and yellow, seen especially in the females of *P. eutropia* suggests mimetic association with a variety of other medium-sized sympatric butterflies. Where young adults are most active in sunlit areas near the forest, the most likely

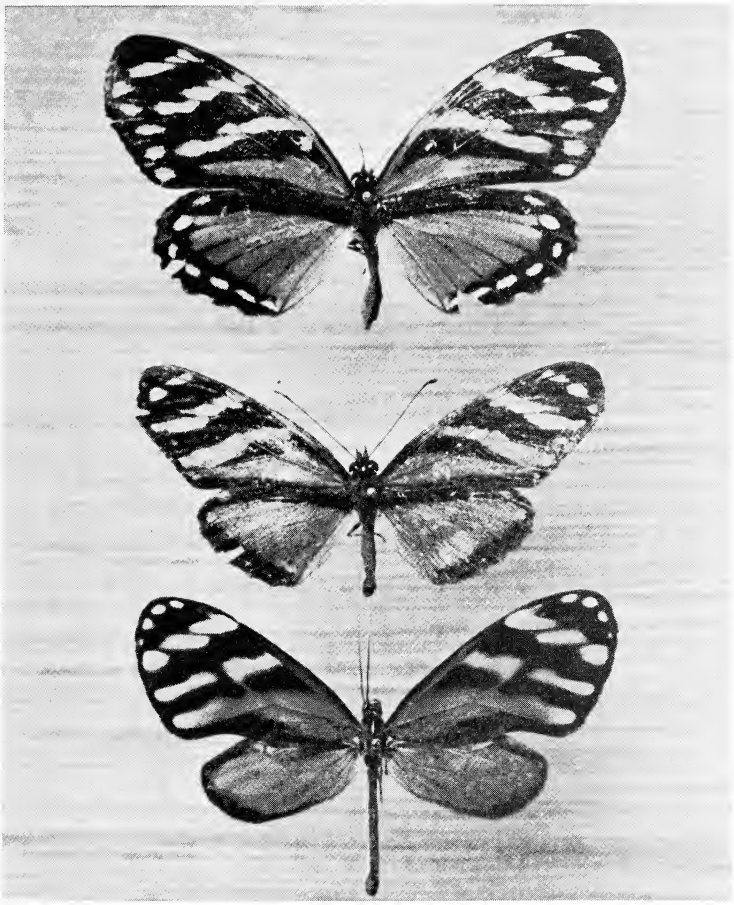

FIG. 4. Probable Batesian mimicry complex involving *Phyciodes eutropia* at Cuesta Angel. From top to bottom: Female *P. eutropia*, male *P. eutropia*, and male *Ithomia heraldica heraldica* (Ithomiidae). Dorsal aspects of all individuals are shown.

candidate for mimetic interaction is *Ithomia heraldica heraldica* (Fig. 4) in the Ithomiidae. This species feeds at the same flowers as *P. eutropia* and generally flies at the same time of day. In the absence of detailed quantitative data on the relative abundances of both species where they occur together and also on the possibly greater interaction of *Ithomia* with male *P. eutropia*, it is difficult to conclude that mimicry is operating between them.

DISCUSSION

The habitat distribution of the adult breeding population of *P. eutropia* at Cuesta Angel is essenitally limited to the moist and shady river-bottom areas

of the ravine where the larval food plant, *Pilea pittieri*, is found. This plant species apparently has low water intolerance and is restricted to very wet microhabitats. The butterfly moves only very little distances from places where the plant is abundant, and even courtship and feeding sites in sunlit patches of young secondary growth vegetation are in close proximity to places of intense oviposition activity. The general lack of *Pilea* farther up the sides of the ravine may be a major contributing factor to the noticeable absence of the butterfly at high places. The butterfly is thus a forest understory species and its populations are limited in spatial distribution to a large degree by the distribution of the food plant. Further studies are needed to define the dispersal abilities of adults, and if it were found that there is low vagility in either or both sexes, gene flow may be restricted and microevolutionary processes in different populations could lead to evolutionary divergence in a variety of phenotypic traits (Ehrlich and Birch, 1967).

Another major aspect of the adaptive strategy of this species concerns predation pressures on adults and immatures. Populations of animals are confronted with the problem of maintaining one or a variety (seasonal) levels of numerical abundance in order to avoid local extinction. At the morphological and behavioral levels of animal organization, selection often favors the evolution of defense mechanisms that reduce the risk of predation or parasitism to reproductively (or pre-reproductively) competent individuals in the population. The intensity and array of predator threats will vary greatly from one population of the species to the other. In butterflies, one major ecological interface that provides an evolutionary matrix for the development and perfection of defense mechanisms is the food-plant–larva (herbivore) association in different populations of the species. There is a substantial body of information that suggests lepidopterous larvae incorporate into their digestive tracts and perhaps body tissues toxic compounds derived from their food plants (see the review in Brower and Brower, 1964), therefore rendering themselves unpalatable to at least some of their predators. This sort of adaptive pattern is dependent upon the coevolutionary interactions between the butterfly species and its larval food plants (Ehrlich and Raven, 1965). An alternative and very different adaptive pattern to similar selection pressures is the apparently *de novo* synthesis of highly volatile compounds that are discharged (upon appropriate stimulus being received) usually from specialized cuticular glands (Eisner, 1970). Not only is the biochemical origin of these two strategies of predator defense very different but unpalatability necessitates the advertisement of the distasteful properties to the attacker, and chemical defense secretions infer that crypsis is the best strategy. In some instances, a single organism may possess both mechanisms of defense (Eisner et al., 1971), where each one is functional against a different array (vertebrate versus invertebrate) of predators.

Clearly the adaptive pattern of the larvae of *P. eutropia* against at least

vertebrate predators is one of crypsis. Here, the morphological and behavioral components of the crypsis have been perfected to the extent that further defense mechanisms would appear to be unnecessary energy expenditures. There is the strong suggestion that the larvae and adults are palatable, receiving little or no defensive compounds from *Pilea*. It is not determined if the larvae or adults give off odoriferous secretions; there is no evidence of this to the human observer when larvae or adults are handled. The presence of highly branched and numerous spines, cryptic coloration, and curling-up defense movements, suggest that the strategy is one of predator avoidance and not advertisement. The gregarious habit of the larvae may be the result of strong selection pressures for cluster oviposition on a food plant with a very patchy distribution and may bear no relation to predation pressures. While cluster oviposition is generally unusual among many species of butterflies studied (Labine, 1968), instances of it and resulting larval gregariousness may be adaptations to a locally scarce food plant (especially if many females are ovipositing in the area, and the interpretation of "many" will vary tremendously with different species and food plants). Under such conditions, it is better to release most of the eggs as soon as possible. An alternative explanation would be that gregariousness imparts some advantage against predators, especially leaf-roaming forms like small amphibians and a variety of arthropods. If each egg cluster is viewed as a kin group, some individuals in the group will be eaten as larvae if they distract predators from the rest of the group. The larvae remain together until pupation and this may be evidence for the existence of some cooperative mechanism by members of the group against predators.

The adults of both sexes may enter into a Batesian mimicry complex with *Ithomia heraldica*, with the latter being the model since the Ithomiidae are reputed to be unpalatable butterflies which results from their larvae feeding on Solanaceae (Brower and Brower, 1964). It is the female *P. eutropia* that appears to resemble *Ithomia heraldica* far more so than the male. Instances of essentially non-mimetic males and mimetic females are very numerous among species acting as Batesian mimics in the New World tropics. The occurrence of sexual dimorphism in *P. eutropia* and the stronger resemblance of the female to an unpalatable species is indirect evidence that Batesian mimicry may be operating at Cuesta Angel. Both species are seen flying and feeding in close proximity at the river bottom and the preference for *P. eutropia* to feed and court in sunny places may be a form of habitat selection enhancing its Batesian association with *Ithomia heraldica*. Vertebrate predators are more likely to associate the two species in sunnier places than in shady places, but ovipositing females in shady forest understory, since they are more mimetic than males, may still stand a better chance of not being attacked, especially during the morning hours.

The strong preference exhibited by ovipositing females for the dark red

form of *Pilea pittieri* and general avoidance of the lighter green form suggests further that crypsis and palatability characterize the adaptive strategy of the larvae against their predators. The larvae would appear more conspicuous against the leaves of the green form owing primarily to the (1) lack of reflectance luster on the leaves of the green form but still present on the larvae, (2) the shadow effects produced by the intricate body spines and reinforced with larval movements, and (3) the gregarious habit of the larvae forming conspicuous large clumps on the small leaves.

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A New South American Genus of Pentatomini (Hemiptera:Pentatomidae)

L. H. Rolston

Department of Entomology,
Louisiana State University, Baton Rouge, Louisiana 70803

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Abstract: *Ladeaschistus*, new genus, is erected to contain four South American species with preapical femoral tubercles. Three species, *L. armipes*, *L. bilobus*, and *L. trilobus* are transferred from *Euschistus* and redescribed. The fourth member of the genus is **L. boliviensis**, NEW SPECIES. The genus is compared to *E. tristigmus*, the type species of *Euschistus*, and to *E. anticus*, a representative of a South American species group.

INTRODUCTION

The South American pentatomids *Euschistus armipes*, *E. bilobus*, and *E. trilobus* differ notably from their current congeners in having the femora armed on the inferior face with conspicuous preapical tubercles (Fig. 18). They differ less obtrusively in having the superior ridge of the pygophore tectiform (Figs. 12, 28, and 37) and in having parameres that bend inversely (Figs. 14, 22, 33, and 41) from those of their congeners (Figs. 2 and 8). Removal of these species from their present genus contributes toward a more practical classification within the Pentatomini. Their unique combination of characteristics necessitates the erection of a new genus to contain them and a new species from Bolivia.

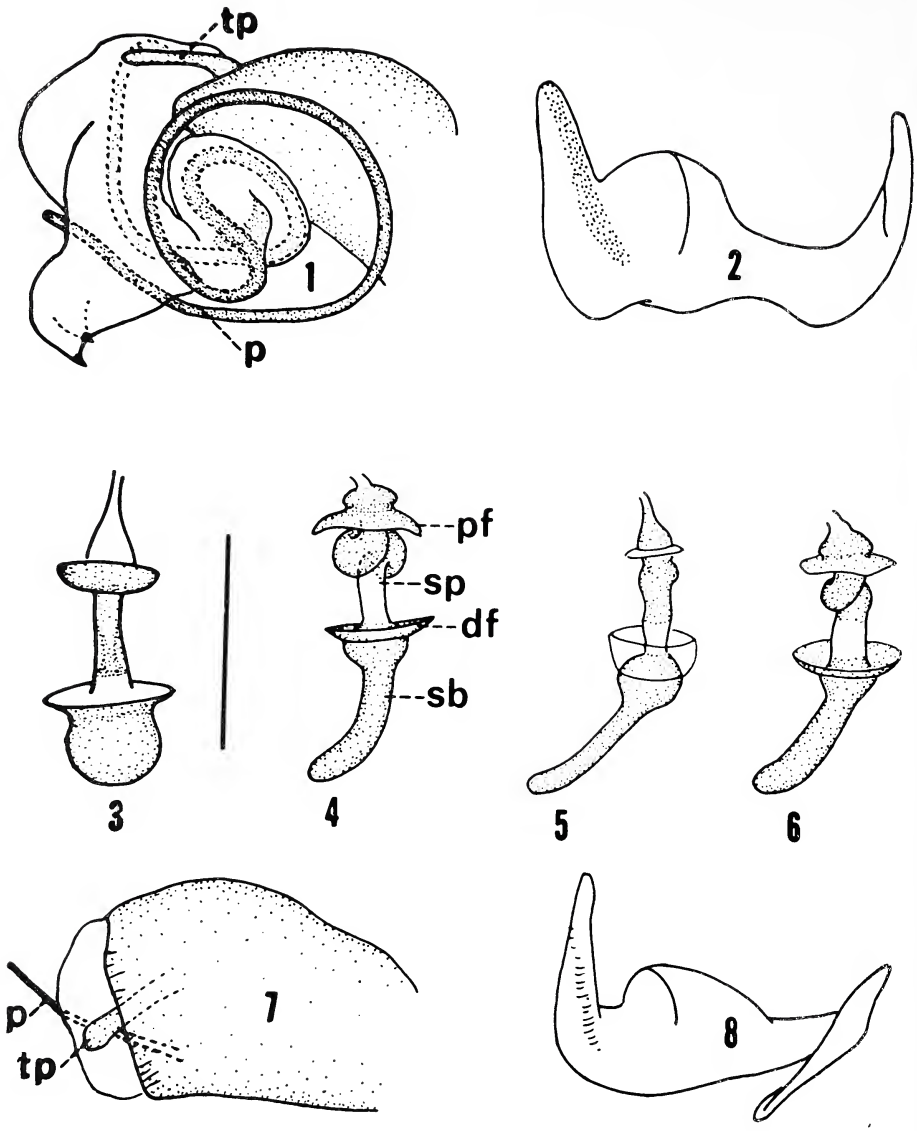
Ladeaschistus, new genus

Width of head across eyes and length subequal. Juga and tylus obtuse at apex, subequal in length, or juga slightly surpassing tylus. Length of first antennal segment placing distal end near apex of head; each of four succeeding segments much longer than first. Bucculae evanescent at base of head; distal end of first rostral segment reaching or slightly surpassing posterior limit of bucculae; apex of rostrum attaining to slightly surpassing metacoxae.

Pronotum about 2.7 to 3.4 times as wide at humeri as long at meson; emargination behind head moderately deep (Fig. 24). Anterolateral angles truncate, contiguous with eyes, extending little or not at all laterad of eyes. Anterolateral margins carinate and denticulate.

Scutellar width at base subequal to length. Frena reaching about 0.6 to 0.7 distance from base toward narrowly rounded apex. Distal margin of coria extending obliquely

Acknowledgment: I am indebted to Dr. Per Inge Persson, of the Naturhistoriska Riksmuseum, Stockholm, for comparing the description and drawings, insofar as possible without dissection, to the lectotype of *Euschistus trilobus* Stål, for confirming the apparent conspecificity of the type series, and for providing data from the labels of these specimens.

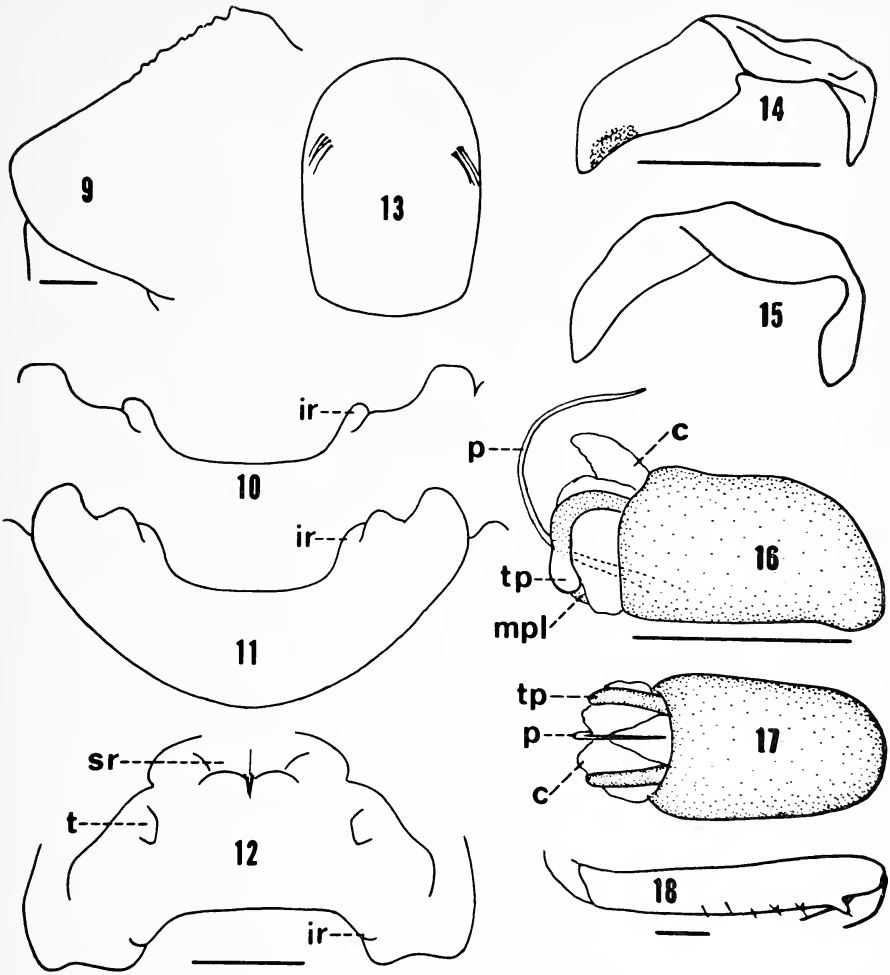


FIGS. 1 and 2. *E. tristigmus*. Fig. 1. Theca and related structures, right lateral aspect; penisfilum (p), thecal process (tp). Fig. 2. Right paramere, lateral aspect.

FIGS. 3 to 6. Spermatheca, distal portion. Fig. 3. *E. tristigmus*. Fig. 4. *L. armipes*; distal flange (df), proximal flange (pf), spermathecal bulb (sb), spermathecal pump (sp). Fig. 5. *E. anticus*. Fig. 6. *L. bilobus*.

FIGS. 7 and 8. *E. anticus*. Fig. 7. Theca and related structures, right lateral aspect; penisfilum (p), thecal process (tp). Fig. 8. Right paramere, lateral aspect.

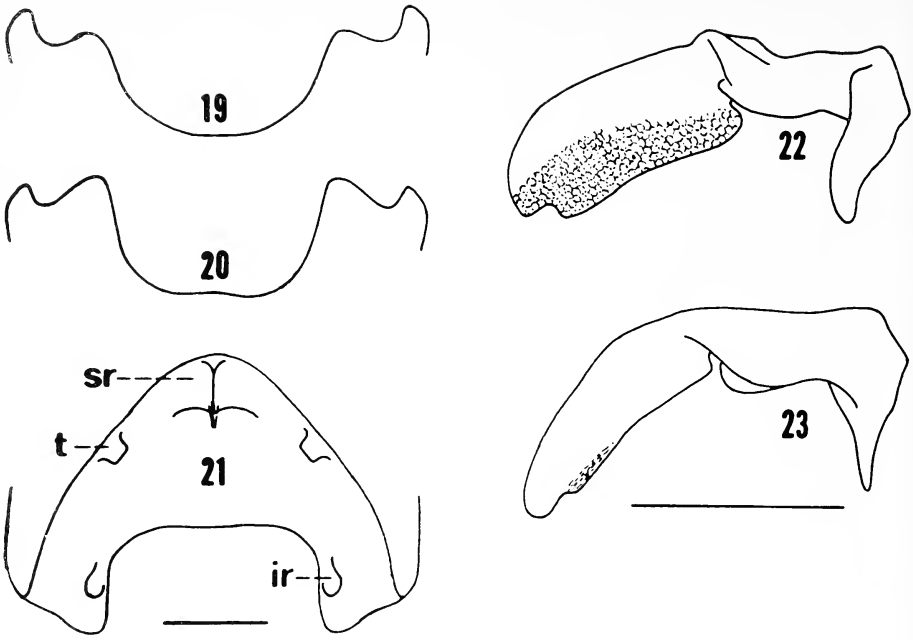
Dimensional lines equal 0.5 mm.



Figs. 9 to 18. *L. armipes*. Fig. 9. Pronotum. Fig. 10. Posterior margin of pygophore, caudal view; inferior ridge (ir). Fig. 11. Pygophore, ventral view with anterior and posterior margins on same focal plane; inferior ridge (ir). Fig. 12. Genital cup, with proctiger and parameres removed; inferior ridge (ir), superior ridge (sr), tubercle (t). Fig. 13. Proctiger. Fig. 14. Right paramere, anterolateral aspect. Fig. 15. Same, rotated 90° toward observer. Fig. 16. Theca and related structures, right lateral aspect; conjunctiva (c), median penal lobe (mpl), penisfilum (p), thecal process (tp). Fig. 17. Same, dorsal aspect. Fig. 18. Left prothoracic femur, anterior face. Dimensional lines equal 0.5 mm.

posterolateral from near apex of scutellum, terminating in acute angle with costal margin above fourth visible segment of abdomen.

Evaporative area on each side extending about halfway from inner margin of ostiole toward lateral margin of metapleuron; ostiolar auricle covering about half of distance along anterior metapleural margin from inner margin of ostiole to lateral limit of elevated



FIGS. 19 to 23. **L. boliviensis** n. sp. Fig. 19. Posterior margin of pygophore, caudal view. Fig. 20. Posterior margin of pygophore, ventral view. Fig. 21. Genital cup; inferior ridge (ir), superior ridge (sr), tubercle (t). Fig. 22. Right paramere, anterolateral aspect. Fig. 23. Same, rotated 90° toward observer. Dimensional lines equal 0.5 mm.

evaporative area. Anterior and middle femora of males armed on inferior face with one or more stout tubercles, these little to much reduced in females; tibiae sulcate. Abdomen without median tubercle or spine.

Superior ridge of pygophore acutely produced, sloping ventrolaterad on each side from median longitudinal ridge, setose at apex (Figs. 12, 21, 28, and 37). Inferior ridge reduced to tumescence located along posterior margin of pygophore on each side of emargination. Parameres bent inversely, with dorsal edge curving ventrad (Figs. 14, 22, 33, and 41). Theca without lobes; thecal processes emerging dorsally (Figs. 17, 32, and 40). Conjunctiva with median lobe above median penal lobes. Penisfilum emerging mesally between median penal lobes.

Spermathecal bulb digitiform; spermathecal pump tightly convoluted at proximal flange (Figs. 4 and 6).

Type species: *Euschistus bilobus* Stål, 1872.

Relationship: The genital morphology of both sexes demonstrates that *Ladeaschistus* species form a homogeneous group whose phylogenetic relationship is much closer to a group of South American *Euschistus* of which *E. anticus* is representative than it is to the type species *E. tristigmus*. In *Ladeaschistus* the spermathecal bulb is digitiform, and the spermathecal pump convolutes tightly at the proximal flange (Figs. 4 and 6). In *E. anticus* the spermathecal bulb is also digitiform, but the spermathecal pump is only sinuous (Fig. 5). Contrarily, *E. tristigmus* has a spherical spermathecal bulb and a cylindrical spermathecal pump (Fig. 3). The seminal duct in *Ladeaschistus* and in *E. anticus* proceeds

directly in a median, ventral position from the ejaculatory reservoir to emerge between the median penal lobes as a short or relatively short penisfilum lying on the vertical median plane (Figs. 7, 16–17, 31–32, 39–40), in stark contrast to the convoluted seminal duct and long, coiled penisfilum in *E. tristigmus* (Fig. 1). *Ladeaschistus* also differs from the species group represented by *E. anticus* in the structure of the genital cup and in the dorsal rather than lateral position of the thecal processes.

The only other pentatomines in the Western Hemisphere with well-developed preapical femoral tubercles are the two species of *Sibaria*. These are morphologically close to but distinct from *Ladeaschistus*. The two genera are readily separable by the short rostrum, which reaches the mesocoxae, and the vertically rounded anterolateral margins of the pronotum in *Sibaria*.

Ladeaschistus armipes (Stål), 1972

Euschistus armipes Stål, 1872, Svenska. Vet-Ak. Handl. 10 no. 4 p. 25; Berg, 1891, An. Soc. Cient. Arg. XXXII p. 277.

Dorsum light castaneous, narrowly ivory bordered on anterolateral margin of pronotum and basal half of costal margin of coria; rather dense punctation dark castaneous, often becoming fuscous on head, in submarginal band along anterolateral margins of pronotum, and exocoria. Brownish-yellow to rufous beneath; punctation concolorous with or a little darker than sclerites. Length of body 10.2 to 11.5 mm without membranes.

Head 2.1 to 2.3 mm wide across eyes; lateral margins tapering sinuously from eyes to apex, nowhere parallel. Antennae pale castaneous; length of segments 0.6 to 0.8; 1.0 to 1.2; 1.3 to 2.1; 1.2 to 2.0; 1.2 to 2.1 mm, last three segments exceptionally variable in length. Distal end of first rostral segment surpassing posterior limit of bucculae.

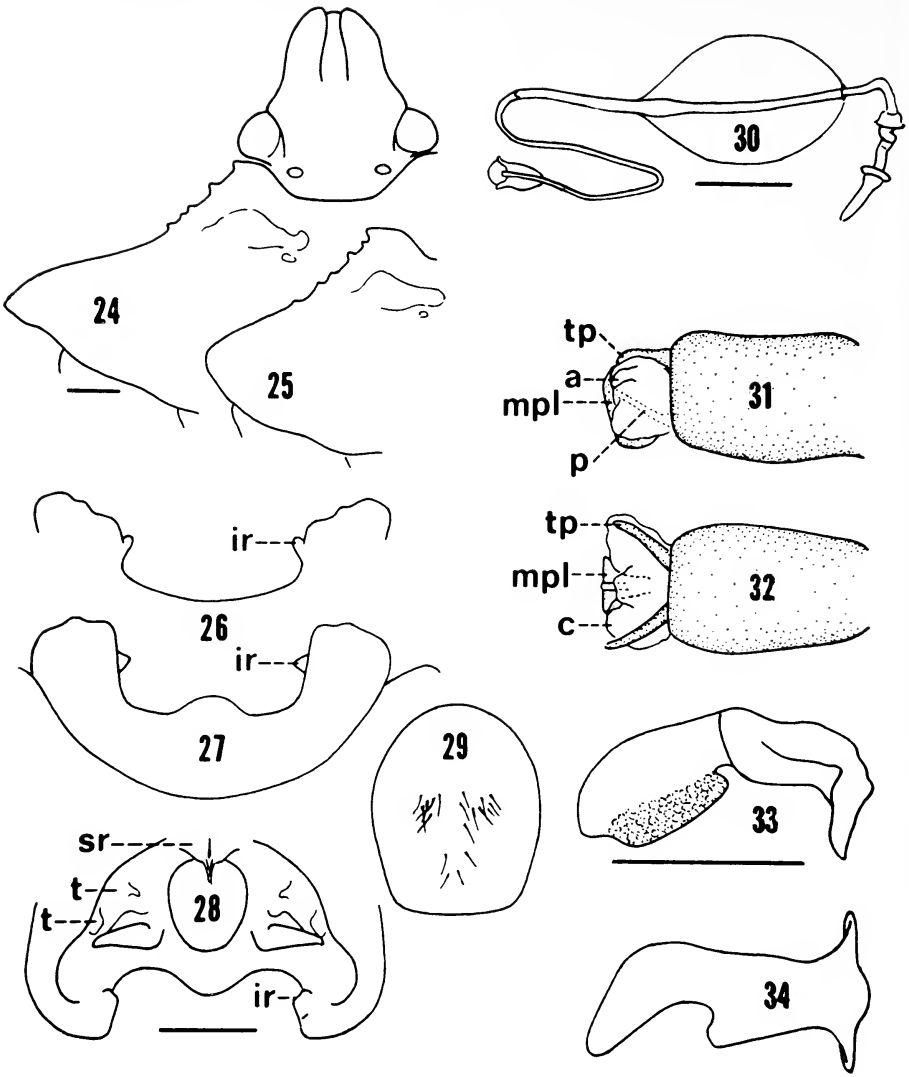
Pronotum 2.4 to 2.7 mm long at meson; anterolateral margins straight, apical half or more denticulate (Fig. 9); denticles and narrow border ivory; humeral angles scarcely produced, obtusely angular; subcalloused spot near posteromesal limit of each cicatrice sometimes pale. Scutellum 4.0 to 4.4 mm across base; weak fovea in basal angles composed of a few confluent shallow punctures; apex punctate, not differentially colored. Membrane of hemelytra brown, fading distally; veins simple or branched. Connexiva narrowly exposed; very margin, intersegmental sutures and subquadrate marginal spot in middle of each segment yellowish.

Punctation unevenly distributed on ventral surfaces of head and thorax, leaving irregular areas impunctate, subcalloused; abdominal venter shallowly punctate. Evaporative areas unicolorous. Legs pale castaneous. Prothoracic and mesothoracic femora armed on inferior face with pair of preapical tubercles; anterior tubercle of pair strong, larger than posterior tubercle; this pair usually preceded by one to four lesser tubercles, paired or not (Fig. 18). One or pair of small preapical tubercles usually present on femora of metathorax. Femoral tubercles generally smaller among females than corresponding tubercles among males. Intersegmental membranes and pseudosutures of abdomen dark castaneous; spiracles somewhat darker than sternites; incisures immaculate at lateral margins.

Broad emargination in posterior margin of pygophore descending in two steps, appearing yet more complex because of remnant of inferior ridge on each side (Figs. 10 to 12). Lateral walls of genital cup armed with large quadrate denticle. Transverse ridge near base of proctiger bearing tuft of setae on each side (Fig. 13). Reticulated area along ventral margin near apex of parameres small (Fig. 14). Thecal processes compressed, cultrate, with hyaline apical enlargement (Fig. 16).

Type. Female, in Naturhistoriska Riksmuseum, Stockholm. Not examined.

Distribution. Brazil: Bahia; Minas Gerais (type locality). Argentina: Misiones. Paraguay.



FIGS. 24 to 34. *L. bilobus*. Fig. 24. Head and pronotum. Fig. 25. Variation in humeral angle. Fig. 26. Posterior margin of pygophore, caudal view; inferior ridge (ir). Fig. 27. Pygophore, ventral view with anterior and posterior margins on same focal plane; inferior ridge (ir). Fig. 28. Genital cup; inferior ridge (ir), superior ridge (sr), tubercle (t). Fig. 29. Proctiger. Fig. 30. Spermatheca. Fig. 31. Theca and related structures, right lateral aspect; conjunctival appendage (a), median penal lobe (mpl), penisfilum (p), thecal process (tp). Fig. 32. Same, dorsal aspect; conjunctiva (c). Fig. 33. Right paramere, anterolateral aspect. Fig. 34. Same, rotated 90° toward observer. Dimensional lines equal 0.5 mm.

Ladeaschistus boliviensis, n. sp.

Size, color, and form of *L. armipes*, differing in dorsal markings, in form of pygophore, and in form and reticulation of parameres.

Numerous small pale subcalloused spots of irregular form scattered over dorsum except on head.

Lateral lobes of pygophore strongly produced at inner angle on each side, resulting in much deeper median emargination than in *L. armipes* (Figs. 19 to 21); inferior ridge visible only from dorsal view; lateral margins of genital cup smoothly arcuate, undivided by vertical ridge as in *L. armipes*. Apex of parameres notched; reticulation extensive (Fig. 22).

HOLOTYPE. Male, labeled Bolivia, Santa Cruz, Prov. Chiquitos, Robore, 300 M. November 1959. Deposited in American Museum of Natural History.

PARATYPE. Female, same data (author's collection).

COMMENT. Although this insect agrees with *L. armipes* in most respects, the differences seem too numerous and of too great a magnitude to be of subspecific value.

Ladeaschistus bilobus (Stål), 1872

Euschistus bilobus Stål, 1872, Svenska Vet.-Ak. Handl. 10 no. 4 p. 25

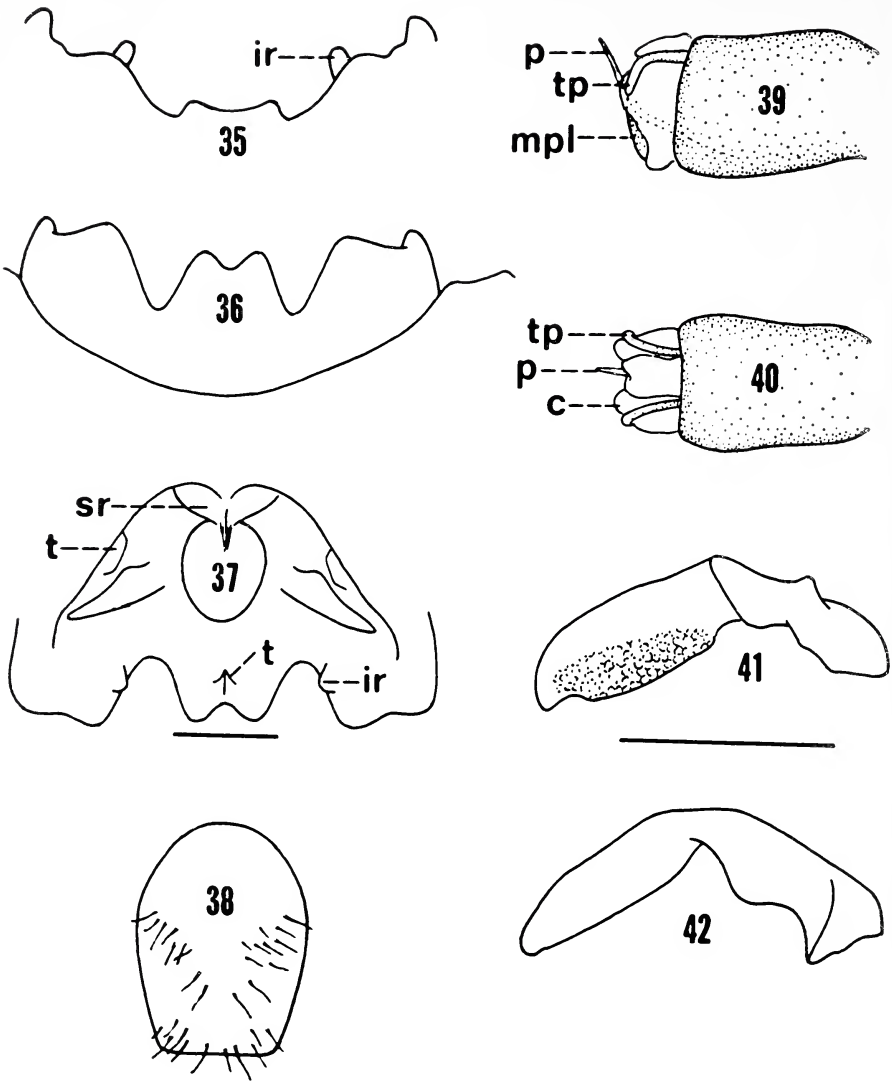
Dorsum medium brown to fuscous with head, anterior portion of pronotum and usually humeri darkest in lighter colored specimens; hemelytra sometimes faintly marked with large dark reticulations; calloused spot near posteromesal border of each cicatrice and small lacuna at distal end of radial vein in hemelytra usually pale; few to many small irregular subcalloused spots scattered on pronotum and scutellum. Ventral surfaces yellowish white, concolorously punctate. Length of body 8.2 to 9.3 mm without membranes.

Head 1.7 to 1.9 mm wide across eyes; disk nearly flat; lateral margins weakly sinuous, tapering from eyes to apex of head (Fig. 24). Basal segment of antenna brownish-yellow, following two segments mottled brown to fuscous, last two segments brown to fuscous except basal fourth to third of each pale yellow; length of segments 0.5 to 0.6; 0.8 to 1.0; 0.9 to 1.1; 1.3 to 1.5; 1.5 to 1.6 mm.

Pronotum 1.9 to 2.0 mm long at meson; anterolateral margins concave, anterior half denticulate; denticles small, mostly subacute and discreet, usually pale in part or whole; humeri obtusely angular to subacute (Figs. 24–25). Scutellum 3.0 to 3.5 mm wide at base, with small foveate cluster of black punctures in basal angles; apex punctate, not differentially colored. Membrane of hemelytra fumose; veins simple or furcate. Connexiva narrowly exposed, black, with narrow arcuate yellowish marginal spot in middle of each segment.

Pleural surfaces of thorax marked by four black dots on each side, one at base of each subcoxae and one near anterior margin of mesopleuron midway between imaginary line drawn through subcoxal dots and lateral margin of metapleuron. Rather small fuscous dots scattered on femora and tibiae; anterior and middle femora of both sexes armed on inferior face with pair of moderate-sized preapical tubercles, these usually preceded by one to four lesser tubercles, most often by a pair; posterior femora armed with one to three small preapical tubercles; anterior tubercle of pair generally a little stouter than posterior tubercle. Spiracles concolorous with sternites. Abdominal margins narrowly bordered in black at basal angles of each segment.

Emargination of pygophore deep, broad from caudal view (Fig. 26) with mesal production of moderate size evident from ventral and dorsal views (Figs. 27–28). Two subquadrate tubercles protruding from each lateral wall of genital cup, one near apex of parameres al-



FIGS. 35 to 42. *L. trilobus*. Fig. 35. Posterior margin of pygophore, caudal view; inferior ridge (ir). Fig. 36. Pygophore, ventral view with anterior and posterior margins on same focal plane. Fig. 37. Genital cup; inferior ridge (ir), superior ridge (sr), tubercle (t). Fig. 38. Proctiger. Fig. 39. Theca and related structures, right lateral aspect; median penal lobe (mpl), penisfilum (p), thecal process (tp). Fig. 40. Same, dorsal aspect; conjunctiva (c). Fig. 41. Right paramere, anterolateral aspect. Fig. 42. Same, rotated 90° toward observer. Dimensional lines equal 0.5 mm.

most horizontal, other entad and nearly vertical. Pair of ridges on proctiger, one ridge on each side about midway between base and apex, bearing numerous setae; additional setae scattered along mesal region between ridges and apex of proctiger (Fig. 29). Reticulated area on anterolateral surface of parameres extensive (Fig. 33). Thecal processes digitiform, not noticeably compressed (Figs. 31–32). Conjunctiva with lobe above median penal lobes and small appendage on each lateral conjunctival lobe.

TYPE. Male, in Naturhistoriska Riksmuseum, Stockholm. Not seen.

DISTRIBUTION. Argentina: Misiones. Bolivia: Huachi. Brazil: Minas Gerais (type locality); Mato Grosso; Parana; Santa Catarina. Paraguay: Horqueta. Peru: Quillabamba. Uruguay.

COMMENT. In recently collected and well-curated specimens of *L. bilobus*, the last two antennal segments without exception are brown or fuscous beyond the pale basal ring of each segment, but in some old specimens of this species, recognizable by the unique male genitalia, the antennae are entirely light-colored, just as they are in *L. trilobus*. These specimens are probably faded, although they may represent a natural variation, and presumably include some females. Such females, and those lacking the two distal segments of the antennae, present a problem in identification because coloration of the antennae seems to be the only means of separating the females of *L. bilobus* and *L. trilobus*.

Ladeaschistus trilobus (STÅL), 1872

Euschistus trilobus Stål, 1872, Svenska Vet.-Ak. Handl. 10 no. 4 p. 24

Size, form, and color of *L. bilobus* except:

Antennae almost uniformly brownish-yellow with basal third of last segment sometimes a little paler; dorsum usually lighter in color with humeri suffused with rufous.

Posterior margin of pygophore trilobed from both ventral and dorsal views (Figs. 36–37); large triangular tubercle located on dorsal surface of middle lobe cephalad of shallow mesal emargination; tumescent remnant of inferior ridge on mesal margin of lateral lobes especially prominent from caudal view (Fig. 35); tubercle on lateral walls of genital cup large, trapezoidal, nearly horizontal.

TYPE. From the syntype series the following specimen is designated as the LECTOTYPE: Male, labeled (a) Minas Geraes (b) Drews (c) Type (d) ♂ (e) Allotypus. The two remaining syntypes, both females, are PARALECTOTYPES labeled as above except one specimen with (d) ♀ (f) typus, and the other with (d) Paratypus.

The labeling suggests a prior designation of lectotype and paralectotype, but this is not the case.

Distribution. Brazil: Bahia; Mato Grosso; Minas Gerais (type locality).

KEY TO SPECIES

1. Anterolateral margins of pronotum straight, narrowly ivory bordered (Fig. 9); posterior margin of pygophore without median lobe (Figs. 10 to 12, 19 to 21) 3

1′ Anterolateral margins of pronotum concave, brown to fuscous, only part or all of most denticles pale (Figs. 24 and 25): posterior margin of pygophore with median lobe (Figs. 27, 28, 36, and 37) 2

2. Antennae almost uniformly brownish yellow; median lobe of pygophore emarginate, nearly as long as lateral lobes, bearing stout acute tubercle on dorsal surface (Figs. 36 and 37) ..... *L. trilobus* (Stål)

2′ Last two segments of antennae normally brown to black beyond pale basal ring; median lobe of pygophore entire, not nearly as long as lateral lobes, without tubercle on dorsal surface (Figs. 27 and 28) ..... *L. bilobus* (Stål)

3. Numerous small pale subcalloused spots of irregular form scattered on dorsum excepting head ..... **L. boliviensis** n. sp.
3′ Pale marks on dorsum confined to spot behind each cicatrice and spot on disk of each corium ..... *L. armipes* (Stål)

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A Review of *Hymenarcys* (Hemiptera: Pentatomidae)

L. H. Rolston
Department of Entomology,
Louisiana State University, Baton Rouge, Louisiana 70803

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Abstract: *Hymenarcys aequalis* (Say) seems to have a phylogenetic origin different from that of *H. nervosa* (Say), *H. reticulata* Stål and *H. crassa* Uhler. A diagnosis of *Hymenarcys* Amyot and Serville and a key to the four included species is given. Parts of the genitalia of both sexes of these species are figured.

INTRODUCTION

This review was undertaken primarily to examine the cohesiveness of the four North American species that comprise the genus *Hymenarcys* and, secondarily, since the only key to all the species (Torre-Bueno) is unsatisfactory, to identify salient characters useful in separating the species. The four species are *H. nervosa* (Say) 1832, the type species, *H. aequalis* (Say) 1832, *H. reticulata* Stål 1872, and *H. crassa* Uhler 1897. The genus is diagnosed, the species are keyed, and parts of the genitalia of both sexes are figured.

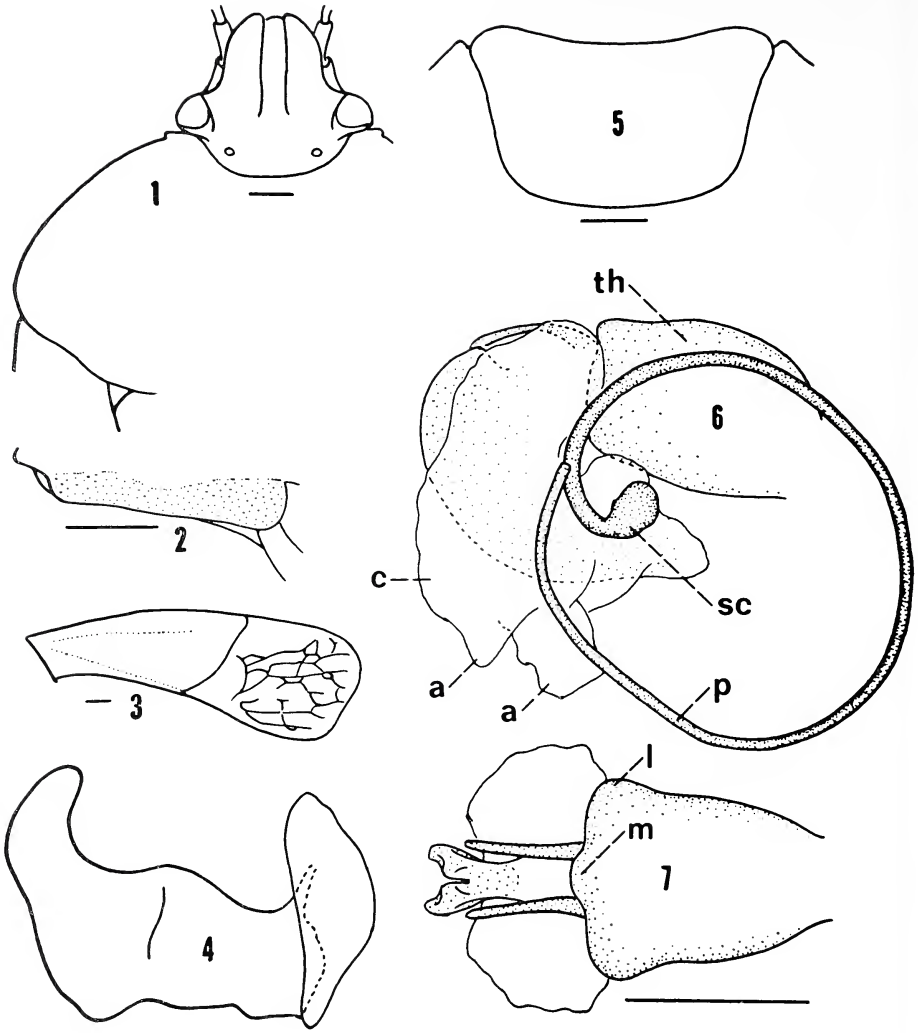
Hymenarcys AMYOT AND SERVILLE, 1843

Amyot and Serville, 1843, Hem.: 124; Stål, 1867, Ofv. Svenska Vet.-Ak. Forh. 24(7): 526; Stål, 1872, Svenska Vet.-Ak. Handl. 10(4): 30; Kirkaldy, 1909, Cat. Hem. 1: 72; Blatchley, 1926, Het.: 122; Torre-Bueno 1939 Entomol. Am. 19: 211, 224; Froeschner, 1941, Am. Mid. Nat. 26: 128, 130.

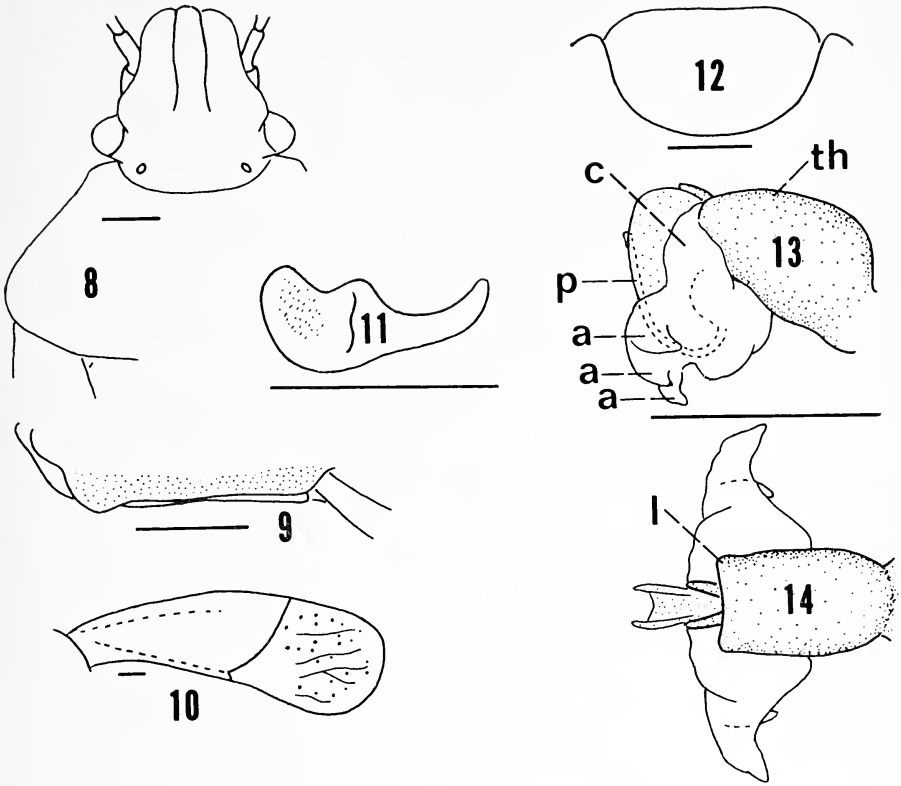
DIAGNOSIS. Juga and tylus subequal in length, obtuse apically. Distal end of first antennal segment approaching apex of head; four remaining antennal segments each longer than first. Posterior limit of bucculae at base of head truncate, abruptly sloping or briefly prolonged caudad as lobe, extending to or slightly past apex of first rostral segment (Figs. 2, 9, 16, and 23). Anterolateral margins of pronotum carinate, entire, at most slightly irregular, neither vertically rugose nor denticulate; humeri not or weakly produced, broadly rounded (Figs. 1, 8, 15, and 22). Basal width and length of scutellum subequal, apex broadly rounded, frena extending 0.5 to 0.6 distance from base toward apex. Distal margin of coria extending obliquely posterolaterad from scutellum as convex curve, the costal angle narrowly rounded or right angular, slightly surpassing apex of scutellum, terminating above fourth visible connexival segment (Figs. 3, 10, 17, and 24). Ostiole auriculate, neither drawn out into sulcus nor accompanied by elongate ruga. Femora unarmed, tibiae sulcate. Abdominal venter without median tubercle or spine.

KEY TO SPECIES

1 Membrane of hemelytra with numerous small dark spots; veins nearly obscure, few, simple or bifurcate (Fig. 10); bucculae sloping abruptly at base of head (Fig. 9); length of body about 6.0 to 8.5 mm. ..... *H. aequalis* (Say)



FIGS. 1 to 7. *H. nervosa.* Fig. 1. Head and pronotum. Fig. 2. Buccula (stippled) left lateral aspect. Fig. 3. Right hemelytron. Fig. 4. Right paramere, lateral aspect. Fig. 5. Pygophore, ventrocaudal aspect with anterior and posterior margins on same focal plane. Fig. 6. Theca and related structures, right lateral aspect; conjunctival appendages (a); conjunctiva (c); penisfilum (p); sclerotized cap (sc); theca (th). Fig. 7. Theca and related structures, dorsal aspect; lateral lobes (l); median lobe (m). Dimensional lines equal 0.5 mm.



Figs. 8 to 14. *H. aequalis*. Fig. 8. Head and pronotum. Fig. 9. Buccula (stippled), left lateral aspect. Fig. 10. Right hemelytron. Fig. 11. Right paramere, lateral aspect. Fig. 12. Pygophore, ventrocaudal aspect with anterior and posterior margins on same focal plane. Fig. 13. Theca and related structures, right lateral aspect; conjunctiva (c); penisfilum (p); theca (th). Fig. 14. Theca and related structures, dorsal aspect; lateral lobes (l). Dimensional lines equal 0.5 mm.

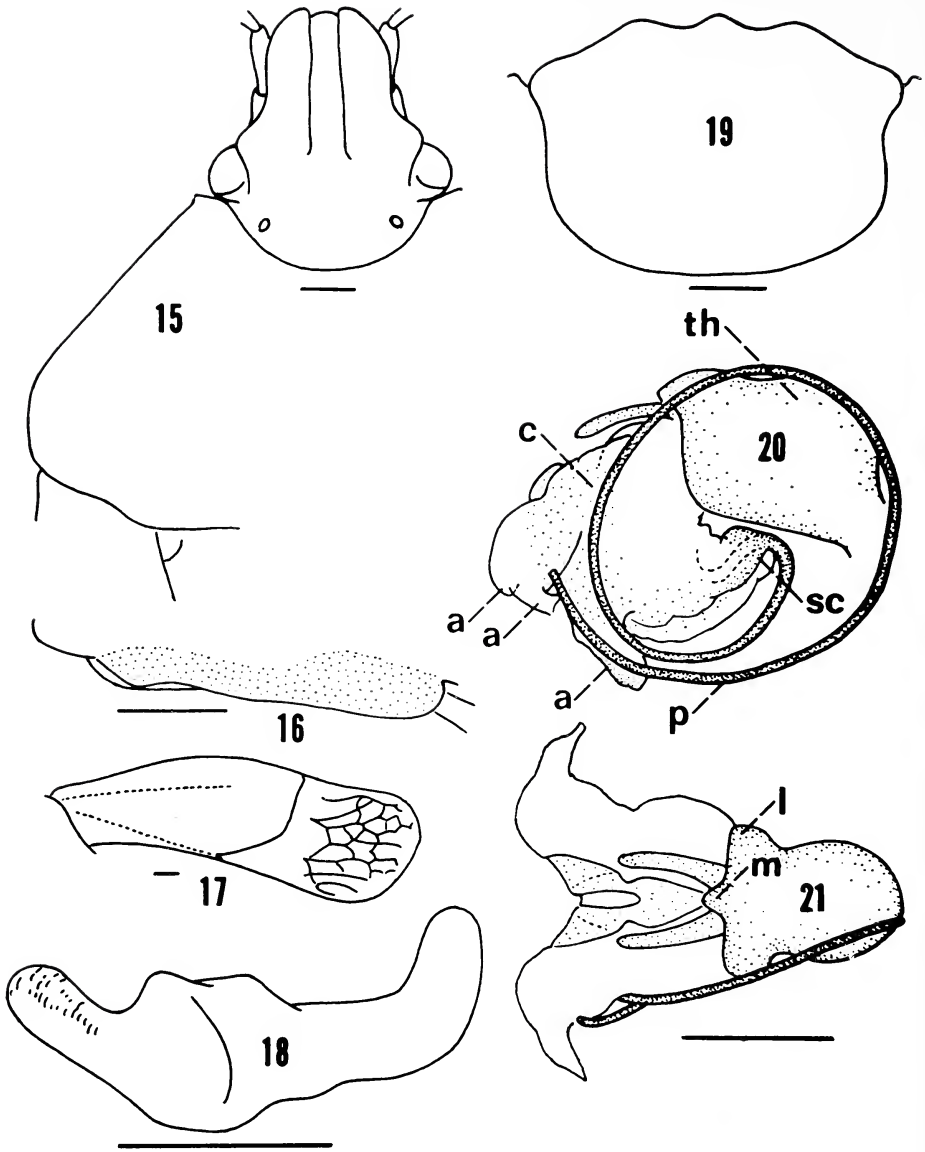
1′ Membrane of hemelytra without spots, brown except along veins or unmarked; venation reticulate (Figs. 3, 17, and 24); bucculae roundly truncate at base of head (Figs. 2, 16, and 23); length of body about 9.0 to 11.5 mm. 2

2(1) Anterolateral margins of pronotum convexly arcuate from dorsal view (Fig. 1); apex of scutellum narrowly pale margined ..... *H. nervosa* (Say)

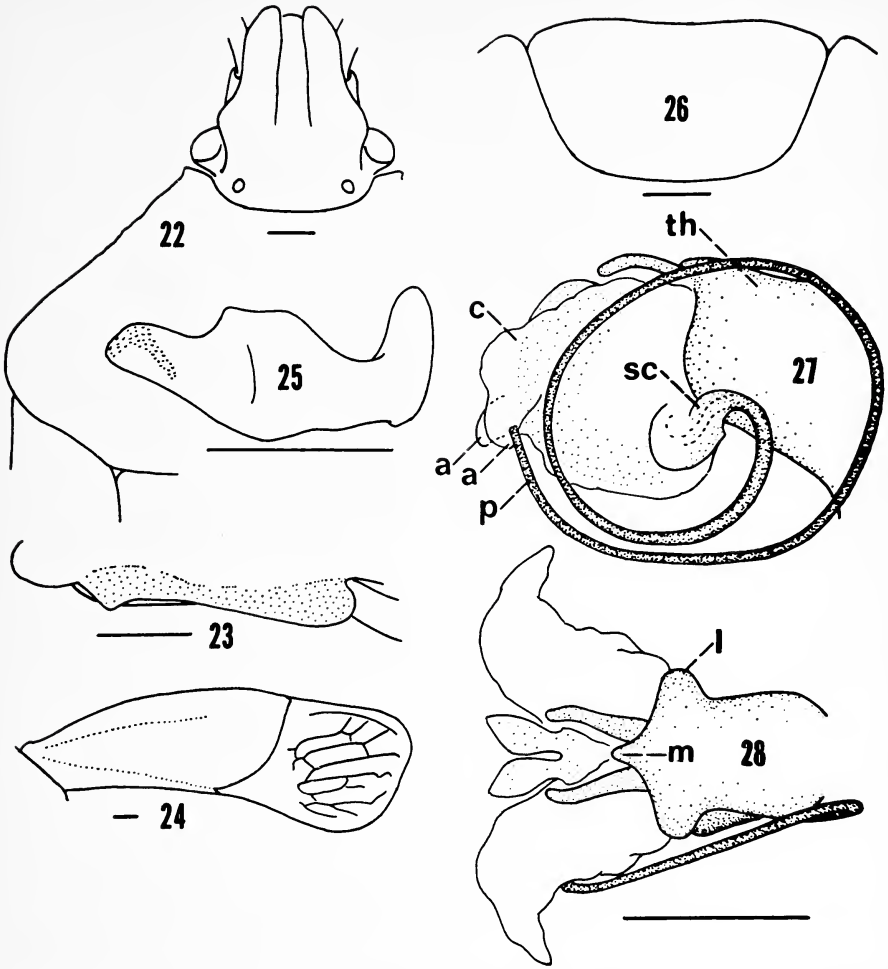
2′ Anterolateral margins of pronotum nearly straight (Figs. 15 and 22); margin of scutellum at apex concolorous with disk 3

3(2) Middle half of posterior margin of pygophore gently concave from ventrocaudal view (Fig. 26); carinate margin of pronotum narrowly subcalloused, impunctate ..... *H. crassa* Uhler

3′ Middle half of posterior margin of pygophore sinuate (Fig. 19); carinate margin of pronotum not at all calloused, punctate ..... *H. reticulata* Stål



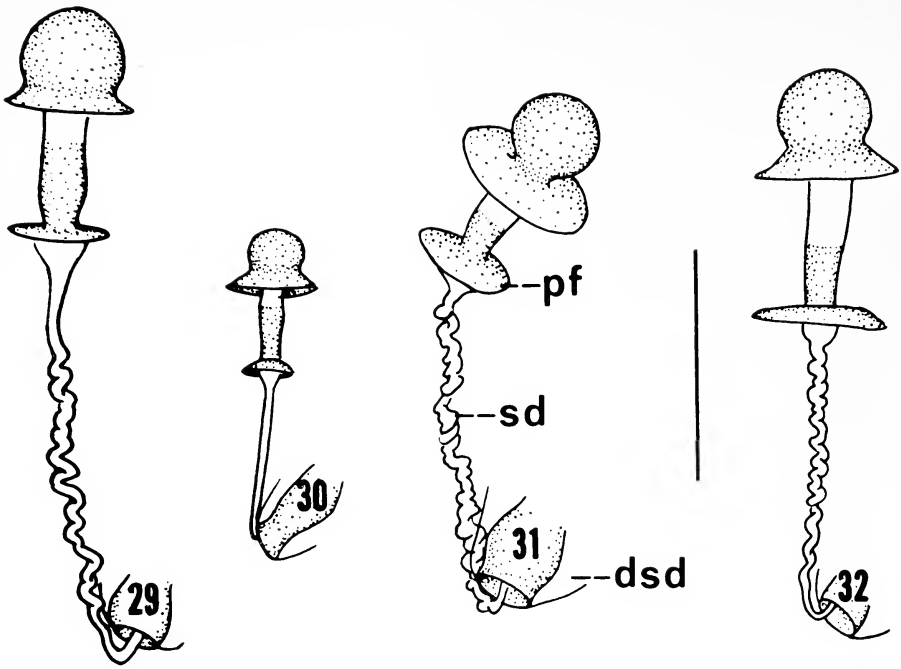
FIGS. 15 to 21. *H. reticulata*. Fig. 15. Head and pronotum. Fig. 16. Buccula (stippled) left lateral aspect. Fig. 17. Right hemelytron. Fig. 18. Right paramere, lateral aspect. Fig. 19. Pygophore, ventrocaudal aspect with anterior and posterior margins on same focal plane. Fig. 20. Theca and related structures, right lateral aspects; conjunctival appendages (a); conjunctiva (c); penisfilum (p); sclerotized cap (sc); theca (th). Fig. 21. Theca and related structures, dorsal aspect; lateral lobes (l); medial lobe (m). Dimensional lines equal 0.5 mm.



Figs. 22 to 28. *H. crassa.* Fig. 22. Head and pronotum. Fig. 23. Buccula (stippled), left lateral aspect. Fig. 24. Right hemelytron. Fig. 25. Right paramere, lateral aspect. Fig. 26. Pygophore, ventrocaudal aspect with anterior and posterior margins on same focal plane. Fig. 27. Theca and related structures, right lateral aspect; conjunctival appendages (a); conjunctiva (c); penisfilum (p); sclerotized cap (sc); theca (th). Fig. 28. Theca and related structures, dorsal aspect; lateral lobes (l); median lobe (m). Dimensional lines equal 0.5 mm.

INTRAGENERIC RELATIONSHIPS

Three species of the genus, *H. nervosa, H. reticulata,* and *H. crassa,* are similar in appearance, in the construction of the male genitalia, and in the form of the spermatheca. Among these species the theca has a prominent median lobe and a distinct lateral lobe on each side (Figs. 7, 21, and 28), and the coiled



FIGS. 29 to 32. Distal portion of spermatheca; sphermathecal duct (sd), dilation of spermathecal duct (dsd), proximal flange (pf). Fig. 29. *H. nervosa.* Fig. 30. *H. aequalis.* Fig. 31. *H. reticulata.* Fig. 32. *H. crassa.*

penisfilum has a sclerotized cap at the base (Figs. 6, 20, and 27). The spermathecal duct between the dilation and proximal flange convolutes tightly in these species (Figs. 29, 31, and 32) and in this respect is unlike that of other Pentatomini species from North America that have been studied (McDonald).

H. aequalis is smaller than its congeners and further differs from them in its weak, simple venation and spotting of the hemelytran membrane. The male genitalia and spermatheca of this species also contrast with those of its congeners. The theca lacks a median lobe, and each side is produced posteriorly but only weakly or not at all laterally as a lobe (Fig. 14). The penisfilum is relatively short, lies almost entirely on the median vertical plane, and lacks a sclerotized cap (Fig. 13). The spermathecal duct between the dilation and proximal flange is a simple tube and innocent of convolutions (Fig. 30).

The evidence seems overwhelming that *H. nervosa, H. reticulata,* and *H. crassa* are closely related species and that *H. aequalis* is phylogenetically distant. Erection of a monotypic genus or subgenus for *H. aequalis* is justifiable, but the four species presently assigned to *Hymenarcys* form a reasonably homogeneous classificatory group and no practical benefit would result from a division of the genus. Oetting and Yonke have summarized the literature

concerning the biology of *H. nervosa* and *H. aequalis*, added field observations on habitats and hosts, and described the immature stages. The two species have similar seasonal histories and have in common some grasses as hosts. Nothing is known of the biology of either *H. crassa* or *H. reticulata*.

DISTRIBUTION

Numerous scattered records of *H. nervosa* indicate a range from the Dakotas through Quebec into New England and southward into North Carolina and Texas. Except for the addition of Saskatchewan, records of *H. aequalis* cover the same territory. However, a male of this species, which I believe to be labeled correctly, was taken by H. R. Burke and J. Hafernik at 4200′ elevation in Pueblo, Mexico. Specimens of *H. crassa* that were examined came from as far east as Burnet Co., Texas, and westward into Piña Co., Arizona. *H. reticulata* is also reported from Arizona and this is probably correct since specimens were seen from Chihuahua as well as Michoacan and Oaxaca, Mexico.

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BOOK NEWS

The Horse Flies of Europe (*Diptera, Tabanidae*). Milan Chvala, Leif Lyneborg & Josef Moucha. Published by Entomological Society of Copenhagen. Copenhagen, 1972. 500 pages, 164 figures, 8 plates (5 colored). In North America available from Entomological Reprint Specialists, P.O. Box 77971, Dockweiler Station, Los Angeles, California 90007. $23.50.

When three of the leading specialists of Palaearctic Tabanidae collaborate to produce a book on the European species, a work of some excellence is expected. The authors have not failed us, and we sincerely regret that the recent tragic death of one of them, Josef Moucha, removed him from a field where he excelled.

The Tabanidae have long been a favorite of taxonomists, and since they are of considerable economic importance as well, "The Horse Flies of Europe" will have a readership extending beyond that of the systematist. It will appeal to workers in the fields of public health and recreation as well as those interested in veterinary and medical science.

The work essentially is taxonomic but chapters cover geographical distribution, biology, collecting and rearing techniques, and medical and economic importance. A useful summary is given of disease organisms for which Tabanidae act as vectors; diseases omitted from this list include anaplasmosis, hog cholera and elaeophorosis.

Fourteen genera are covered and the generic concepts and species included are handled as they would be by a worker in North America dealing with Nearctic species, allowing of course for legitimate differences of opinion on the status of certain species and the utility of some subspecific names. The one exception is the species described by Kröber as *Corizoneura hispanica* which the authors place in *Stonemyia*. It is unlikely that any worker in North America would place it in this genus. Although *Glaucops* is usually placed as a subgenus of *Tabanus*, its treatment as a full genus is acceptable and possibly preferable. When information on ecology and biology is available, it is included under each species, a desirable addition to any taxonomic treatise.

Except in *Pangonius* and *Chrysops*, subgenera are placed in synonymy and related forms are treated as species groups. This may be subject to some criticism but I regard it as highly desirable. In general, variants, whether described as varieties or subspecies, are placed in synonymy although they may be mentioned in the text. Some subspecies, with a reasonably distinct geographic range, are recognized.

For the average reader, this volume probably has as much information as he needs. The specialist is likely to wish that some additional information were included. I would like to know where the type of each species is located and its condition and the type species of genera placed in synonymy would be useful. Distributional maps would have added much, but this may have required a work of two volumes.

Some students of the Palaearctic tabanid fauna may question some of the synonymy, including some older names which may be *nomina oblita*. The male of *Hybomitra polaris*, given as "unknown," was described by Kauri in 1954. The index is reasonably complete but *Haematopota variegata* Fabricius (1805) is not found under that name and it takes much page turning to find it transferred to *Silvius*, while the species passing under that name for over 160 years is finally discovered under *Haematopota pandazisi* (Kröber). *Hybomitra montana* is listed as Holarctic on pages 31 and 169 but on page 228 it becomes only "very closely related" to the Nearctic *H. frontalis*; considering the variability of both forms, this hedge may be justified.

The drawings in the text are excellent as are the colored plates of adults and photographs of wing patterns of *Chrysops* and *Haematopota*. A very useful book.

L. L. PECHUMAN
Department of Entomology, Cornell University

Scabies. Kenneth Mellanby. E. W. Classey Ltd., Hampton, Middlesex, G.B. 1972. 81 p. $3.50.

This readable little volume is the second edition of this text; the first was issued in 1943 as part of the Oxford War Manual. In a very clear style it describes in ten chapters the parasitological and medical aspects of scabies, "the itch."

Chapter I, The Anatomy and Life History of the Itch Mite, identifies and describes the Sarcoptes scabies var. hominis parasite and includes a very well written description of a technique of isolation of it from a skin burrow in order to provide the diagnosis. Chapter II, The Parasitology of Human Scabies, demonstrates the role of the ovigerous female in the pathogenesis of human scabies and the sarcoptic mange in animals. Chapter III, The Development of Symptoms, gives a very good description of the clinical manifestations of the disease, and it also emphasizes a less well known fact, that these signs are a result of sensitization and secondary infection following a relatively asymptomatic incubation period of several weeks. The initial asymptomatic burrows are practically impossible to diagnose in a clinical setup. Chapter IV, Secondary Pathological Conditions Induced by Scabies Infection, clearly points out the clinical problem of persisting secondary changes after eradication of the mite via adequate antisarcoptic treatment. Failure to recognize this fact may easily lead to overtreatment with generally irritating antisarcoptic agents, leading to further deterioration. Also, vice-versa, failure to recognize scabies may lead to unsuccessful treatment of secondary eczema or suppurative dermatitis. Chapter V, The Transmission of Scabies, shows that appreciation of this facet may contribute to interruption of the spread of infection with relative ease. The mite will die within 10 minutes at 50°C (120°F), and will not survive longer than 2 days in a drying cupboard (on garments). Also, ordinary processes of laundering are adequate to eradicate the parasite. Chapter VI, The Incidence of Scabies, provides the author's contribution via his interesting hypothesis (and documentation) on the role of sensitization and immunology in the 20 to 25-year cycle of recurrent peak incidence of the disease. From this standpoint the occurrence of World War II during the last epidemic of scabies was coincidental and not causative. This would also explain the current increase of the disease in Great Britain. Chapter VII, The Prevention of Scabies, centers around (a) individual and (b) public health aspects. It is of interest to note that contrary to common thinking the author maintains that washing (hygiene) does not prevent scabies, does not remove burrowed mites, and may even be detrimental: "If the cuticle is filthy it may offer a less favorable harborage to the parasite." Chapter VIII, The Treatment of Scabies, is divided into two parts: (a) The Treatment of Parasitic Infection with sulfur or benzyl benzoate interestingly is as up-to-date in 1973 as it was in 1943. Several other modalities of treatment quoted in the text are today of no more than historic significance. A second part, (b), of this chapter, The Treatment of Secondary Infection, is completely outdated. It should have been either updated or simply omitted. As published in this otherwise authoritative text it may easily convey wrong impressions and mislead an uninformed (i.e., non-M.D.) reader. Chapter IX, Conditions Which May Be Confused with Scabies, enumerates several disorders to be considered in differential diagnosis but lacks the precision and clarity of previous chapters. It may be interesting to quote the author in mentioning pediculosis corporis in differential diagnosis, that is, that "a lousy individual not infrequently has scabies as well," or, regarding pediculosis capitis, "a high proportion of female scabies patients have lousy heads" (page 66). Chapter X describes very briefly (with adequate illustrative drawings), eight other mites of medical and veterinary importance (order Acarina).

The Appendix is of historical interest. It provides recipes to prepare (1) Berlese's fluid (serves to "mount mites and pieces of tissue containing burrows" for microscopic study), and (2) benzyl benzoate emulsion for treatment of the itch.

A three-page index completing this volume is adequate.

This volume provides a multitude of interesting data usually not found in standard medical texts. The timeliness of this second edition is illustrated by the recent increase of scabies in Great Britain and parasitic diseases elsewhere, including New York State (case of tick paralysis on Long Island). Thus, this book will be a valuable addition to university and college libraries, especially medical and veterinary schools, and will be of value to public health officers, school physicians and nurses, military physicians, parasitologists, and veterinarians.

J. P. DUIC, M.D.
240 Garth Road, Scarsdale, New York

An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada. Harrison Morton Tietz. Published by A. C. Allyn for the Allyn Museum of Entomology, iv + 1042 pp., in 2 vols., obtainable only from Entomological Reprint Specialists, Los Angeles, California, 90007. $25.00.

The last catalog of the early stages of North American Lepidoptera was that of Henry Edwards, published in 1889. Although quite complete, it contained only 147 pages. Subsequently Davenport and Dethier (1938) and Dethier (1946) published lists of references to the butterflies. Obviously there has long been a serious need for an up-to-date catalog, especially because of the enormous amount of information published in recent years. This index prepared by Tietz will do much to fill this need. However, it covers the literature only through about 1950, so that the last 22 years have not been indexed. It also omits the microlepidoptera, but even so will prove an invaluable reference to anybody interested in almost any phase of work on the butterflies and macromoths. It is quite complete (although a couple of omissions were found in a casual check). In preparing it the author consulted 226 periodicals and 127 separate works, which are listed. The nomenclature is that of McDunnough's 1938 Checklist; this is now quite outdated in many groups but, as the most recent complete list, gives a definitive standard. The plant nomenclature follows that of Gray's Manual (Fernald, 1950), also somewhat outdated, but at least a consistent point of reference.

The chief section deals with the Lepidoptera covered, arranged alphabetically by species (and with their families cited) and thus placeable by the McDunnough index. The listing is of specific names treated as valid by McDunnough, but all other species-group names listed by McDunnough, including those placed in synonymy, and all infrasubspecific names, are included in this index and cross-referenced to the valid names. There is also a listing by common names, cross-referenced to the scientific names. These do not necessarily correspond to the common names of the "official" list of the Entomological Society of America, but they do correspond with general popular usage.

Taken all together, one can begin with either the scientific or common name of a species and find references to the host plants from which it has been recorded; or can begin with either the scientific name of a plant or a group of plants (e.g., pines) and find references to the macrolepidoptera that have been recorded on it. In both ways this index can and will be of great service, and is certainly a must for all serious workers, as well as for naturalists. It is a pity that it ends just at about the date when a great outburst of life history work began; but doubtless the period after 1952 will eventually be covered in similar fashion.

The author attempts to deal with the two chief troubles that bedevil all workers, namely

misidentifications of plants or animals, or both; and the listing of food plants eaten in captivity but not in nature. But he could hardly do much about these. It may be noted, however, that food plants mentioned merely as wild guesses have been listed without question or any qualification. The user must, therefore, beware.

The typography is a bit difficult to use, and there are quite a few typographical and spelling errors. Nevertheless this is an important book, and one that will be extremely useful for a great many years.

Alexander B. Klots
The American Museum of Natural History

Proceedings of the New York Entomological Society

(Meetings held in Room 129 of the American Museum of Natural History unless otherwise indicated.)

Meeting of March 6, 1973

The meeting was called to order by Dr. Howard Topoff, President, at 8:10 p.m. 12 members and 4 guests were present. The minutes of the meeting of February 20, 1973, were approved as read.

Ms. Katharine Lawson of Hunter College and Ms. Iris Goldfarb of CCNY were elected to Student Membership. Ms. Lawson's interest is in ants, social insects, sensory-perceptual and social development. Ms. Goldfarb's interest is in development of orienting responses in spiders.

Mr. Les Greenberg of City College was proposed for Student Membership, and Mr. Roosevelt Hunt, Jr., was proposed for Active Membership. Mr. Greenberg is interested in social behavior in insects; Mr. Hunt's entomological specialties are Lepidopterans and Hymenopterans.

program. Dr. Karl Maramorosch introduced the speaker Dr. George Saul, Visiting Professor at Boyce Thompson Institute for Plant Research. Dr. Saul's talk on "Non-reciprocal cross incompatibility in the parasitic wasp *Mormoniella*" focused upon mechanisms involved in extranuclear inheritance.

The meeting was adjourned at 9:35 p.m.

Peter Moller, *Sec.*

NON-RECIPROCAL CROSS-INCOMPATIBILITY IN THE PARASITIC WASP MORMONIELLA

Mormoniella vitripennis (Walker) [= *Nasonia vitripennis* (Walker)] is used for studies in genetics, behavior, and host-parasite relations. Males are normally haploid and develop from unfertilized eggs; females develop from fertilized eggs and are normally diploid. About 85 percent of the progeny of mated females are female. Unmated females produce only male offspring.

Of more than 350 mutations which are now maintained in stocks, many affect eye color, and a high percentage of the eye-color mutations are alleles at the complex locus *R*. The *R* locus is composed of at least seven "factors," or series of completely linked genes. Four of the factors contain eye-color genes; the others contain genes affecting female

fertility or male viability. Many *R* locus genes are mutant in two or more factors.

In the early 1950s, the *R* locus mutation $R^{dast277}$ produced many spontaneous mutations when it was heterozygous. Two of these are the *R* locus mutations R^{pe-333} (peach, *pe*) and R^{ti-277} (tinged, *ti*). Both are mutant in two factors, are recessive to their wild-type allele, and change the reddish-brown wild-type eye color to light pink. In 1956, it was found that *ti* females gave no female progeny when crossed to wild-type males, and that crosses of *pe* females to wild-type males gave only about 8 percent female progeny. The reciprocal crosses gave normal frequencies of female progeny, so the cross-incompatibility is termed "non-reciprocal." Normal frequencies of females occur in each stock. With regard to incompatibility, *pe* and *ti* show the same characteristics as wild type when crossed with each other, showing that the incompatibility associated with *pe* differs from that of *ti*. Both types of incompatibility have appeared in stocks of other *R* locus mutants that arose from heterozygous $R^{dast277}$.

The *pe*-type incompatibility is transmitted from stock females to the few daughters that arise from crosses with wild-type males. Repeated backcrosses of such daughters to wild-type males for up to twenty backcross generations indicate that the strength of the incompatibility is influenced by the genome, but that the pattern of maternal transmission remains. Crosses of wild-type females by *pe* or *ti* males, followed by up to twenty generations of backcrossing of female progeny to males from the incompatible stock, yield no evidence of *de novo* incidence of incompatibility. The incompatibility is therefore maternally transmitted through the egg but is not transmitted by sperm. It is influenced by the genome but is not a gene product. It appears to be under extranuclear control.

The incompatibility is infectious and can be transmitted to wild-type females by injection or feeding of solutions prepared from homogenates of *pe* or *ti* females. In *ti* eggs, the incompatibility factor acts by preventing the formation of chromosomes by sperm pronuclei following fertilization of the eggs by wild-type sperm. Only a tangled mass of chromatin is formed, and the eggs develop as gynogenetic haploids. Incompatibility is not characterized by death of eggs or embryos.

Electron microscopy is currently being used in an attempt to find the incompatibility factors and determine their action on sperm pronuclei.

GEORGE B. SAUL 2ND

Meeting of March 20, 1973

The meeting was called to order by Dr. Howard Topoff, President, at 8:30 P.M., in the Fifth Floor Lecture Room. 22 members and 46 guests were present.

The minutes of the meeting of March 6, 1973, were approved as read. In a short public relations speech President Topoff called for new members.

Mr. Les Greenberg of City College was elected to Student Membership. His interest is in social behavior in insects. Mr. Roosevelt Hunt, Jr., was elected to Active Membership. His interest is in Lepidopterans and Hymenopterans. Mr. William D. Sumlin III, of San Bernardino, was proposed for Active Membership. Mr. Sumlin's interests are bionomics and systematics of the adephagan Coleoptera.

PROGRAM. Before introducing the speaker Dr. Roman Vishniac, President Topoff expressed his thanks to Dr. John Cooke for his activities in the New York Entomological Society. Dr. Cooke is leaving the country and is going back to England. The audience thanked Dr. Cooke with enthusiastic applause.

Dr. Vishniac vividly remembered the days when he was President of the New York

Entomological Society, in 1941, and then talked about the "Romance of Entomology." His talk was illustrated by a series of color slides, the superb quality of which was most impressive.

It was announced that on April 3, 1973, our speaker will be Dr. Dominick J. Pirone, of Fordham University and Manhattan College, who will talk about "An insect Collector in Costa Rica."

The meeting was adjourned at 10:00 P.M.

Peter Moller, *Sec.*

Meeting of April 3, 1973

The meeting was called to order by Dr. Howard Topoff, President, at 8:15 P.M. 18 members and 14 guests were present.

The minutes of the meeting of March 20, 1973, were approved with the correction that Dr. Roman Vishniac *joined* the New York Entomological Society in 1941.

Mr. William D. Sumlin III, of San Bernardino, was elected to Active Membership; his interest is in bionomics and systematics of the adephagan Coleoptera. Mr. Bernard H. Marcus, of Batavia, New York, was proposed for Active Membership; his interest is in aquatic insects.

PROGRAM. Father Sullivan introduced the speaker Dr. Dominick J. Pirone, Fordham University and Manhattan College, who talked about his impressions and experiences as "An Insect Collector in Costa Rica."

It was announced that on April 17, 1973, our next speaker will be Dr. Charles L. Remington, Yale University, whose talk will be about "Ultraviolet Reflectants in Mimicry and Sexual Signals."

The meeting was adjourned at 9:40 P.M.

Peter Moller, *Sec.*

Meeting of April 17, 1973

The meeting was called to order by Dr. Howard Topoff, President, at 8:15 P.M., 18 members and 18 guests were present.

The minutes of the meeting of April 3, 1973, were approved as read.

Bernard A. Marcus, Assistant Professor of Biology of Genessee Community College was elected to Active Membership. Oskar Dorfmann, of Steffisburg, Switzerland, was proposed for Active Membership. His interest is primarily in Lepidoptera.

PROGRAM. Dr. Charles Remington of Yale was introduced by Father Sullivan. Dr. Remington gave a most interesting and exciting talk drawn from his investigations of the "Relations of Ultraviolet Reflective Patterns as Mimicry and Sexual Symbols in the Lepidoptera." Showing two slides simultaneously of the same mimicry complexes, one taken by normal human-eye viewing light and one in ultraviolet light, he compared the two as seen by insect eyes and man's.

The next meeting of the Society, on Tuesday, May 1, will present Dr. Norman Lin on the "Evolution of Social Behavior in Insects," Father Sullivan announced.

The meeting was adjourned at 10 P.M.

Joan M. DeWind, *Sec. Pro Tem*

ULTRAVIOLET REFLECTANCE IN MIMICRY AND SEXUAL SIGNALS IN THE LEPIDOPTERA

This talk was dedicated to the late Dr. Frank E. Lutz, long of the American Museum of Natural History, whose pioneering studies of ultraviolet (U.V.) perception in insects were carried out here almost exactly 50 years ago.

Reflectance patterns in the U.V. were investigated in a majority of the lepidopterous mimics of North and South America and Africa. Published work shows that it is likely: 1) that the birds and other vertebrate predators are the primary mimefactors controlling natural selection for aposematic (conspicuous signal) coloration in Lepidoptera; and 2) that insects but not vertebrates can see significantly into the near-U.V. (c. 300 to 380 nm). These two factors would have allowed insects to evolve U.V. reflectance signals for their own visual communication, separate from the limitations imposed by pressure for adaptive coloration in the visual range of potential vertebrate predators (c. 380 to 760 nm). My studies included inspection of wide-ranging geographic samples of several hundred species, by means of the Sony VCK portable video camera with a U.V. transmitting lens capped with a U.V. transmitting filter. From this survey the most interesting models, mimics, sexual morphs, and crepuscular species were then photographed with both U.V.-filtered reflectance and normal visible light.

Some mimicry results: 1) The appearance in U.V. versus visible light was substantially different in 18 of 20 models and 26 of 33 mimics scanned (some models have more than one mimic). 2) Among the 26 mimics with a U.V. reflectance pattern distinct from that in the visible, the resemblance to the model in U.V. was close in 10 of 13 from Africa, but in only 2 of 6 from South America and 2 of 7 from North America. Possible explanations are that more of the predators in Africa than in the New World can see in the U.V., or that mimetic selection has been developing longer in the African complexes and has been perfected there even in such minor expressions as appearance in the U.V.

Sexual signals tend to be monomorphic in U.V. reflectance for species in which the appearance of females is di- or polymorphic in our visible spectrum. This is spectacularly true in *Papilio glaucus* L., in which the blackish mimetic female form is essentially identical in U.V. to the yellow malelike form. *Hypolimnas bolina* (L.) shows the same U.V. similarity for visible female morphs in the Solomon Islands (but not in Fiji). In a major American model swallowtail, *Battus philenor* (L.), males and females appear much more unlike in U.V. than in visible reflectance, because in U.V. the submarginal pale spots absorb in males and reflect in females; again, the sexual recognition signal is simpler in U.V. than visible reflectance.

The possible role of U.V. reflectance in antihybridization signals is suggested in several genera of butterflies and diurnal moths. Interspecific differences are strong in U.V. in some groups of sympatric species that are near relatives, e.g., male *Colias eurytheme* Bdv. and *philodice* Gdt., *Alypia langtoni* Couper and *octomaculata* (Fabr.), and several *Actinote* species. In the moth genus *Annaphila*, *arvalis* H. Edw., *depicta* Grote, and *mera* Harvey are much more alike in visible than in U.V. reflectance.

A sampling of supposed crepuscular Lepidoptera showed, as predicted, a marked tendency for strong U.V. reflectance on pale areas. Notable examples are *Opsiphanes staudingeri* G. & S., *Stichophthalma camadeva* Westw., an undetermined crepuscular riodinid from Uruguay, several *Hepialus* (s. lat.), certain sematurid moths of the genera *Homidiana* and *Coronidia*, and the giant Indo-Malayan uraniid moths of the genus *Nyctalemon*. Presumably this functions for intraspecific recognition in low illumination.

Hypotheses to explain the early evolution of U.V. reflectance patterns in Lepidoptera were passed in review.

CHARLES L. REMINGTON
Yale University

Meeting of May 15, 1973

The meeting was called to order by Dr. Howard Topoff, President, at 8:20 p.m. 19 members and 11 guests were present.

The minutes of the meeting of April 17, 1973, were approved as read.

The regular meeting scheduled for May 1, 1973 was cancelled to avoid an overlapping with the James Arthur Lecture.

Mr. Oskar Dorfmann of Steffisburg, Switzerland, was elected to Active Membership. His interest is primarily in Lepidoptera. Mr. Christian Thompson of New York was proposed for Active Membership. His interest is in flowerflies. Mr. Richard P. Seifert of SUNY at Stony Brook was proposed for Student Membership; his interest is in tropical ecology, Sphingidae, and Sphecidae.

Since this was the last meeting of the 1972–1973 season it was moved to elect the proposed candidates at the same meeting and not to wait for the next meeting as required by the by-laws. The vote in favor of the motion was unanimous. Mr. Thompson was elected to Active Membership and Mr. Seifert to Student Membership.

program. Dr. Topoff introduced speakers Mr. Herbert Loebel, who showed three insect nature filmlets on—among other fascinating topics—the fate of the male praying mantis, and Miss Alice Gray, of the American Museum of Natural History, who introduced the audience to the art of Japanese origami, i.e., paperfolding. After completion of the requirements of this mini-course, folding one bug and one butterfly, members and guests participated in the Second "International Honey Tasting."

The meeting was adjourned at approximately 10 p.m.

Peter Moller, *Sec.*

INVITATION TO MEMBERSHIP

The New York Entomological Society was founded in 1892 and incorporated the following year. It holds a distinguished position among scientific and cultural organizations. The Society's **Journal** is one of the oldest of the leading entomological periodicals in the United States. Members and subscribers are drawn from all parts of the world, and they include distinguished professional naturalists, enthusiatic amateurs, and laymen for whom insects are only one among many interests.

Your are cordially invited to apply for membership in the Society or to subscribe to its **Journal** which is published quarterly. Regular meetings are held at 8:00 P.M. on the first and third Tuesdays of each month from October through May at the American Museum of Natural History, the headquarters of the Society. A subject of general interest is discussed at each meeting by an invited speaker. No special training in biology or entomology is necessary for the enjoyment of these talks, most of which are illustrated. Candidates for membership are proposed at a regular meeting and are voted upon at the following meeting.

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Genetic symbols: follow recommendations of Demerec, et al. (Genetics **54:** 61, 1969)

Biochemical abbreviations: follow rules of the U.I.P.A.C. -I.U.B. (J. Biol. Chem. **241:** 527, 1966)

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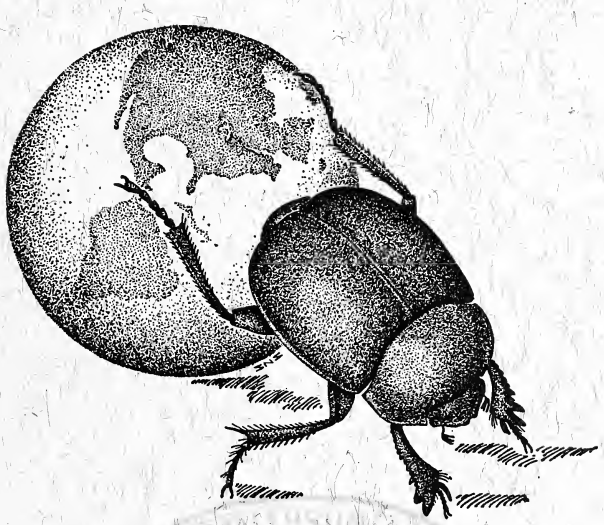

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The New York Entomological Society
Incorporating The Brooklyn Entomological Society
Incorporated May 21, 1968

The New York Entomological Society
Organized June 29, 1892—Incorporated February 25, 1893
Reincorporated February 17, 1943

The Brooklyn Entomological Society
Founded in 1872—Incorporated in 1885
Reincorporated February 10, 1936

The meetings of the Society are held on the first and third Tuesday of each month (except June, July, August and September) at 8 P.M., in the AMERICAN MUSEUM OF NATURAL HISTORY, 79th St. & Central Park W., New York, N. Y. 10024.

Annual dues for Active Members, $4.00; including subscription to the Journal, $9.00.

Members of the Society will please remit their annual dues, payable in January, to the Treasurer.

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American Museum of Natural History, New York 10024

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Mailed October 9, 1973

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Journal of the New York Entomological Society

VOLUME LXXXI OCTOBER 9, 1973 No. 3

CONTENTS

Moths of the subfamily Ennominae (Geometridae, Lepidoptera) of the Belvedere Expedition to the Gulf of California, Mexico

Frederick H. Rindge

Curator, Department of Entomology, The American Museum of Natural History

Received for Publication May 25, 1973

Abstract: The Belvedere Expedition of 1962 to the Gulf of California brought back 85 specimens of moths of the subfamily Ennominae (Geometridae). These represent 17 species; two of these have been placed only to genera. One new species, *Glaucina* **ugartei**, n. sp., is described in this paper. Locality data are given for the species taken on the expedition, as well as for the general distribution of each of the species. Apparently three species are endemic to region in which they were collected.

INTRODUCTION

Relatively little is known about the moths of the family Geometridae from the peninsula of Baja California, Mexico. Generally speaking, this large area is believed to have a relatively sparse representation of this family; this is borne out by what little collecting has been done there. Very few people have done any collecting on the eastern coast of the peninsula, and this is one of the great values of the specimens from the Belvedere Expedition. Prior to this trip, only two others come to mind that were actively engaged in catching moths and published results about them. The first was the expedition of the California Academy of Sciences to the Gulf of California in 1921; the geometrid moths were published by W. S. Wright (1923). He included 11 species; of these, several belonged to the Ennominae. The second field trip was not confined to the Gulf but collected in a number of areas in the Territory, including some Gulf localities. This was the Margaret M. Cary–Carnegie Museum Expedition to Baja California, Mexico, 1961; for its itinerary and localities, see Fox (1963). The Ennominae were studied by Rindge (1969), and included 32 species.

The Belvedere Expedition began on March 15, 1962 at Bahía de los Angeles and ended at La Paz on April 21. Lindsay (1962) gave a general account and a detailed itinerary of the expedition, including maps of the route followed. Mr. Charles F. Harbison, then Curator of Entomology of the San Diego Natural History Museum, collected the Lepidoptera on this trip; the moths were taken at lantern light (Lindsay, 1962, p. 41).

In the text of this paper the data for each species are given in a somewhat abbreviated form. As all the specimens were captured in 1962 by Charles F. Harbison, these two items are omitted. The reader is referred to Lindsay's

paper for the exact localities that are cited. The bibliographical references are minimal; they include only citations to the original description, recent revisionary studies, and previous Baja California records.

A total of 85 specimens, representing 17 species, has been studied. Two of these species, both represented by single specimens, are not given specific names. Of the remaining 15, seven (including one in this paper) have been named by me in my revisionary studies published since 1959.

The moths were collected at ten different localities. The northernmost of these, Bahía de los Angeles, is at the southern end of the lower Colorado Valley region of the Sonoran Desert (Shreve and Wiggins, 1964); the one species that was taken here has been collected primarily in the Coachella Valley of southern California. The remaining nine localities are all in the Central Gulf Coast region (Shreve and Wiggins, 1964), a relatively narrow strip of land extending from just below Isla Angel de la Guarda, south to almost the end of the peninsula, and including the islands visited on the trip. As far as we know now, three of the species that were taken are to be found only in this region; they are *Pterospoda kinoi* Rindge, *Pterotaea salvatierrai* Rindge, and the species of *Glaucina* described as new in this paper.

SPECIES ACCOUNTS

Pterospoda kinoi Rindge

Pterospoda kinoi Rindge, 1969, p. 26, figs. 1 (holotype male), 2 (paratype female), 7 (male genitalia), 8 (female genitalia).

RECORD: Isla San Marcos, March 28, six male and five female paratypes.

REMARKS: This species occurs on opposite sides of the Gulf of California, being known from Bahía San Carlos, Sonora, and from three other localities in Baja California Sur, extending as far south as La Paz, Arroyo San Bartolo (Cary–Carnegie Expedition), and San Venancio. This species not only has an interesting distribution, but it is the only seasonally dimorphic one known to me in the genus.

Fernaldella fimitaria angelata Wright

Fernaldella fimitaria angelata Wright, 1923, p. 114. Rindge, 1969, p. 31.

RECORD: Isla Espíritu Santo, April 20, one male.

REMARKS: This subspecies is known from the gulf coast of the peninsula, from the type locality at Bahía de los Angeles and in the La Paz area. Material is needed in series to see whether or not this is a valid subspecies, or whether *angelata* should be placed as a synonym of *fimitaria*.

Semiothisa colorata Grote

Semiothisa colorata Grote, 1883, p. 7. Rindge, 1969, p. 32.

RECORDS: Punta Púlpito, April 2, 7, one male, one female; Isla Coronados, April 3, one female.

REMARKS: This is a common species of the arid southwestern United States, extending from western Texas to southern California. It has also been taken in Sonora, and on the gulf in

both the State and Territory of Baja California. Wright (1923, p. 115) records two specimens as *Phasiane colorata* Grote from Angeles Bay (Bahía de los Angeles), June 25; I have not examined these, but the identification could be correct. This is one of the commonest and most widespread of the Baja California geometrids.

Semiothisa sp.

Semiothisa sp.: Rindge, 1969, p. 33.

RECORD: Punta Púlpito, April 2, one male.

REMARKS: This species is allied to *nigricomma* Warren; it is known from Arizona and Baja California Sur.

Semiothisa sirenata McDunnough

Semiothisa sirenata McDunnough, 1939, p. 254. Rindge, 1969, p. 33.

RECORD: Isla Cerralvo, April 16, one male.

REMARKS: This species occurs in Arizona, southern Nevada, southern California, Sonora, and both the State and Territory of Baja California.

Semiothisa cyda (Druce)

Eubolia cyda Druce, 1891–1900 (1892), p. 177; 1881–1900 (1893), pl. 58, fig. 4 (lectotype male).

Semiothisa cyda: Rindge, 1959*b*, p. 8, figs. 2 (male ventral plate), 6 (male genitalia), 10 (female genitalia); 1969, p. 33.

RECORDS: Puerto Santispaquis, April 1, one female; Punta Púlpito, April 2, one female; Isla Cerralvo, April 16, one female.

REMARKS: This species was known, incorrectly, for years as *s-signata* Packard; I corrected the terminology in 1959. This species is one of the commonest and most widespread species of the southwestern United States and much of Mexico; see my 1959 paper for a complete list of the states involved as they were then known. The moth occurs along the gulf in both the State and Territory of Baja California.

Itame sobriaria Barnes *and* McDunnough

Itame graphidaria sobriaria Barnes and McDunnough, 1917, p. 239, pl. 24, fig. 9 (holotype male).

Itame sobriaria: Rindge, 1969, p. 35.

RECORDS: Isla Coronados, April 3, two females; Isla Cerralvo, April 16, one female.

REMARKS: This species is known from Arizona, New Mexico, western Texas, Chihuahua, and the Territory of Baja California. Insufficient material is available to determine whether or not the peninsular population is subspecifically different or not.

Glaucina biartata Rindge

Glaucina biartata Rindge, 1959*a*, p. 275, pl. 23, figs. 5, 6 (holotype male, paratype female), text figs. 3 (front), 20 (distribution), 39 (male genitalia), 75 (female genitalia).

RECORD: Isla Cerralvo, April 16, five females.

REMARKS: The type series was from northwestern Baja California and San Diego, California. Since the appearance of the original description a number of other specimens of this species

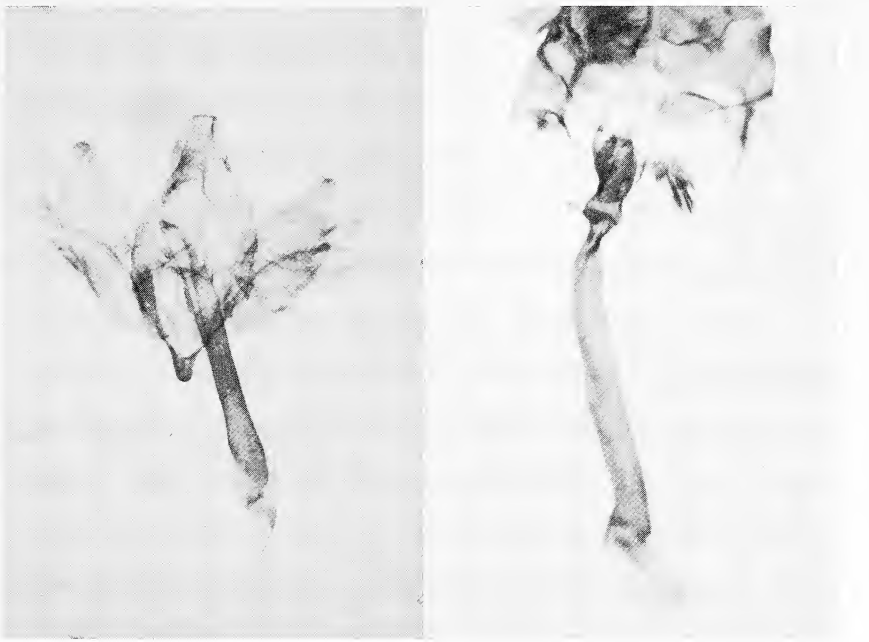

Fig. 1. Genitalia of *Glaucina* **ugartei**, n. sp. Holotype male (left) and allotype female (right).

have been seen from both the state and territory of Baja California, thus indicating that it is one of the more widespread species of this genus on the peninsula. The specimens from the southern part of the range tend to be smaller and somewhat more contrastingly marked than do those from the northwest coastal area.

Glaucina ugartei, n. sp.

Fig. 1

DIAGNOSIS: This species is similar to *ouden* (Dyar) but may be distinguished by its slightly smaller size, grayer, almost immaculate forewings, and by the distinctive genitalia. The male genitalia are characterized by the broadly truncate apex of the uncus and the very long, slender aedeagus; the female genitalia by the extremely long and slender corpus bursae.

MALE: Head with vertex and front having mixture of dark grayish brown and pale gray scales; front flat, raised, slightly wider than high; palpi rising above lower margin of eye, extending beyond front, dark grayish brown, the scales with narrow white tips; tongue normal; (antennae partly missing). Thorax grayish brown above; below, and legs slightly paler. Abdomen grayish brown above and below.

UPPER SURFACE OF WINGS: Forewings unicolorous grayish brown; maculation absent except for faint trace of nebulous gray t. p. line; terminal line narrow, dark grayish brown; fringe concolorous with wing. Hind wings pale gray, slightly darkening outwardly, with anal area grayish brown; without maculation; terminal line and fringe similar to those of forewing.

UNDERSURFACE OF WINGS: Forewings unicolorous gray; hind wings grayish white; without maculation except for darkened veins on hind wings, and for narrow terminal line on all wings.

LENGTH OF FOREWING: 8.5 mm. (holotype).

FEMALE: Similar to male but with palpi rising almost to middle of eye.

LENGTH OF FOREWING: 9.5 to 10.5 mm.; allotype, 10.5 mm.

MALE GENITALIA: Uncus broad, apical portion with parallel sides and truncate apex; gnathos with median area elongate, bluntly pointed; valves with costa convex medially, produced apically, apex narrowly spinose, maximum width less than one-third of width of base of uncus, uniting at base with narrow sclerotized strip that joins broader sacculus; sacculus with bases joined by short, narrow transverse bar, sclerotized, slightly longer than wide, sacculus arm arising from this basal area, elongate, slender, evenly and outwardly curved, extending to margin of sacculus, apex with short spinelike point, less than one-fifth width of base of uncus; sacculus with membranous portion broad, outer margin curved, with a few minute setae near base; anellus small, sides slightly concave, in length about four-fifths width of base of uncus; saccus about equal in length to tegumen, extending beyond sacculus as elongate tubular point; aedeagus longer than combined lengths of uncus, tegumen, and saccus, slender, very slightly narrowed medially; vesica with very narrow, apically bifurcate, sclerotized strip, less than half length of aedeagus.

FEMALE GENITALIA: Sterigma membranous; ductus bursae mainly situated dorsad of tube from sterigma, extending posteriorly as small sac, then curving anteroventrally to meet corpus bursae; ductus seminalis arising ventrally at junction of ductus bursae and corpus bursae; latter extremely long (3 mm.), slender, and lightly sclerotized, then enlarged into small membranous sac; signum absent.

TYPES: Holotype, male, allotype, female, and two female paratypes, Isla San José (24°59′ N., 110°38′ E.), Gulf of California, Territory of Baja California Sur, Mexico, April 12, 1962 (C. F. Harbison). The genitalia of the holotype are mounted on slide FHR No. 11531, and of the allotype on No. 11488.

The holotype and allotype are in the collection of the American Museum of Natural History on an indefinite loan from the San Diego Museum of Natural History; paratypes are in the collection of the latter institution.

REMARKS: This species is a member of group III of *Glaucina*, as described in my revision (Rindge, 1959*a*, p. 301). This small group contained only three species heretofore; one from the deserts of southern California, a second from Guerrero, Michoacan and Puebla, and the third from Chihuahua. *Glaucina* **ugartei** is intermediate in some characters between the first two species, *bifida* Rindge and *ouden* (Dyar). The moth might be mistaken for Dyar's species, but the genitalia are more like those of *bifida*.

ETYMOLOGY: This species is named after Father Juan de Ugarte, S.J. (1660–1730), one of the outstanding pioneer missionaries of California. Father Ugarte, a native of Honduras, served on the peninsula from 1701 until his death.

Glaucina lowensis (Cassino and Swett)

Coenocharis lowensis Cassino and Swett, 1925, p. 35.

Glaucina lowensis: Rindge, 1959*a*, p. 324, pl. 26, figs. 7, 8 (male, female), text figs. 29 (distribution), 63 (male genitalia), 95 (female genitalia).

RECORD: Punta Púlpito, April 2, one female.

REMARKS: When I did my revision of *Glaucina* in 1959, this species was known from southern California and adjacent northwestern Baja California. Since that time one other female of this species has been studied from Todos Santos, on the west coast of the peninsula near the southern end. Thus the species appears to be much more widespread than previously known.

Eubarnesia ritaria arida Rindge

Barnesia ritaria Grossbeck: Wright, 1923, p. 113.
Eubarnesia ritaria arida Rindge, 1959*a*, p. 347, pl. 27, figs. 16, 17 (paratypes male and female), text fig. 36 (distribution); 1969, p. 36.

RECORDS: Punta Púlpito, April 2, one male; Puerto Escondido, April 6, one male: Isla Cerralvo, April 16, one male, one female.

REMARKS: This subspecies extends from southern and southeastern California, around the head of the Gulf of California into Sonora, and for the length of the peninsula of Baja California. The earliest recorded specimens from the Gulf were by Wright, who reported eight moths from Angeles Bay. The type series included 40 specimens from San Felipe; in my 1969 paper two localities were added from the southern end of the peninsula. This subspecies is apparently rather widespread on the peninsula.

Anacamptodes pseudoherse Rindge

Anacamptodes pseudoherse Rindge, 1966, p. 218, pl. 24, fig. 8 (paratype male), text figs. 24 (male genitalia), 47 (female genitalia); 1969, p. 38.

RECORD: Punta Púlpito, April 2, one male paratype.

REMARKS: This species is widespread throughout much of Mexico, with two specimens being known to me from Baja California Sur; both paratypes are from the eastern portion, one being on the coast and the other (Arroyo San Bartolo; Cary–Carnegie Expedition) from just inland.

Anacamptodes cerasta Rindge

Anacamptodes cerasta Rindge, 1966, p. 221, pl. 24, fig. 11 (paratype male), text figs. 28 (male genitalia), 48 (female genitalia); 1969, p. 39.

RECORD: Isla Cerralvo, April 16, one female.

REMARKS: This species is endemic to the Territory of Baja California; the type locality is La Paz. The single specimen is rather battered but has the maculation more clearly defined than in most of the specimens examined. The determination was made by a study of the genitalia.

Pterotaea crickmeri (Sperry)

Stenoporpia crickmeri Sperry, 1946, p. 138.
Pterotaea crickmeri: Rindge, 1968, p. 73; 1970, p. 284, figs. 3 (distribution), 20 (holotype male), 57 (male genitalia), 88, 89 (female genitalia).

RECORD: Bahía de los Angeles, March 25, one male.

REMARKS: This is the only specimen known from Baja California. The species occurs in the desert areas of Riverside and San Diego counties, California.

Pterotaea salvatierrai Rindge

Pterotaea salvatierrai Rindge, 1970, p. 285, figs. 3 (distribution), 21 (holotype male), 59 (male genitalia), 90 (female genitalia).

RECORDS: Isla San Marcos, March 28, 11 male and two female paratypes; Punta Púlpito, April 2, 19 male and 11 female paratypes.

REMARKS: This species is endemic to the eastern coast of Baja California Sur.

Pergama inviolata (Hulst)

Stenaspilates inviolata Hulst, 1898, p. 218.

RECORDS: Isla San Marcos, March 28, one female.

REMARKS: The species was described from Arizona; it also occurs in the desert areas of southern California, and in both parts of Baja California.

Somatolophia (?) sp.

RECORD: Isla Santa Catalina, April 10, one male.

REMARKS: This may be an undescribed species, apparently related to *obliterata* Warren and *ectrapelaria* Grossbeck. The specimen is rather worn and abraded, with the resulting loss of most of the maculation, and so it is not being described at this time. Revisionary work on *Somatolophia* and *Apicia* Guenée is badly needed; this species may belong in the latter genus.

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BOOK REVIEWS

Jamaica and Its Butterflies. F. Martin Brown and Bernard Heineman. 1972. E. W. Classey, Ltd., London. Entomol. Reprints, Los Angeles, U. S. Distributor. 478 pp. $44.00.

This is an unusual book in many respects. It has been written by two close friends, who collected butterflies in Jamaica for many years and who decided in 1950 to write a book and finally did so, for our benefit. The book is delightful to read; it gives a warm, personal account of the extensive collecting of the authors and their wives that resulted in this definitive publication. The Prologue by Bernard Heineman gives a refreshing touch that is followed by a description of Jamaica and a very interesting account of the early butterfly collectors and the more recent collections by the authors. Chapters on butterfly anatomy and biology, habitats, and zoogeography follow. The last 350 pages are devoted to the descriptions of fourteen families and 133 species of Jamaican butterflies. Of these, 31 species are endemic. The ten color plates at the end, and one plate at the beginning, illustrate all known species. A bibliography, glossary, checklist of Jamaican butterflies, and index to scientific names complete the book. The illustrations by Marjorie Statham Favreau and color plates are of very good quality and the artistic outlay of the book is an additional bonus. This book belongs in every entomological library, and no collector of tropical butterflies will want to miss it. The book will prove useful to anyone seriously interested in butterflies. The more general parts of it might also be of interest to those who go to Jamaica for a brief vacation even if they are not especially interested in butterflies, because there is a wealth of information about the Jamaican scene.

KARL MARAMOROSCH
Boyce Thompson Institute
Yonkers, N.Y.

Errata and Additions to Valiela, I. 1969. **The Arthropod Fauna of Bovine Dung in Central New York and Sources on its Natural History.** *J. N. Y. Entomol. Soc.*, 77:210–220.

Dr. J. G. Matthysse of the Department of Entomology, Cornell University, has pointed out the erroneous designation of a mallophagan named "*Damalinia bovicola*" in the paper. Dr. R. C. Dalgleish has subsequently identified the specimen as *Sturnidoecus* sp. This louse remains an accidental member of dung fauna since only a single specimen was found during three summers of collecting.

The name of the staphilinid *Aleochara bipustulata* is misspelled *A. bipostulata* in the text.

Two additional references containing information on the natural history of dung beetles are:

LANDIN, J. 1967. On the relationship between the microclimate in cow droppings and some species of *Sphaeridium* (Col. Hydrophilidae). Opuscula Entomologica, **32:** 207–212.

RAINIO, M. 1966. Abundance and phenology of some coprophagous beetles in different kinds of dung. Ann. Zool. Fenn., **3:** 88–98.

The Biology of the Butterfly *Dione juno huascama* (Nymphalidae: Heliconiinae) in El Salvador

ALBERTO MUYSHONDT
101 AVE. N., 322, LOMAS VERDES, SAN SALVADOR, EL SALVADOR

ALLEN M. YOUNG
DEPARTMENT OF BIOLOGY, LAWRENCE UNIVERSITY, APPLETON, WISCONSIN 54911

ALBERTO MUYSHONDT, JR.
ESCUELA NACIONAL DE AGRICULTURA, SAN ANDRES, DEPARTMENTO LA LIBERTAD, EL SALVADOR

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Abstract: Various aspects of the life cycle and natural history of the heliconiine butterfly *Dione juno huascama* (Lepidoptera: Nymphalidae) were studied in the vicinity of San Salvador, El Salvador, at various times over approximately three years. These studies emphasized: description of life cycle and developmental time, larval food plant specificities, and the behavior of adults and immatures. Mortality factors operating on immature stages were also studied in a preliminary manner. The findings are discussed with respect to previously published reports on other subspecies of *D. juno* as well as for other species of the genus in other regions. Furthermore, an attempt is made to discuss various aspects of population biology and heliconiine phylogeny in light of the new data on *D. juno huascama*. Emphasis is also placed on the association of *D. juno* with a cultivated plant species around San Salvador and the notable absence of many other heliconiines from this larval food plant.

INTRODUCTION

It is becoming increasingly evident that our understanding of the population biology and community ecology of neotropical families (and subfamilies) of butterflies is dependent largely upon a thorough knowledge of the fundamental biology (life cycle, natural history, etc.) of individual species in selected habitats. The impetus for this approach has come primarily from studies and discussions emphasizing the coevolutionary interactions between insects and plants (Ehrlich and Raven, 1964; Janzen 1967*a*, 1970; Breedlove, 1972). And while it is known that certain components of the fundamental biology of a butterfly species, such as food plant preference for oviposition and larval development, vary substantially in different habitats (e.g., Singer, 1971), it is nonetheless essential to study methodically the biology of selected species within a family or subfamily so that both phylogenetic and contemporary ecological properties are revealed and distinguished (Birch and Ehrlich, 1967).

A substantial effort has been made with this approach to the ecology of neotropical butterflies owing to the recent biological studies of the subfamily

Acknowledgment: We thank Lee D. Miller of the Allyn Museum of Entomology for identifying the species and subspecies.

Heliconiinae in Trinidad (e.g., Beebe, Crane, and Fleming, 1960; Alexander, 1961*a*, *b*; Brower, Brower, and Collins, 1963; Crane, 1957; Turner, 1968; and many others) and Brazil (Brown, 1970, 1972; Brown and Mielke, 1972). The Heliconiinae are famous for their strong dependence upon Passifloraceae as larval food plants, a factor undoubtedly responsible in part for their participation in mimicry complexes throughout the tropics (see comments in Brower and Brower, 1964). But biological studies of the Central American fauna have been virtually nonexistent, and the purpose of this paper is to describe various aspects of the biology of a "pre-*Heliconius*" species (Emsley, 1965), namely *Dione juno huascama* Reakirt, in El Salvador. Our report brings together various observations on life cycle, larval food plants, and natural history (mainly descriptions of behavior patterns of adults and immatures) and attempts to discuss them in terms of other studies on the genus *Dione* (Alexander, 1961*a*, *b*) and the general pattern of adaptive radiation and field behavior of the subfamily, using the interpretations of Brown (1972). And although other subspecies of *D. juno* have been studied in other parts of tropical America (Brown, 1944; Alexander, 1961*a*, *b*; Brown and Mielke, 1972) our report comprises the first account of the biology of *huascama*, and for the species in El Salvador. To our knowledge the biology of *D. juno* has not been previously studied in Central America.

DESCRIPTIONS OF STUDIES

Field collections of eggs and other immature stages of *D. j. huascama* were made at intermittent times between 1970 and 1973 from various localities in San Salvador and its vicinity (San Andres, Apopa) where there exist small commercial plantations of *Passiflora*. The butterfly is generally very abundant here at various times of the year; breeding populations are confined to plantations, scrub areas, old fields, and marginal secondary growth habitats along streams and small ravines. Since virtually no virgin rain forest remains in San Salvador, the butterfly has been forced to occupy a variety of secondary habitats.

Our basic technique for studying life cycle was to obtain eggs in the field and bring these into a room (laboratory) where rearing was done in clear plastic bags. The food plant was refreshed as needed in these cultures. Using this approach, the butterfly was reared no fewer than eight times, with two batches of eggs usually being studied each time. The cultures were examined periodically to note the external morphology of eggs, larvae, and pupae, in addition to measuring egg-adult developmental time. All rearings on different occasions were done in the same room, and the temperature here was usually 22–25°C. Specimens of all life stages were preserved from time to time in 70 percent ethanol, and these are available for examination upon request. Our lack of a good microscope limited us to the study of the external morphology in detail on

fresh specimens; egg morphology was examined with a low power (10 ×) microscope.

Field studies consisted of witnessing on several occasions the oviposition behavior pattern, and activities of caterpillars, including defense, feeding, resting, and pupation. Since eggs, caterpillars, and pupae are gregarious (see below), we were also interested in measuring the amount of biotic mortality (parasitism, predation, fungus disease) and abiotic mortality (desiccation) in these life stages.

In addition to rearing caterpillars on natural food plants, as based on oviposition records and subsequent performance of caterpillars, an attempt was made to offer caterpillars other species of food plants in captivity. Our interest here was an estimate of the spectrum of food plant acceptability for species of *Passiflora* found in the San Salvador region.

RESULTS

Life Cycle

The eggs are laid in large clusters on petioles and ventral sides of leaves of *Passiflora edulis* L. (Fig. 1-A, B) and each egg is initially bright yellow, but subsequently darkens to red. The egg is elongate, ovoid, and truncated at the bottom; there is a conspicuous depression on the top in the center. A series of ten vertical ridges arranged in pairs extend into the depressed center at the top. This arrangement of ridges is accompanied by a series of five shorter vertical ridges with each of these being between two pairs of the longer ridges; the shorter ridges diminish and disappear before reaching the depressed apical area. All ridges have a corrugated appearance. In addition, there are very faint horizontal ridges between the vertical ridges, but these were very difficult to count. The incubation period is six days.

Upon hatching, the first instar does not usually devour the eggshell. Prior to the first feeding, the first instar is white with a brown head; there is also a black prothoracic shield with about six setae, and at the future attachment point of each body spine there is a round black pinacullum bearing a seta. Neither the head nor body of the first instar has spines. The larva is about 2.5 mm long when it begins to feed, and the body becomes brownish-yellow; by the first molt (after three days), they are about 4 mm in length.

Both head and body of the second instar are uniformly brown (Fig. 1-C), but the head now bears very clearly bifid epicrania, terminated by a short spine on each, and sparse setae. The body bears many short spines bearing setae. The distribution of spines is as follows: (1) prothoracic segment bears a lateral pair of spines over the spiracula (and the spiracles of this segment are larger than those of other segments), and a smaller pair of spines just under the shield; (2) mesothoracic segment with one pair of spines over the spiracles

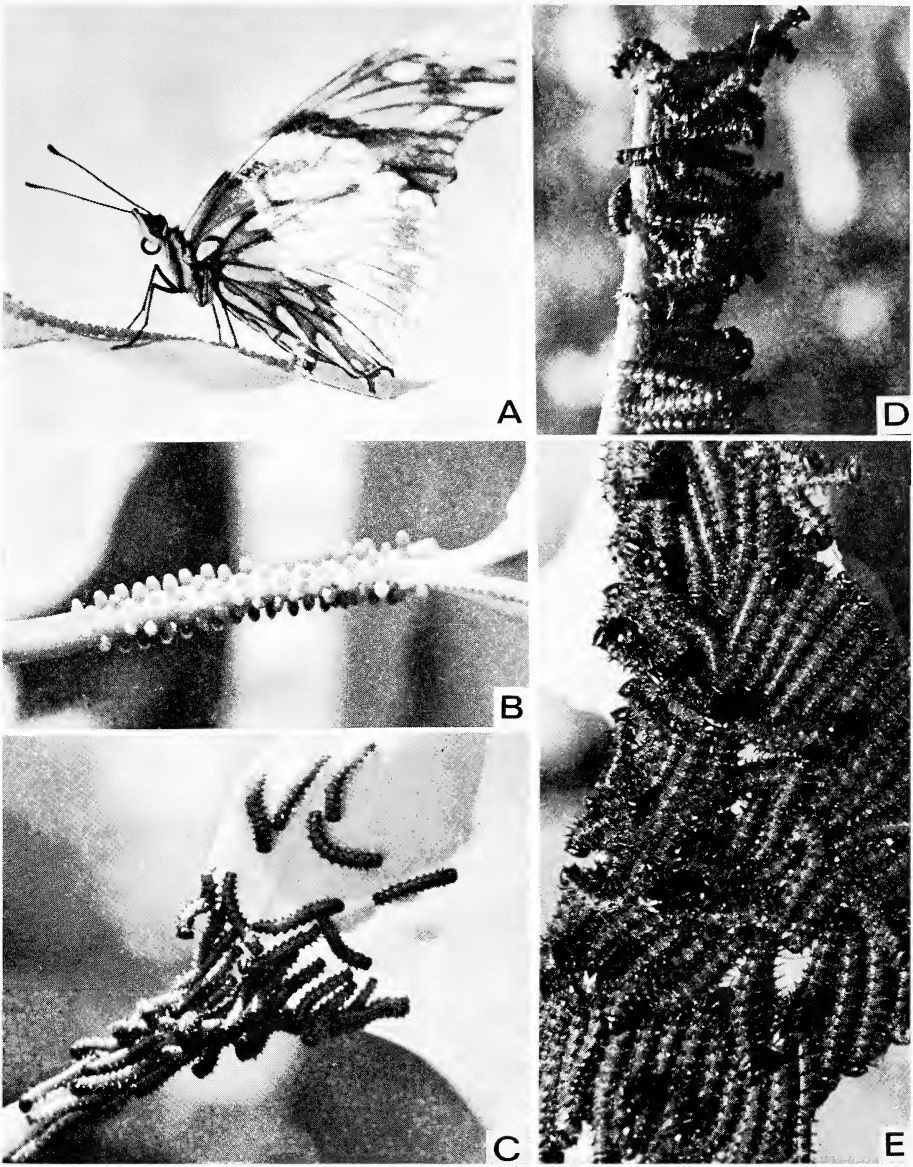


FIG. 1. Life cycle of *Dione juno huascama*. (A) Female laying several eggs on ventral side of a leaf of *Passiflora edulis* L. (the picture is upside down for clarity). (B) Egg cluster from a single female on the petiole of *P. edulis* leaf. (C) Second instar larvae in locomotor activity. (D) Third instar larvae on petiole after completely eating a leaf. (E) Fourth instar larvae resting on a leaf, illustrating the coordinated resting positions among individuals.

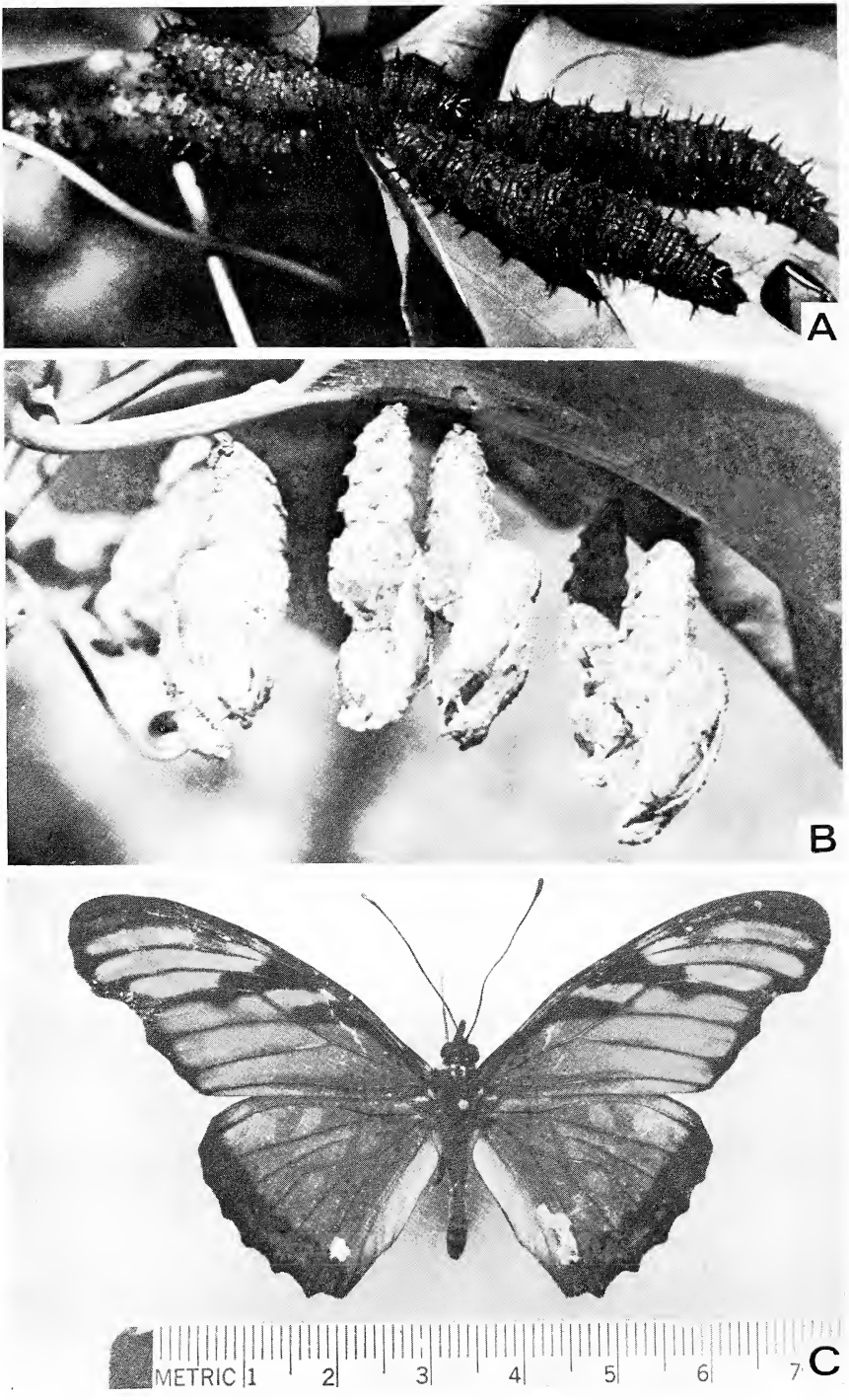
and another slightly subdorsally; (3) metathoracic segment has one pair of spines subdorsally; (4) all abdominal segments, except the ninth and tenth, with a pair of spines just above the spiracles, another just below them, and a third pair slightly subdorsally; (5) the ninth abdominal segment has one pair slightly subdorsally and the tenth has one pair just above the spiracles. All spines bear fine setae and these also occur at the base of legs and prolegs. The spiracles, excluding those of the first thoracic segment, are small, black, and inconspicuous. The second instar attains a size of about 10 mm and it lasts three days. The remaining three instars (Fig. 1-D, E; Fig. 2-A) retain the same arrangement of spines and head structure, but there is a tendency for the coloration to become more mottled through successive instars. Especially in the fifth instar, the coloration is distinctive, being a mottled light brown. The third instar lasts two days and they are 14 mm long; the fourth instar lasts four days and the larva attains a size of about 30—40 mm in length. The prepupa is a slightly shortened version of the fifth instar and it lasts about one day.

The pupa is 20—25 mm in length and dark brown (Fig. 2-B) and the cremaster is even darker brown, as are the spiracles. In terms of profile and form, the abdomen is incurvated to the wing cases, and the latter are strongly projected ventrally. There are three rows of protuberances in the upper region of the abdomen: one row along the meson and two subdorsal rows. The prothorax is strongly arched and there is a marked indentation dorsally between the abdomen and thorax; the head region is much narrower than the prothorax. The pupa stage lasts seven days, giving a total egg-to-adult developmental time of about 30 days in the laboratory. The adult (Fig. 2-C) exhibits some sexual dimorphism in wing coloration, with females being lighter with less distinctive black markings.

It should be pointed out that our measurements of body size and developmental time were taken from large numbers of individuals reared at different times, and although records were not kept on the numbers measured, probably several hundred larvae were involved. Also, we did not use developmental time data for individuals that were unusually slow within the group; such data would add a strong bias to the estimation of the true developmental time.

Food Plant Studies

Although we know of only one natural food plant for *D. j. huascama* in the San Salvador region, namely *Passiflora edulis* L. (and probably two subspecies involved), we discovered that larvae complete development successfully (i.e., they perform as well) on several other species of *Passiflora* found here: *P. coriacae* Jussieu, *P. capsularis* L., *P. pulchella* H.B.K., and *P. salvadorensis* Donn. Smith. Interestingly enough, they will not accept *P. foetida* L., *P. gossypiifolia* Desvaux, and *P. quadrangularis* L. Non-passifloraceous food


A
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plants have not been found. Eggs and larvae have only been found on wild and cultivated *P. edulis* L.

Adult Behavior

Our major concern here was the description of oviposition behavior, since this is obviously a very important component of plant-herbivore associations, as seen in butterflies. As we know virtually nothing about the searching movements of mated female *D. j. huascama* and how it relates to the spatial distribution of food plants for egg-laying, we limit ourselves to the acts that ensue once a food plant has been found by the butterfly.

If eggs are to be laid on a leaf, the female usually selects a medium-sized leaf, given the range of leaf sizes and shapes on the particular vine in question. The placement of eggs on the leaf is very coordinated since all eggs are evenly spaced from one another, and a given group or cluster may contain more than one hundred eggs. In older females captured in the wild and dissected, the range in number of developed eggs is 80 to 140, suggesting that an average female lays more than one egg cluster during her lifetime. Dissection of recently eclosed females yielded no eggs, indicating that the bulk of egg maturation occurs after mating. The eggs are always laid ventrally in this species, and sometimes eggs are laid in a cylindrical fashion around petioles (Fig. 1-B), although fewer eggs per cluster are usually found in this arrangement. Oviposition usually occurs between 10:00 and 14:00. The rate of egg-laying changes considerably as more eggs are laid in a cluster: initially the rate is about one egg every seven seconds, going to one every 15 seconds about 15 minutes later, and 45 minutes later, to one egg every two minutes! Indeed, egg-laying is apparently laborious in this butterfly. Also, a female will often rest intermittently during oviposition.

Behavior of Caterpillars

The most striking feature of the behavior of caterpillars in this species is very clear gregarious or communal living, with traces of social behavior. Not only are the caterpillars gregarious, as a direct result of clustered egg-laying in this butterfly, but they have exploited this preadaptation to a high degree by the evolution of group behavior patterns.

Upon hatching, individual caterpillars within an egg cluster do not eat either their own eggshells or eggshells of other individuals. The first instar larvae feed on the underside of the leaf, eating only the lower layer of tissue,

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Fig. 2. Life cycle of *Dione juno huascama*. (A) Fifth instar larvae. (B) Communal pupation as shown here by the empty pupal shells. (C) Adult *Dione juno*.

eventually giving the leaf a crumpled and wilted appearance. When the larvae move from one leaf to another, they do so in a solid column or line, and not individually, a behavioral feature retained in later instars. More importantly, there are no indications of cannibalism on eggs and each other under natural conditions; there is a high level of tolerance evident for individuals toward one another. The possibility of intergroup tolerance has not been studied in depth, and it would be interesting to see if larvae displaced from one group into another are tolerated in the new association. We do know, however, that at times when eggs of different females are present on the same leaf, the larvae from the first egg batch to hatch do not cannibalize the other egg batches or the larvae when they eventually hatch. This is very suggestive of well-developed intergroup tolerance, at least in the early stages of this heliconiine. When a group of larvae is initially very large, say 100 individuals or more, we have noted that eventually, in later instars, the group will become subdivided on the food plant, and that these subgroups may even be divided further, depending largely on the size of the food plant and distribution of leaves. By the time of pupation, groups may be very small, and although pupation is also done communally in this species, the usual range in number of pupae per group is three to ten. At no time, however, do larvae exhibit intolerance and aggressiveness toward one another, and the breakdown of groups through successive instars should be interpreted primarily as an adaptation to redistribute the group of herbivores efficiently over the available food supply. Thus group subdivision is a result of the manner in which the larvae feed. From the second instar on, they place themselves vertical to the leaf edge, very tightly packed together on both sides of the leaf. As the leaf is consumed (all tissues), more and more larvae cannot find a feeding spot and move to another leaf; this process is intensified as larvae grow larger and eventually involves movement onto several new leaves rather than just one. In the laboratory, however, in the absence of an adequate amount of fresh food, larvae of various instars will become cannibalistic, with most attacks being on individuals in the process of molting. Similar cannibalistic predation by caterpillars also occurs with pupae being eaten (in a contrived situation where two very different age groups are put together with a limited food supply and one group pupates earlier than the other).

Feeding and resting periods are highly coordinate group activities in caterpillars of this butterfly, and defense behavior may also be included here. Feeding occurs throughout the day in all instars and the size and composition of resting groups is dependent upon proximity of neighbors while feeding: Larvae close together during feeding form small resting groups while those individuals that moved far away on the plant form other groups. During all instars, and most notably in the last one, caterpillars emit a very disagreeable odor when the

branch they are on is shaken. Furthermore, if a shadow is projected over them, or the vine bent drastically, the whole group reacts as a unit with all individuals making spasmodic movements of the anterior part of the body. These movements can be directed laterally or vertically. But we have not observed any indication of chemical defense secretions from spines or glands on the larvae. In our field experiences, we have noted that several other heliconiines (*Heliconius*), in the larval stage, are quite capable of producing a mild rash when the spines are rubbed gently on the back of the hand, perhaps involving release of a chemical secretion from spines piercing the skin. Despite repeated tests, we have not observed this phenomenon in *Dione*. The possibility of pre-*Heliconius* genera like *Dione* lacking chemical defense mechanisms that are found in *Heliconius* warrants further investigation. Clearly the length of spines of *Heliconius* larvae are greater and the spines more highly branched, suggesting an increased defensive role of these structures in the course of heliconiine evolution.

That the caterpillars have been successful in the evolution of an effective group defense behavior is suggested by our failure to find evidence of parasitism in several groups collected in different places and at different times of the year. It has also been seen that various species of birds active in the vines, along with a few species of arboreal lizards, do not feed to any great extent on the larvae. There was one instance in which a large, fat, green lizard was seen eating several fourth instar larvae, and similar predation by other lizards inhabiting the trelliswork of vines has also been noted at various times. We have no observation of an entire group being destroyed by such predation. Even though birds are active in the vines, females of *D.j. huascama* continue to lay eggs and do not appear to be frightened away. In fact, we have repeatedly observed that various birds attempt to catch females of this butterfly, but with no success.

Miscellaneous Observations

Although we have no precise data regarding annual cycles in adult abundance for *D.j. huascama*, there is some preliminary evidence to support the idea that immature populations are vulnerable to abiotic mortality more so at certain times of the year than at other times. Whereas populations may not suffer appreciable reductions in numbers from biotic mortality factors (although we certainly need more data on this aspect), the strong tropical dry season associated with San Salvador may influence population numbers. On February 4, 1973, several groups of caterpillars, in different instars, were discovered in a large plantation of *Passiflora*, along with several groups of pupae. The interesting observation was that most of the pupae were killed, most likely from desiccation, judging from their condition. In fact, some of them had the dead butterfly, partially eclosed but still attached to the pupa shell. A total of 23 pupae were examined on this date, and only three of these had produced the imago

without any apparent difficulty. In addition, three of the remaining had the dead adult partially eclosed, while the other 17 were intact but completely shriveled up. Upon closer examination in the laboratory, it was apparent that death was not due to parasitic attack or predation. We attribute this high incidence of pupal mortality as the result of injuries suffered by the pupae from very strong winds blowing across this region, very typical of the dry season here. This effect, along with resulting mechanical abrasion with dry vines surrounding them led to substantial loss of internal fluids and traumatic death. But at the same time, larvae present on this date were healthy and females were seen ovipositing. If this pupal mortality is the result of wind effects, and assuming for the moment that it kills a lot of pupae, we interpret it as a dry season effect since the winds are very diminished during the wet season. We are attempting to obtain a more quantitative picture of pupal mortality in both wet and dry seasons in this population.

We have also observed that there is a superabundance of females laying eggs between July and September (wet season) in commercial plantations of the food plant while they become scarce during March and April (dry season) in these places. This suggests strong seasonal fluctuations in adult numbers perhaps in response to the seasonality of vegetative growth in the food plants.

DISCUSSION

The various kinds of data presented above can be meaningfully discussed in terms of the implications for population biology and in relation to the phylogeny of heliconiine butterflies.

Implications for Population Biology

The early stages of *Dione juno andicola* and *D. moneta moneta* have been studied by Brown (1944), but our report is the first account for *D. j. huascama*. Emsley (1963) states that *huascama*, although having a broad geographic distribution from northern Mexico through Central America and into Colombia (grading in the east to *juno*), this butterfly seldom occurs above altitudes of 1500 meters. In El Salvador, there appears to be an altitudinal separation between *D. juno* and *D. moneta*: *juno* is generally found in elevations from 500 to 1000 meters, while *moneta* is found between 1500 and 2000 meters. Very interesting is the fact that we have found the solitary larvae of *moneta* only on *P. edulis*, the larval food plant of *juno*. Competitive exclusion for larval food plant exploitation might have been involved in the apparent altitudinal displacement of the two closely related species. Regardless of its ecological relationship with *moneta*, it is very likely that the population biology of *D. juno* will vary greatly along altitudinal gradients in the tropics, and we might expect substantial subspeciation and other forms of divergence to occur along an altitudinal

transect at any tropical latitude; there is a greater opportunity for ecological specialization in the tropics for species with broad distributions along altitudinal transects (Janzen, 1967*b*). Any account or study of population biology for *D. juno* should include altitudinal variations influencing larval food plant selection and population dispersion. This point is especially well taken for *D. juno* since it is known that although the butterfly has a wide geographic distribution in Brazil, breeding populations tend to be very localized (Brown and Mielke, 1972), a condition very amiable for microevolutionary divergence within separate populations rather than for the species as a whole (Birch and Ehrlich, 1967).

In our experience, *D. juno huascama* shows some flexibility in larval food plants in the laboratory, and this may be an important adaptation underlying greater ecological flexibility in El Salvador. Alexander (1961*a*) noted that *D. juno juno* caterpillars has two natural food plants, *P. laurifolia* and *P. serratodigitata*, but that they accept a third species, *P. auriculata*, in the laboratory; but he noted a reduction in larval performance on this species. Brown and Mielke (1972) give several species of *Passiflora* as food plants for two subspecies of *D. juno*, namely *juno* and *suffumata*; it is interesting that there is some nonoverlap in food plant preferences between these two subspecies, suggesting divergence in feeding habits.

In El Salvador, *D. juno* is strikingly associated with a single species only of commercially grown *Passiflora* (*edulis*). Even in the wild, when we occasionally encounter small patches of this species in association with wild species such as *coriacea*, *gosypiifolia*, *salvadorensis*, and others, larvae of *juno* occur only on this species. With the exception of *D. moneta*, the only other heliconiine we have found on this species is *Agraulis vanillae*, another pre-*Heliconius* species. Most species of heliconiines exploit wild species of *Passiflora* as indicated by observations on *Heliconius charitonius*, *H. petiveranus*, *H. hortense*, *Dryas iulia*, and *Eueides aliphera* in El Salvador. In fact, in our experience, it is not uncommon to find larvae of all of these species on the same individual vine in lowland regions! The evolutionary history of relatively few species, like *D. juno*, *D. moneta*, and *A. vanillae* (the latter also feeds on two wild species of *Passiflora*) on *P. edulis* before this plant became widely cultivated in El Salvador, permitted these butterflies, most notably *D. juno* around San Salvador, to become very abundant locally when the plant came under cultivation for commercial purposes.

Another aspect of population biology relevant here concerns the extent of cohesiveness within a deme or breeding unit. Although eggs and caterpillars are aggregated, and with the latter showing social behavior, it is not known if the adult population shows similar high cohesiveness. Gregarious roosting in adult heliconiines has been considered to be a highly evolved trait associated with home-range movement and unpalatability (Benson, 1971). In

Benson's scheme, pre-*Heliconius* genera such as *Agraulis, Podotricha, Dryadula,* and *Dione* are considered primitive not only in terms of morphology (Emsley, 1963) but also in terms of lacking communal roosting in the adult stage as well as home-range movements. It is generally held that unpalatability to vertebrate predators with well-developed visual and learning abilities is a more highly evolved trait in many butterflies (Brower and Brower, 1964) and that it possibly evolved in the Heliconiinae through kin selection (Benson, 1971). Clearly mark-recapture experiments on adult movements and roosting within populations must be done for heliconiines like *D. juno* to test these ideas. Egg clustering and larval gregariousness as seen in *Dione* argue against a correlation with phylogeny and palatability because many *Heliconius* have single egg-laying and solitary caterpillars (see Appendixes I and II in Brown and Mielke, 1972; and also in Alexander, 1961*a*, *b*). Adult population cohesiveness may still be high in the absence of communal roosting and home-range movements (if eventually verified) in breeding populations of *D. juno* owing to the spatial arrangement of the preferred food plants for oviposition and larval development: a commercial crop species of *Passiflora* in San Salvador, such as *P. edulis*, may represent a large resource patch for a population with minimal vagility necessary, while a wild species of *Passiflora* with a more patchy distribution (and considerably smaller patch size) would necessitate high adult vagility and a different distributional pattern of reproduction for food plant exploitation. Any combination of multiple utilization of different food plant species with the two distributions would give a mixed strategy. While the distribution of eggs over the available food supply by searching mated females is dependent in part upon the egg-clustering habit of *D. juno*, it is equally apparent that other congeneric species, such as *D. moneta poeyii*, lay their eggs singly on tendril tips. This may be an adaptive response to utilization of more patchy (rare) food plant species by this butterfly.

The social behavior and gregariousness of immatures has been studied in depth for *D. juno juno* in Trinidad by Alexander (1961*a*, *b*) and little can be added here for the subspecies *huascama*. We wish to add, however, that an investigation of chemical defense properties in caterpillars of *D. juno* and how these may relate to gregarious behavior including coordinate defense responses would be very interesting to study.

The question of seasonal changes in population size as seen in several heliconids is an interesting one both from the standpoint of responses by the insects to tropical dry seasons, and the seasonal patterns of vegetative growth of the food plants. Gilbert (1969) noted substantial annual variations in numerical abundance of adult *D. moneta* in North America and suggested that such seasonality might be related to seasonality of vegetative growth of food plants. In Gilbert's experience, adults are most abundant in late summer and early

fall, suggesting a gradual buildup in numbers as the growing season progresses. Emmel and Leck (1970) noted a buildup in adult numbers of *D. juno* during the late wet season in Panama, and general wet season abundance has been also seen for *D. moneta* in seasonal habitats in Brazil (Brown and Mielke, 1972). From our experience with *D. juno* in El Salvador, we wish to add that in strongly seasonal habitats, the dry season may act as an environmental bottleneck through substantial mortality on the pupae, leading to a reduction in adult numbers during the dry season; the effect should increase as the dry season progresses. Of course, such mortality is also very dependent on the structure of the forest canopy and position of the food plant in the plant community: Open, exposed crop stands of *Passiflora* and their herbivores would be more susceptible to strong wind effects than other patchily distributed species in forests and old secondary-growth communities.

Relation to Heliconiine Phylogeny

Emsley (1965) has emphasized with morphological data that there is a distinct subgroup of several closely related genera, namely, the *Dryadula-Agraulis-Dione-Podotricha* subgroup, within the Heliconiinae. Fleming (1960) emphasized earlier that *Agraulis* and *Dryas* were very close to the nymphaline stock that gave rise to the subfamily. Other morphological and behavioral studies of the immature stages (Beebe, Crane, and Fleming, 1960; Alexander, 1961*a*, *b*; Brower, Brower, and Collins, 1963; Brown and Mielke, 1972) have supported these views. As a result (at least in part), of these studies, Brown (1972) proposed an interesting array of generalizations contrasting primitive and advanced heliconiine species, based on field data of representative species (his Table 4, p. 59). We will attempt to apply our data on *Dione juno* to his scheme.

In his formulation, a primitive species is one that: (1) is narrowly restricted to a single faunal range and locally to one habitat, say a forest; and (2) possesses rigid behavior patterns such as male-promenading over large areas, low intermale tolerance, high flying, females shy and rarely observed, and strong diurnal rhythmicity in flower visitations. If there is good correlation with the primitive phylogenetic position of *Dione* based on morphological data with ecological data, then this genus should be primitive also, according to Brown's scheme for field characteristics. Our work permits us to examine some aspects of the scheme for *Dione juno huascama* in El Salvador.

The early faunistic study of Brown (1944) indicated that *Dione juno* has a broad geographical distribution, and our experience in El Salvador is that it occurs at a variety of elevations. Also, it occurs in a variety of habitats, especially those created by man. In El Salvador, there is virtually no undisturbed forest left, and this is conspicuously the case for the San Salvador region. Here, butterfly species are faced with the problem of adapting to a variety of

habitats created by man. Part of the apparent success for *D. juno* in doing this may be related to the choice of food plant species, where at least one crop species is exploited. These two characteristics relating to geographical distribution and habitat selection indicate that *D. juno* is an advanced species in Brown's scheme. As for behavioral patterns of adults, our general experience, in the absence of more quantitative data, has been that various aspects of adult activity are very flexible. Most noticeable is the presence of both sexes together and general feeding at flowers throughout the day, suggestive of advanced species in the scheme. We have not done mark-recapture analyses of individual adult movements, and this would have been desirable to study male-promenading or other movement patterns in this species.

These preliminary results suggest that more primitive heliconiines possess more flexibility in terms of ecological and behavioral adaptations. It is certainly imperative to test Brown's scheme with all of the pre-*Heliconius* genera and to perform experiments on courtship movements of males and general cohesiveness of adult populations in selected species.

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"Artifacts" and "Mimics" of DDT and Other Organochlorine Insecticides[1]

Ralph W. Sherman[2]

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Abstract: Existence of artifacts and mimics of DDT and certain other organochlorines has been demonstrated by a few investigators over a period of eight years. This paper is a selective review of relevant world literature by these investigators. The presence of such artifacts (extraneous substance occurring in nature) and mimics (simulants) had theretofore been obscured by interferences. It was determined that such interferences are inherent in the early colorimetric and total chlorine analytical methods employed prior to the advent of the gas-liquid chromatograph. Such artifacts and mimics are masked by DDT if DDT is present. They give identical analytical reactions as DDT when the two pioneer analytical methods are used. It was disclosed in 1966 that polychlorinated biphenyls are widespread in the ecosystem. Also, PCBs were found to simulate DDT. This discovery negated the putative data that were the basis for previous alleged sensational charges against DDT. Included herein are illustrations of charts obtained from gas-liquid chromatographic analysis of pre-DDT origin soil and of PCBs. These show the presence of artifacts and mimics. The implications of these findings in view of the hazards attributed to DDT are also discussed.

INTRODUCTION

One of the least publicized and hushed-up research findings concerning DDT (dichloro diphenyl trichloroethane) is that a substance occurs in nature that gives identical analytical results as DDT. The first inkling I had that such a bizarre situation exists came about quite accidentally. During a 1962 speaking engagement in Vincennes, Indiana, I toured the Agricultural Research Service's insecticidal laboratory there. Just to make conversation I asked the then-head of the pesticide analytical work, "With all this reporting of DDT found in such unlikely, far-out places, is it possible that there occurs in nature a substance that gives the same analytical reactions as DDT?"

"Oh, yes," he replied, "chemists have had reactions identical with those of DDT when they analyzed materials that have never been exposed to an insecticide. For lack of a better name these unknowns are called 'artifacts' of DDT."

"Why, then," I asked, "hasn't this fact been publicized to show that everything that is being attributed to DDT contamination could just as readily be a naturally occurring substance?"

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[1] This paper presented in abbreviated form at the 14th International Congress of Entomology, Canberra, Australia, August 24, 1972.

[2] Consulting Entomologist. Formerly Chief Staff Officer, Plant Quarantine Division, A.R.S., U.S.D.A. Current address: 1713 Luzerne Avenue, Silver Spring, Md. 20910.

"Well," he answered, "with our present knowledge we are unable to identify these materials."

DISCUSSION

It was not until some years later that I learned of a published scientific paper that furnished proof positive that a "naturally occurring extraneous substance" appearing in pre-DDT soil gave the same retention times as DDT and DDE, its metabolite, when analyzed in a modern, sophisticated gas-liquid chromatograph (GLC). This proof is documented in full detail, including chromatograms by Bowman et al. (1965). In a quick perusal of the published abstract and the paper's contents, one could readily overlook the fact that the paper recorded a real breakthrough when compared to previous analyses quantitating DDT. In gas chromatograms (Fig. 1) reproduced by the authors, the peaks resulting from analysis of untreated soil were identical with peaks resulting from standard extracts of several chlorinated insecticides. More startlingly, however, identical peaks to those of *p,p'*-DDT and *p,p'*-DDE (isomers of DDT and DDE) were obtained from an extract of untreated soil previously held in a sealed 20-gallon container since 1940. The investigators found that although the untreated soil had been taken from an area believed to be free of insecticides, it was initially suspected of being contaminated with 35 p.p.b. *p,p'*-DDE, 62 p.p.b. *p,p'*-DDT, as well as trace amounts of two other organochlorine insecticides. This led the authors to caution that the use of retention times of these peaks as the sole identification of these insecticides was misleading. This was confirmed by the analysis of the same type of soil from the 1940 container. Although this soil antedated the advent of chlorinated insecticides in the United States, the retention times of the zones corresponded to those of the untreated soil. There was less extraneous material in the extract of the 23-year-old sample. In light of these data, the zones in the soil extracts of both untreated and pre-DDT soil were regarded as being due to naturally occurring interferences from this type of soil. Thus, the untreated soil used in the experiment was considered to be essentially free of chlorinated insecticides. The "apparent" insecticidal contaminants therefore qualified as coming under the adopted name "artifacts."

An additional example of the appearence of "apparent" residues of such compounds is described by Frazier et al. (1970). Gas chromatograph charts resulting from the analysis of 34 soil samples that had been stored continuously in tightly sealed glass jars since collection between 1909 and 1911 disclosed some "apparent" insecticide residues in 32 of 34 samples analyzed. The authors concluded that the peaks arose from co-extracted indigenous soil components. The peaks showing the most pronounced apparency corresponded to those of the organochlorine insecticides aldrin and heptachlor epoxide.

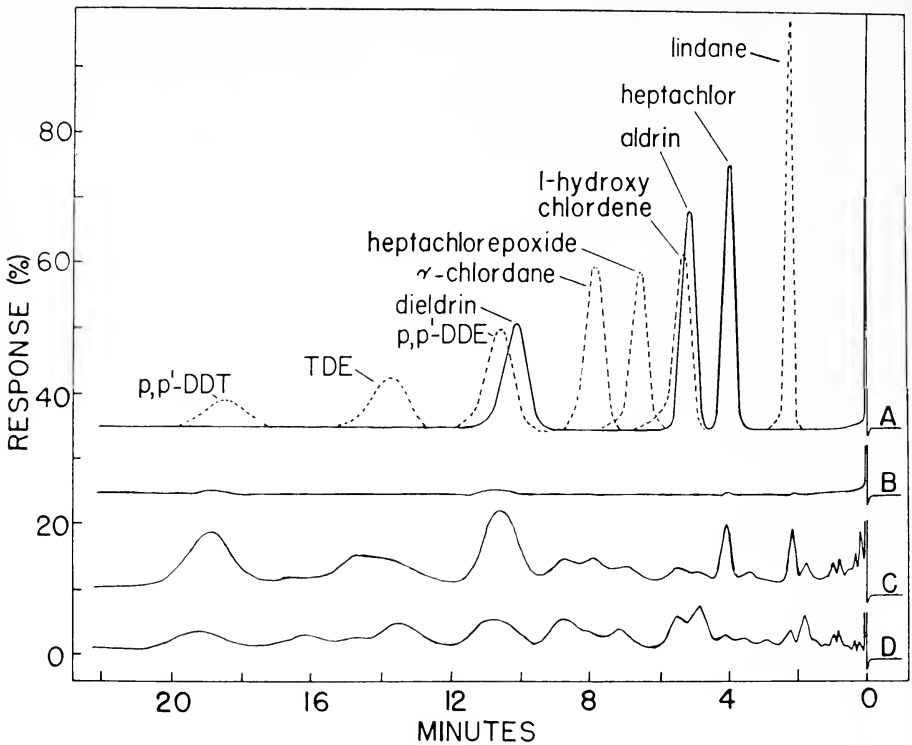

Figure 1. Gas chromatograms: (A) Hexane solution (5 μliter) containing 1 ng quantities of several chlorinated insecticides and related compounds; (B) and (C) extracts equivalent to 2.5 and 25 mg of the untreated soil, respectively; and (D) extract equivalent to 25 mg of untreated soil previously held in a sealed container since 1940. Reprinted from the J. Econ. Entom., vol. **58**, no. 5, October 1965, page 898. Copyright 1965 by the Entomological Society of America. Reprinted by permission of the copyright owners and the authors (Bowman et al., 1965).

That the Food and Drug Administration has also been guilty of just such an erroneous determination is highlighted in Senate Report No. 1578 (United States Senate, 1964). This report accompanied H.R. Bill 3642. The bill in question conferred jurisdiction upon the United States Court of Claims, "to hear, determine, and render judgment on the claims of Mike Mizokami, Sam Mizokami, Tom Mizokami, and Hatsuyo Mizokami, of Blanca, Colorado, based upon damages allegedly sustained as the result of erroneous determination by the F.D.A. in 1962 that spinach grown by them was contaminated by the pesticide heptachlor." The private bill was passed and was approved by the President on December 6, 1964. The comedy of errors that led to the enactment of this bill is described in the Senate Report, reading, in part, as follows:

...as part of the Food and Drug Administration's pesticide program, a sample of fresh spinach was collected from Mizokami Bros. Produce. The sample was tested by the Administration's Denver District office for the presence of pesticide residues. On August 2, 1962, the test results apparently indicated the presence of heptachlor. In the language of the report of the Department of Health, Education and Welfare, "there is no established tolerance" for heptaclor in spinach. Ultimately, as a result of further testing, the Government found that the evaluations of the original tests were erroneous and that the spinach was not adulterated.... The initial test was performed by gas chromatography and indicated the presence of heptachlor residue for which there is no established tolerance. The New York district of the Administration was immediately advised and on August 6, 1962, samples of spinach were collected in New York from a carload shipment by Mizokami Bros. Produce. Residue tests on these samples were performed by paper chromatography, because the gas chromatography equipment was not yet installed in New York. Both tests apparently indicated the presence of heptachlor.

On August 9 the New Jersey consignee was informed that the spinach was adulterated and was requested to hold the spinach available for a State embargo and for Federal judicial seizure. Seizure of 418 20-pound bushel baskets was effected on August 20, 1962, pursuant to court order. The approximate value of the seized spinach was $1,024.

Subsequent tests of the seized spinach established that evaluations of the original tests were erroneous and that the spinach was not adulterated. On September 17, 1962, the seizure action was terminated but by this time the spinach had decomposed and was worthless.

On September 24, 1962, the Food and Drug Administration addressed a letter to Mizokami Bros. Produce, advising them of the reversal of the Government's position and expressing regrets for the occurrence of the incident.

In brief, there was involved in the Mizokami Bros. Produce debacle an erroneous determination by gas chromatograph at Denver. A second sample taken from a carload of this producer's spinach upon its arrival in the East likewise gave a false reading of heptachlor when analyzed in New York by still another analytical method, paper chromatography. Not until a representative of a chemical manufacturer determined that no heptachlor had been used on the spinach nor anywhere in the vicinity of the growing crop were the findings of the F.D.A. questioned. When the facts were outlined to the Administration, the remaining reserve sample was forwarded to the F.D.A. Division of Food in Washington for check examination. The check examination, using gas chromatographic procedures, failed to confirm either the first gas chromatographic analysis in Denver or the paper chromatography examination in New York.

In other words, F.D.A.'s examinations are not infallible. Since their report on H.R. 3642 states that "an occasional mistake is certain to occur" and that the Mizokami's "situation is not unique," it is logical to conclude that many similar instances have occurred over the years, but the aggrieved parties have not contested what H.E.W. has termed, "good faith mistakes."

At the September 1966 meeting of the American Chemical Society in New York City, Francis B. Coon, Head of the Chemistry Department of WARF

Institute, Inc., Madison, Wisconsin, presented a paper (F. B. Coon, 1966), the abstract of which reads as follows:

Animal tissues of a chronological age known to precede the advent of chlorinated insecticides were analyzed by an electron capture gas chromatographic procedure. The purpose of the study was to find, if possible, background levels which could be applied to chlorinated insecticide residue analysis. The gas chromatographic charts so obtained were compared to similar charts of authentic chlorinated insecticides. Some of the tissues studied showed peaks which were at or near the retention time of known insecticides. The levels found, when calculated as individual insecticides, are of the order of 0.05 p.p.m.

After considerable searching of the files, Mr. Coon was able to supply a copy of the unpublished paper showing the results he obtained at WARF Institute in analyzing selected samples of authentic pre-DDT origin. In this report, Mr. Coon tells of one of WARF's early insecticide-residue projects to determine the DDT and DDE content of fish taken from sprayed areas in forest lands of the West. Control fish from areas of no known DDT contact, as well as the test fish, were analyzed by the Schechter-Haller method (Schechter et al., 1945). A fly bioassay followed to confirm the colorimetric findings. Low levels, 0.05 to 0.5 ppm, of both DDT and DDE were found in all fish tested. Even the control fish showed levels of 0.05 to 0.1 ppm. WARF was unsuccessful at that time in locating fish that did not give a positive response to this form of analysis.

With the introduction of the gas-liquid chromatograph the search was continued. Requests were made to several individuals and museums for representative samples of known pre-DDT origin. In this 1965 solicitation for pre-DDT specimens for analysis at WARF specific mention was made that the material should have had no environmental contamination with chlorinated hydrocarbon insecticides.

As a result of this search many excellent specimens were obtained. All specimens were properly documented, sampled, and assayed, using electron capture gas chromatography. Among the chromatographic charts presented by Mr. Coon were the following:

A graphic presentation of 0.25 nanograms each of DDE, DDD, and DDT.

A similar chart resulting from analysis of the liver from a male *Hylobates* gibbon collected January 31, 1935, at Tasu, Burma. The specimen had been stored in an unopened tank since 1935. One of the peaks on this chart had the same retention time as DDE.

Three additional charts presented refer, respectively, to the kidney, testes, and intestinal fat from the same gibbon. All three show a peak with the same retention time as DDE. All have other similarities and some differences.

In addition to the data reported by Mr. Coon in his 1966 paper, he has also supplied photographs of heretofore unpublicized chromatographic charts of a 1938-collected fledgling robin supplied by Dr. J. J. Hickey, Department

of Wildlife, University of Wisconsin. These charts were retrieved from WARF Institute files only after persistent search. The chromatographic chart of the robin shows peaks with the retention times of DDT and DDD (dichlorodiphenyl dichloroethane, TDE). Further, a chart of the formaldehyde from this robin shows a peak with the same retention time as DDT.

Two artifacts of dieldrin (an epoxide of aldrin) have been found in the green leaves of alfalfa, wheat, corn, kale, clover, and grass, but not in soil, water, or nongreen plants (Glotfelty and Caro, 1970). The artifacts discovered were not easily detected under normal GLC conditions and resisted removal by the common cleanup procedures for plant material. Under certain circumstances a completely symmetrical "dieldrin" peak was secured, so that the presence of the artifacts was completely disguised. It was also found that multicolumn analysis at normal column temperatures could lead to false conclusions about the presence of dieldrin in the test sample. The authors conclude that the artifacts are non-halogenated, pigment-related natural products, found only in photosynthetic tissue. Indirect evidence suggests that the artifacts are xanthophyll esters.

Swedish scientist Soren Jensen's announcement (Anonymous, 1966) of the discovery of polychlorinated biphenyls (PCBs) in fish, birds, and humans alerted some scientists in the United States to the possibility that unidentified compounds that long had been interfering with (or more specifically, "mimicking") the identification and quantification of organochlorine insecticides might be PCB.

As a result of reoriented analytical searches, a comprehensive review of complications introduced by PCBs was compiled (Risebrough et al., 1968). The authors described the 1967 collection in Baja, California of an unhatched, abandoned egg of a peregrine falcon. Unknown peaks present in the chromatograms of the extract of the egg were unidentified until the PCB announcement led the investigators to search for the compound. The retention times of the unknown peaks in the peregrine extracts proved to be identical with those of several PCB compounds. The authors tabulated the results of analyses of 137 specimens from three species of fish and thirty-one species of birds. With a solitary exception, every sample that was positive for DDT or DDE was also reported to contain PCB in varying amounts.

A rather surprising disclosure appeared in what might be termed a transitional article between the years when DDT and its metabolites were the major compounds used as standard comparisons and the reoriented analytical procedures required after the ubiquitous nature of PCB was discovered (Anderson et al., 1969). Close attention is necessary to certain tabular material in this article to comprehend its full import. Results are shown of residue estimates of five cormorant and pelican egg pools at different time intervals.

Table 1. Comparison of plasticizers and insecticides by GLC. Reprinted from the J. Econ. Entom., vol. **62**, no. 4, August 1969, page 763. (Lichtenstein et al., 1969).

Plasticizer Aroclor		% weight chlorine	GLC I[a] No. of peaks	GLC I[a] Identical with[c]	GLC II[b] No. of peaks	GLC II[b] Identical with[c]
1221-2[d]	A	21	1	None	5	LI
1232-2	B	32	15	LI, HE, AL, DE, DI, TD, DT	15	LI, HE, HO, DE
1242-2	C	42	14	LI, HE, AL, DE, DI, TD	14	LI, HE, HO, DE,
1248-2	D	48	15	LI, HE, AL, DE, DI, TD, DT	15	LI, HE, HO, DE DT
1254-2	E	54	11	AL, DE, DI, TD, DT	10	HO, DE, TD, DT
1260-2	F	60	15	TD, DT	13	DI, TD, DT
1262-2	G	62	12	TD	13	DI, TD, DT
1268-2	H	68	7	None	8	None
4465-2, 3	I	65	11	TD	11	DI
5442-3	J	42	3	None	7	LI, HE, HO
5460	K	60	3	None	0	None

[a] Packard gas chromatograph, column 5% SE 30 on 60/80 chromosorb W. Oven temp. = 190°C.
[b] Jarrell-Ash chromatograph, column 5% QF-1, 5% DC 200 (1:1) on 80/90 Anakrom AS. Oven temperature = 190°C.
[c] LI = Lindane, HE = Heptachlor, HO = Heptachlor epoxide, AL = Aldrin, DI = Dieldrin, DT = *p,p'*-DDT, DE = DDE, TD = TDE.
[d] 2 = chlorinated biphenyls, 3 = chlorinated triphenyls.

Analyses by standard GLC in 1965, prior to the PCB announcement, showed the respective egg pools to contain *p,p'*-DDT at the following ppm: 0.30, 2.80, 1.40, 0.20, and 0.20. When the same egg extracts were reanalyzed by standard GLC in 1969, this time with the knowledge that PCBs may have been inaccurately measured and the DDT content thereby exaggerated, the ppm of DDT were 0.00, 0.00, 0.44, 0.00, and 0.05. Thus, the original analyses were 100 percent wrong in three instances, with an overall 90 percent deviation from the original evaluations.

Lichtenstein et al. (1969) supplied a thorough explanation of the multiple interferences of various PCBs with most organochlorine insecticides. Eleven polychlorinated bi- and triphenyls were analyzed with two different columns in separate gas chromatographs. The observed retention times were compared with those obtained after the injection of the organochlorines lindane, heptachlor, heptachlor epoxide, aldrin, DDT, DDE, and TDE. The injection of nearly all the PCB plasticizers resulted in chromatograms with a multiple of peaks, sometimes as many as fifteen. The authors' tabular material (Table 1) shows that Aroclors 1232, 1242, 1248, and 1254 gave identical peaks with DDE in both chromatographs and that Aroclors 1232, 1248, 1254, 1260, and 1262 gave identical peaks with *p,p'*-DDT in one or both chromatographs. Photographs of thin layer plates used in the analyses show that Aroclors 1221, 1232, 1242, 1248, 1254, 1260, and 1262 result in spots identical with the standard *p,p'*-DDE. At least three each of the Aroclors produced identical spots with lindane, heptachlor, heptachlor epoxide, aldrin, dieldrin, and TDE.

A clear explanation of the total interference of PCBs with the organochlorides is furnished by Gustafson, 1970. The gas chromatographic charts illustrating the article (Fig. 2) show conclusively that when PCBs are present in a sample they give a pattern of several GLC peaks, whose retention times are similar to those of DDT, DDE, aldrin, and heptachlor epoxide.

These multiple interferences are also confirmed by Reynolds, 1969. In Reynold's investigations it was found that peaks of each of the commonly found pesticides have corresponding PCB peaks. The PCB peaks, therefore, would interfere with the pesticide peaks if PCB were present in the same extract. Reynolds called attention to the ease with which one could report false results, especially if use is made of the GLC results without further confirmation. Even when thin layer chromatography (TLC) is used as a confirmatory method, Reynolds found that one could quantify the whole as being the pesticide and be out by many factors depending on the ratio of the two compounds giving rise to the GLC peak.

An analytical chemist of the Division of Foods, Food and Drug Administration, told me several years ago that a zero tolerence for anything is no longer possible. "You name it," he said, "and we'll find it." And he's right.

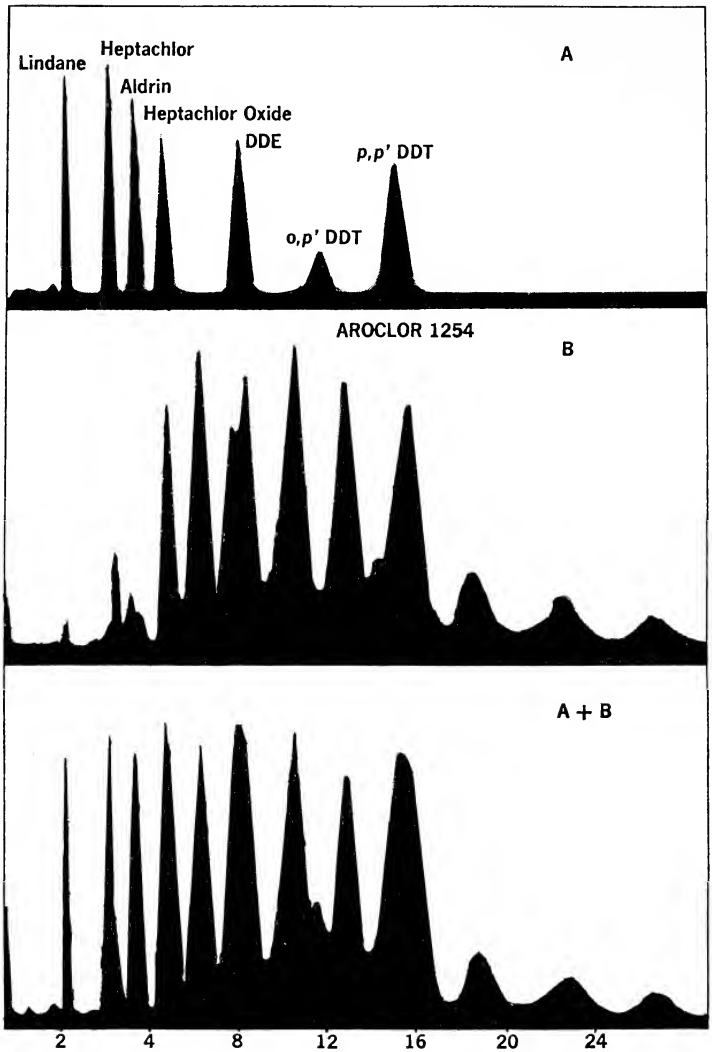

Figure 2. Gas chromatogram A is of a standard pesticide mixture, B is typical of Aroclor 1254, and A plus B is the chromatogram of a 50:50 mixture of both. The concentration of Aroclor 1254 is approximately 10 times that of the pesticides in A; hence it is understandable why PCB's were not readily recognized in pesticide chromatograms. Reprinted from Environmental Science and Technology, vol. 4, no. 10, October 1970, page 817. Copyright 1970 by the American Chemical Society. Reprinted by permission of the copyright owner and the authors (Gustafson, 1970).

New methods of residue analysis now make possible the detection of minute amounts of chemicals that were previously undetectable. The state of the art is now such that one needs to learn lower mathematics, to extend one's imagination to comprehend a microgram (one-millionth of a gram), a nanogram (one-billionth part), and a picogram (one-trillionth part). To envision one part per trillion, think of the size of a football compared with the spaciousness of the Houston Astrodome. Despite zero or no-residue restrictions imposed on pesticides, analyses of foods will continue for years to come and for some "apparent" pesticides, in perpetuity, to show peaks identical with DDT, DDE, and other organochlorides. Such peaks may be caused by artifacts of these compounds, by PCBs, or by persisting trace amounts of the actual organochlorides.

RESULTS AND INTERPRETATIONS

The abundant evidence showing that artifacts and mimics of DDT have been reported as authentic DDT, despite the fact that they were "apparent" rather than "real," carries many implications. The outstanding impact is that all analyses performed either by the Schechter-Haller colorimetric method or the total chlorine method are not only suspect but are invalid until reassessed by modern techniques. The Schechter-Haller method was the classical one employed from its introduction in 1945 until the advent in the United States of the gas chromatograph in the early 1960s. The transition in method is illustrated by two publications by Turner (1965, 1970), reporting on the analysis of fish from Connecticut rivers. The results reported for 1963 were obtained by the Schechter-Haller method. The reports of tests in 1966 were based on GLC charts confirmed by paper chromatography.

The fallibility of the Schechter-Haller colorimetric method is apparent from the erratic results of early analyses run at WARF Institute (Coon, 1966). Gunther (1955) states that most aromatic compounds will interfere with this procedure. Also, the Food and Drug Administration's 1967 Pesticide Analytical Manual, in commenting on this method, states that numerous compounds closely related to DDT, such as chlorobenzilate and methoxychlor, are known to produce a color similar to that of DDT.

For a time the total chlorine method of analysis was popular and competed, more or less, with the Schechter-Haller method. Gunther (1955) states that any chlorine-containing compound will interfere with this method of analysis. One of the latest citations of the inadequacy of this method appears in an Environmental Protection Agency publication (Curley et al., 1971). In summarizing the evolution of analytical methods, the authors note that total organic chlorine analysis in 1948 provided for the first determination of DDT storage in man. They also state that since this method has no specificity for

DDT, the total organic chlorine would not preclude the presence of other organic-chlorine-containing moieties. As a result these investigators employed a combination of GLC and mass spectrometry (MS).

Also, in a 1970 publication by investigators of the Food and Drug Administration's Perrine, Florida, Laboratory (Biros et al., 1970), a combined GLC-mass spectrometry system was used in the determination of PCBs in human adipose tissue.

Of the approximately 535 bibliographical references cited in Rachel Carson's *Silent Spring* (1962), approximately 75 are of 1960 origin, 50 of 1961, and a dozen are attributed to 1962 origin. A check of the individual citations listed for the 1960s and a review of the narrative drawn from these sources disclose that the analyses of DDT on which they are based were performed by methods that have since been discredited and abandoned. Such methods gave results that failed unequivocably to determine with absolute specificity whether the residue detected was DDT; an extraneous substance occurring in nature; or PCB, the presence of which prior to 1966 had been detected as DDT or one of its metabolites. Prior to the introduction of the GLC, the then-existing state of the art of DDT residue analysis is best described as one of relative ignorance.

From current analytical chemical literature, combined GLC/MS is now considered the preferred standard method for accurately measuring and identifying organochlorine residues. Thus far there have been few attempts to replicate and validate by currently acceptable methods the sensational claims of the 1948–1962 period.

During the period 1942 through 1962, DDT carried piggyback naturally occurring extraneous substances plus PCBs, both of which gave identical colorimetric responses, total chlorine results, and GLC peaks as DDT, its metabolites, and several other organochlorine insecticides. DDT thus has been the scapegoat for these artifacts and mimics.

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(Note from the editors: This paper focuses attention on the importance of using proper tests for identification of DDT and other compounds and stresses the fact that some of these compounds were erroneously identified by gas chromatography. The emphases and conclusions are those of the author and do not necessarily reflect the views of the editors.)

Notes on the Life Cycle and Natural History of Butterflies of El Salvador

I A.—*Catonephele numilia esite* (Nymphalidae-Catonephelinae)

Alberto Muyshondt

101 Avenida Norte #322, San Salvador, El Salvador

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INTRODUCTION

This is the first article of a second series (elsewhere we have presented a first series dealing with the subfamily Charaxinae), describing what my sons and I have found about the life cycle and natural history of butterflies of the Catonephelinae group of the Nymphalidae found in El Salvador, the smallest country of Central America.

It is our understanding that the life cycle of many species of neotropical Rhopalocera is at least incompletely known and therefore they have been classified based exclusively on the adults' morphological characteristics. According to E. B. Ford (1945), "Any classification must take into account as many as possible of the external and internal structures not only of the adult but of the early stages." With this in mind, we undertook the task of rearing from egg to adult as many of the local species as possible, photographing the different stages of the metamorphosis, recording the measures and the time elapsed on each one. Specimens of the early stages have been preserved in alcohol and are sent to museums where they are kept and are available to students of the groups.

A major difficulty has been the determination of the species described, as we are dependent on A. Seitz (ed.), 1924, "Macrolepidoptera of the World." Vol. 5, The American Rhopalocera, 1907–14, a book that is, according to Klots (1960), "replete with errors that cause much confusion." To solve this problem we have requested the valuable assistance of Drs. A. B. Klots and F. D. Rindge of the American Museum of Natural History and L. D. Miller of the Allyn Museum of Entomology, who have kindly identified the material submitted to them.

Acknowledgments: We express our deep obligation to Dr. Alexander B. Klots who, in the course of three years, has given much needed encouragement and guidance from his vast experience in studying butterflies and has taken the time to read this manuscript to help to make it presentable. We are grateful also to Dr. F. D. Rindge who identified the species described and gave valuable counsel. My appreciation also goes to Drs. A. M. Young and S. D. Steinhauser who provided reference material. The senior of the Muyshondt family gives due credit to his sons, in particular, Albert, Jr., and Pierre, for their unfailing enthusiasm in the fieldwork.

In our article on *Prepona omphale octavia* Frühstorfer (Muyshondt 1973 A), we made a rough description of the country, its climatic zones, and other pertinent information, so as to form an understandable picture of the habitat of the species described.

We have observed *Catonephele numilia esite* Felder at altitudes ranging from 500 m. to 1200 m., always in the neighborhood of coffee plantations (that are manmade forests owning to the local technique of planting the coffee under shade trees), mostly between June and November, that is, mostly during the rainy season (May to October).

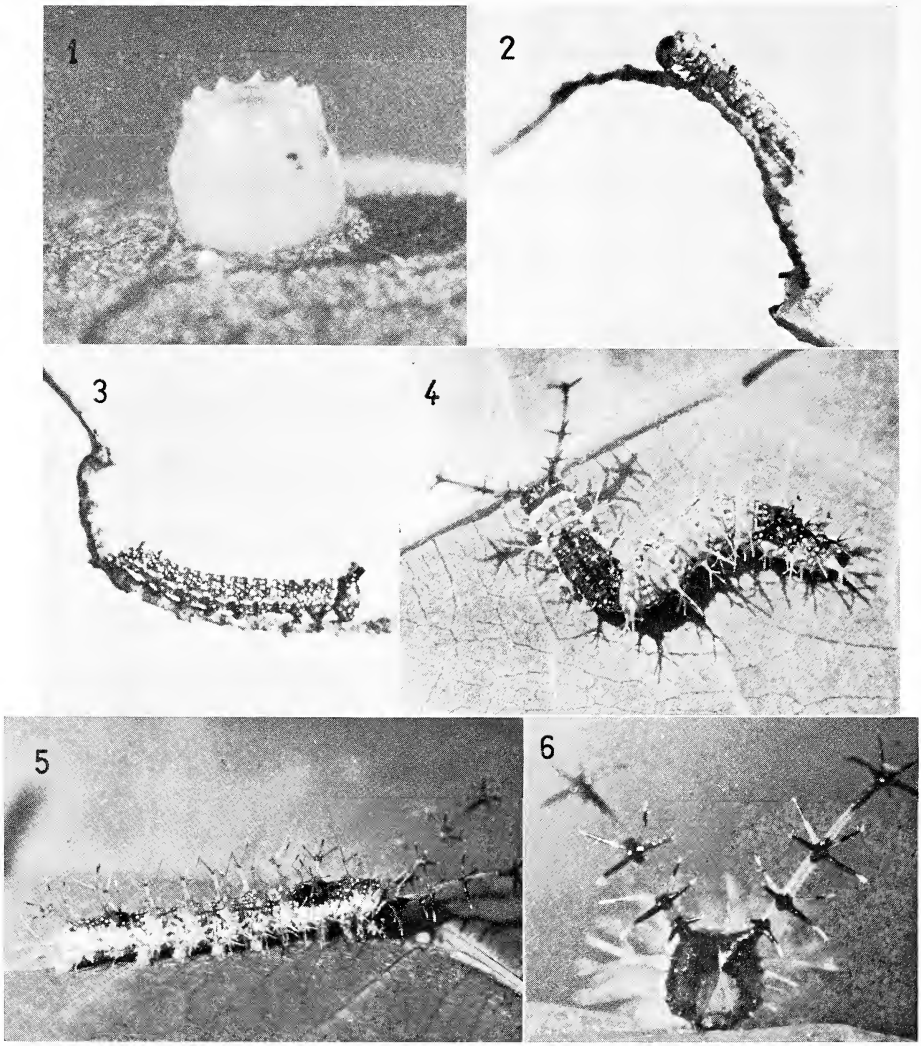
On September 8, 1969, my eldest son captured two identical and for us unknown larvae on a very broad-leaved tree known locally as "Tepeachote" (later identified as *Alchornea latifolia* Swartz). The larvae pupated the following day without feeding on the leaves on which they were found and produced, on September 19 and 20, two different butterflies, which were later identified as *C. numilia esite* male and female.

Assuming that the plant on which the larvae were found was the foodplant, weekly searches were made for them. On July 24, 1970, my eldest son again saw a female ovipositing on a tree of the same species in the neighborhood of Nuevo Cuscatlán, a village located about 8 km. southwest of San Salvador, capital of El Salvador. Nine eggs were collected then, put in individual transparent plastic bags, and brought back to our insectarium. Photographs were taken of the eggs and of the larvae that hatched from them until the adults emerged. Records of the time and measures of the different stadia were kept and specimens of the various instars and of the pupa were preserved in alcohol. During the whole process, the bags were under ambient light and temperature conditions. No moisture control was maintained, but the amount of moisture was high on account of the plastic bags, even if they were opened every day to clean them. Since that time we have reared this species many times, during different months of the year, except April and May, with about the same results. The specimens of the early stages and adults have been placed with the American Museum of Natural History, New York.

LIFE CYCLE STAGES

Egg. Truncated cone, about 1 mm. long and 1 mm. laterally at widest point. White with a bright yellow zone around the micropyle located on the center of the convexity tipping the egg. Around this convexity there is a crown of eleven thick and short prominences. From each prominence originates a vertical rib, of the same color as the rest of the egg, which reaches the base of the egg. They turn yellowish one day before hatching, which takes 4 to 5 days.

First instar larva. Head naked, dark brown, roundish, slightly thicker than body. Body dark green with caudal segments brownish-orange, naked with brown true legs. About 2 mm. when recently hatched and 5 mm. before moulting. 3–5 days.



FIGS. 1–6. *Catonephele numilia esite* Felder.

FIG. 1. Egg, about 1 mm. long.

FIG. 2. First instar larva ready to moult, on prolonged vein. Frass pellets can be seen stuck to body. About 5 mm. long.

FIG. 3. Second instar larva on prolonged vein. About 9 mm. long.

FIG. 4. Third instar larva with typical "S" attitude. About 1.2 cm.

FIG. 5. Fourth instar larva with straight attitude. About 2.3 cm.

FIG. 6. Fourth instar larva. Closeup of head.

Second instar larva. Head brown with white peppering. One stubby horn ending in a rosette of tiny spines on apex of each epicranium. Body olive-green dorsally, brown below spiracula, all mottled with white dots. Thoracic segments with four short branched white spines each. All abdominal segments with a transversal row of seven short, branched, white spines each, except the last two segments: the last one with only two lateral spines, the one before last with four lateral spines. It grows to about 9 mm. in 3–4 days.

Third instar larva. Head shiny black with white line around cervical triangle and long horns on epicranial apex, with three rosettes of spines each horn: the basal and median rosettes with four spines, the apical with five. Horns greenish with black zones at the base of the rosettes. Body olive-green with black areas dorsally from second thoracic segment to second abdominal segment, and from seventh abdominal segment caudad. Long forked spines cover the body now, following the same arrangement as in second instar. It grows to 1.2 cm. in 3–4 days.

Fourth instar larva. Same general aspect as in third instar, except for longer horns and orange-red areas on the head at the base of horns and in front. Thin spines at lateral margin of epicrania from base of horns to ocelli. It grows to 2.1 or 2.5 cm. in 4–6 days.

Fifth instar larva. Head mostly reddish-orange except lateral black margins of epicrania from base of black and green horns to mouth parts. Long and thin spines around margin of epicrania and shorter spines between horns. Body all green, mottled with white dots. Dorsal spines orange with black forks, the rest green with black forks. It grows to 4.2 cm. in 8–11 days.

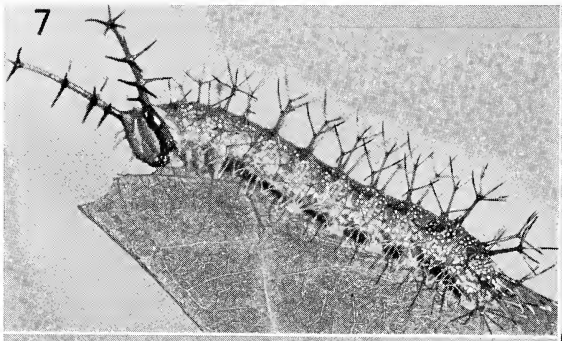
Prepupa. Much shorter and thicker, but same colors as fifth stadium. 2.5 cm. long. Duration, 1 day.

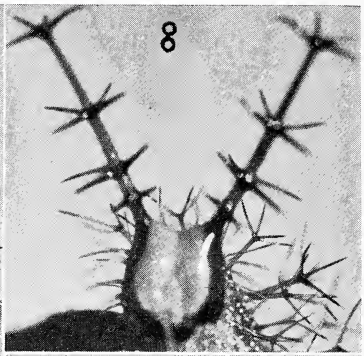
Pupa. Green of various shades, except for brown margin on wingcase on thoracic area, and small orange spiracula. Abdomen thickening gradually from cremaster to wingcase, then about the same thickness to thorax, separated from abdomen dorsally by indentation, then tapering gradually to bifid head. Cremaster has a flat base armed with crochets that permits the pupa literally to "stand" on the silken pad. Measures 2.3 or 2.8 cm. long, .9 or 1.0 cm. laterally at widest point, and .8 or .9 cm. dorsoventrally at widest point. Duration, 8–11 days.

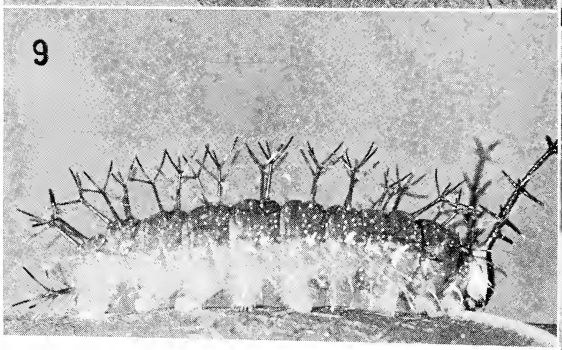
Adult. Both sexes have about the same shape. Forewing with projected angle at apex, then sharp concavity (more so in females), then rounded convexity to tornus; inner margin straight. Hind wing rounded with outer margin slightly sinuose. Colors drastically different in males from females, dorsally.

Males. Dorsally basic color dark brown on both wings. Forewing with roundish orange zone at discal area, and smaller orange round spot at subapical zone. Hindwing with a squarish orange zone at discal area, a bluish zone at outer margin and a blue dot at anal angle. Ventrally both wings a combination of brown of different shades, from very light to very dark, except a yellowish area in forewing from basal to discal zones.

Females. Dorsally dark brown both wings as in male, but with four elongated yellow spots in line on discal area, and a line of two small yellow and one small reddish spots in subapical area. On the hindwing some bluish lines parallel to outer margin, from outer angle to anal angle. Ventrally combination of brown of different shades, darker than in males. There is a replica of the dorsal discal yellow spots on the forewing. Sizes average 6.0 cm. in males, 6.6 cm. in females, from tip to tip of spread forewings. Total developmental time varies from 34 to 47 days, females taking longer than males usually.







FIGS. 7–11. *Catonephele numilia esite* Felder.

FIG. 7. Fifth instar larva feeding at edge of leaf. About 4.1 cm. long.
FIG. 8. Fifth instar larva. Closeup of head.
FIG. 9. Prepupa on top of leaf. About 2.5 cm. long.
FIG. 10. Pupa lateral view. About 2.5 cm. long.
FIG. 11. Pupa dorsal view.

NATURAL HISTORY

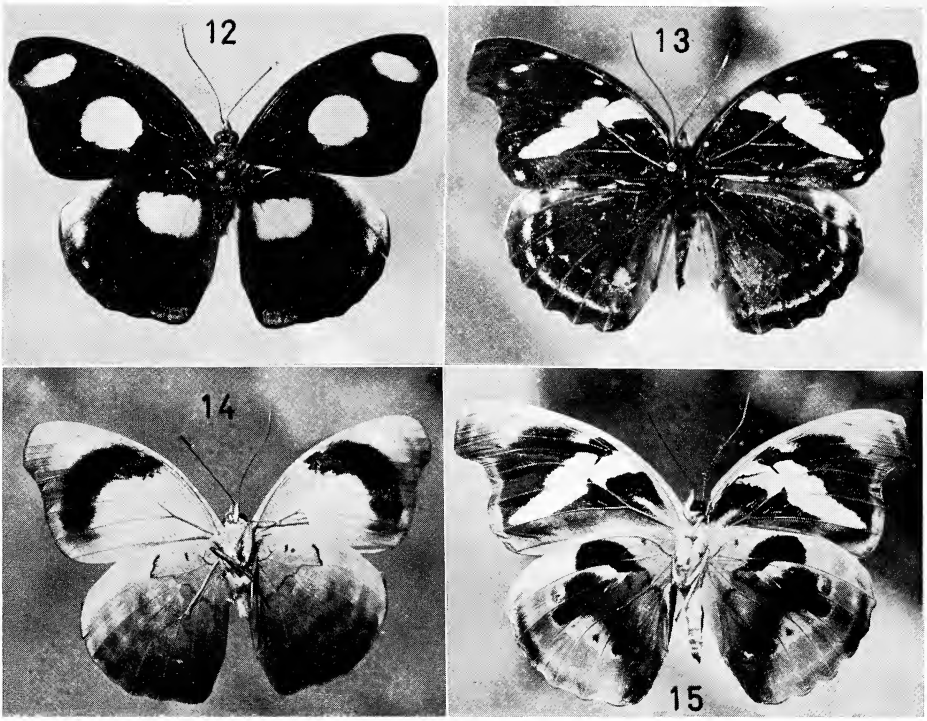
The foodplant of *Catonephele numilia esite*, *Alchornea latifolia*, is a medium-sized tree (up to 20 m. tall), locally called Tepeachote, with alternate, long-petiolate, broadly ovate, about 25 cm. long leaves with crenated margin; it belongs to the Euphorbiaceae family. The tree is found in coffee plantations where it is used, even if sparsely, as a shade tree and for its wood. Its range covers from 500 m. to 1500 m. of elevation.

The eggs of *C. n. esite* are deposited singly on the underside of mature leaves, mostly near the middle of the leaf, and even if the eggs are rather small, their white color contrasts against the green of the leaf, so they can be located with relative ease. At times more than one female oviposits one egg on a single leaf, so that more than one can be found on an individual leaf.

The recently emerged larvae eat the top of the eggshell and even part of the walls, but we have never seen them devour the eggshell completely. Shortly after feeding on the eggshell, the tiny larvae crawl to the edge of the leaf and start nibbling around the terminal of a vein until it is bare, and at the same time they affix the small frass pellets to it with silk, so that soon the vein seems to project beyond the leaf limits. To do this the larvae bend their bodies backward and with their mouthparts grab the pellet that is being expelled and then place it on the bared vein, weaving silk to affix it. It is not uncommon to find first and second instar larvae with several pellets of frass stuck with silk to their body. The larvae use this prolonged vein as a resting place at all moments while not feeding and during the first and second stadia, keeping the head pointing outward.

During the third, fourth, and fifth instars the larvae move about the plant, usually on the upper surfaces of the leaves, and, while resting, adopt two characteristic attitudes: one, the body straight, and two, the body "S" shaped. In both cases the head is bent forward so that the long horns are parallel to the leaf surface. If touched with a thin object the larvae strike suddenly with the horns with a back or side movement, depending on their physical position. Sometimes more than one larva move to the same leaf and accidentally touch another. When this happens the touched one reacts violently and strikes the offender with its horns, usually puncturing its body fatally; or both might strike simultaneously with similar results. We have found two larvae with their horns locked in such a way that they had succumbed to starvation. This might cause selection against any social habit.

When ready to pupate the larvae weave a silk pad, usually on the upper surface of the leaf, and affix to it their anal prolegs, keeping the body straight, resting on the leaf surface, the horns upraised or bent forward. Shortly before doing so they clean the digestive tract by ejecting an amount of green liquid mixed with excrements.



FIGS. 12–15. *Catonephele numila esite* Felder.

FIG. 12. Male, dorsal view. About 6 cm. from tip to tip of spread forewings.

FIG. 13. Female, dorsal view. About 6.5 cm from tip to tip of spread forewings.

FIG. 14. Male, ventral view.

FIG. 15. Female, ventral view.

The pupae, due to their relatively large, flat surface armed with crochets on their cremaster, keep themselves "standing" at an angle on the upper surface of the leaves. Sometimes they seem to hang when the supporting surface is the underside of a leaf or a twig, but if the object is turned over it becomes evident that the pupae are not hanging, but standing on it, as they maintain the same angle regardless of the object's position. There are times when the pupae get punctured by their own exuvia in the process of affixing the cremaster to the silken pad and disposing of the crumpled larval skin. The pupae when molested respond with violent lateral swings or move in an accordionlike fashion. In both cases they produce a faint, but audible, squeaking sound somewhat like that of cerambicid beetles.

The adults of this species emerge rapidly from the pupa shell and walk to a surface from which they can hang, and in about 15 minutes their wings are rigid and ready to fly. During this process they eject an amount of reddish meconium.

We have dissected recently emerged females and none of them had eggs in their abdomen.

Both sexes are strong flyers. Males favor treetops where they can be seen standing alertly and darting swiftly to chase other males of the species, but they permit other species (mostly *Anaea* spp.), to use their chosen treetop without attacking them. Females are seen flying at lower levels and alighting on tree trunks with their heads pointing downward. The females are slightly larger than males.

Recently emerged couples have been kept in a cage for as long as 10 days, feeding on fermenting banana, without obtaining copulation.

When ready to oviposit the females fly around the chosen tree a few times, alight on the underside of a mature leaf, near its middle, deposit one egg thereon, and immediately resume flying. They repeat the process some eight to ten times before departing. Oviposition occurs usually between 10:00 and 14:00 hours.

In the fields both sexes feed greedily on a variety of fermenting fruits, usually on the ground, and on animal excrements. While feeding they lose their alertness and can be netted with facility. We have never seen adults of this species on flowers.

We have found eggs of *C. numilia esite* the year around but mostly during the rainy season (May to October).

DISCUSSION

J. Röber (1914) described very well the fifth instar larva and the pupa of *Catonephele numilia* and reported the foodplant, in South America, to be *Alchornea iricura* Cas. and *A. cordata* Müller Arg. However, apparently this is the first complete life history description with photographs of this species.

Ebert (1969) groups under Catonephelinae other genera besides *Catonephele* (*Cybdelis*, *Epiphile*, *Myscelia*, and *Temenis*), some of which are represented in El Salvador lepidopterous fauna, plus others: *Pyrrhogyra* and *Pseudonica*, whose eggs, larvae, pupae, and behavior during the early stages are so similar to that of *Catonephele numilia esite* that we do not hesitate to group them together. We even dare to suggest that the genus *Pyrrhogyra* probably is the intermediate between Catonephelinae and Callicorinae, because the eggs of *Pyrrhogyra* are more like the later group than *Catonephelinae*, although the larvae are not. Ebert (loc. cit.) groups the genera *Callicore*, *Diaethria*, and *Paulogramma* under Callicorinae. (We add, for the same reasons as above, the genus *Catagramma*.) If the characteristics of the early stages and their behavior mean anything, it is evident that the two groups are at least very closely related.

In addition to *C. numilia esite*, we have reared from egg to adult *Epiphile*

adrasta adrasta Hewitson (manuscript in preparation), *Temenis laothöe liberia* Fabricius (manuscript in preparation), *Pseudonica flavilla canthara* Doubleday, *Pyrrhogyra hypsenor* Godman & Salvin of the Catonephelinae group, and *Diaethria astala* Guérin and *Catagramma titania* Salvin of the Callicorniae, besides other species we have studied incompletely that belong to either group. From this experience we agree with Holland (1914) that "species which are related to one another show their affinity even in the form of their egg," and with Brower, Brower, and Collins (1963) on "... characters on which the forces of centripetal selection resist change to a greater degree. Classically these are the external morphological characters of the eggs, larvae, pupae and adults." ... This criterion is reinforced by the similarity of the behavior of the immature stages of the mentioned species belonging to the two groups, which, according to Crane (1957), is an important factor in determining phylogenetic relationships. This will become most apparent as the following articles of the intended series are presented.

The first and second instar larva of *C. numilia esite* and the other species mentioned behave similarly in the way the eggshell is eaten: Just the upper part of it and sometimes part of the wall are consumed by the recently emerged larvae. Again, all of them have the same habit of moving to the edge of the leaf, nibbling around a vein, prolonging it with frass stuck with silk, and using this vein as a resting place while not feeding.

Catonephele n. esite and others use the bared vein as described during the first and second instars only, while others use it even during the third stadium. All of them, during the fourth and fifth instars, wander about the upper surface of the leaves, and, when resting, adopt the same attitudes: the "S" shaped and the straight ones, with the head bent forward to keep the horns parallel to the leaf surface. Besides the behavioral similarities there are striking morphological ones: First and second instars can very easily be taken for one another. From the third stadium on, there are differences not only in coloration but in the spines that cover the body: They are more or less abundant or almost lacking, but the head and its horns keep the same pattern. The pupae of all these species also have the same general aspect with minor differences; all of them have the cremaster with the flat surface that permits them to "stand" on the leaf; and all of them produce the defensive sound when molested. Only three of the local species included in the Catonephelinae group show a drastic sexual dimorphism when adults: *Catonephele numilia esite, C. nyctimus* Westwood, and *Epiphile adrasta adrasta*. In the Callicorinae only the *Diaethria* spp. show a certain sexual dimorphism. We have then a consistent similarity of basic morphological characteristics and of behavior during the early stages, and some adaptive differences in some of the adults.

In relation to the foodplants used by the two groups, only two Catonepheli-

nae, *C. n. esite* and *C. nyctimus,* were found on Euphorbiaceae. All the rest of the Catonephelinae and all of the Callicorinae of the local fauna were found exclusively on several species of Sapindaceae; this is another factor in common between the two groups.

During the several years we have studied *Catonephele numilia esite* in our insectarium the only cause of mortality we have noticed, besides the larval fights, as been a diarrhea that provokes a softening of the body tissues and inevitably ends in death of the larvae by bursting of the body. This always happened when the larvae were fed on slightly decaying leaves of the foodplant.

In the fields many first instar larvae die of desiccation during the dry season, mostly when the trees are located near dirt roads and the leaves are covered by a heavy layer of dust. Up to the present we have not found any cases of parasitism in this species.

C. n. esite shows a cryptical defense mechanism during some of the early stages (first and second instars), very similar to the one used by Charaxinae (Muyshondt 1973 A, B, and C), when the young larvae on the bared vein imitate portions of leaf tissue still attached to it. The pupae also might be considered mimetic by their green color, even if they are usually standing on top of the leaves and not hidden under them. But third, fourth, and fifth instar larvae of this species seem to rely rather on the mechanical defense provided by the long horns on the head and the profusion of forked spines that cover the body. These spines are not urticant, but very sharp. The adults, even if they are strong flyers, use the flash and hide effect obtained from their showy dorsal colors contrasting with the cryptical brown of their underwings. A puzzling aspect of the adults of *C. numilia esite* is the drastic difference in dorsal coloration between the two sexes for no apparent benefit. None of the two sexes mimics any of the classically considered "protected" species of the local fauna pertaining to the Danaidae, Heliconiidae, Ithomiidae or Papilionidae.

The defensive strategy of *C. n. esite* is quite complex; it at times points to a palatable condition for predators, as would be a logical consequence of the lack of aromatic or bitter compounds in the foodplant used by the larvae, *Alchornea latifolia,* but then during other phases of development suggests protection by unpalatability, manifested by the rather showy colors the larvae display and their way of resting exposed on the tops of leaves. This peculiarity of behavior made us wonder about the qualities of the foodplant. It is known that many Euphorbiaceae contain not only violent poisons but terribly caustic juices (Planchon and Collin, 1895). Others apparently produce hydrogen cyanide (Brower and Brower, 1964). It would be interesting to investigate the foodplant of *C. n. esite* for deleterious components that could be accumulated in the body of the feeding larvae, becoming concentrated gradually and starting to function as predator-deterrents after the larvae

reach a certain state of development, in this case the third instar. Such an investigation of the foodplant might therefore explain the change of behavior.

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Retention of Insect Virus Infectivity in Mammalian Cell Cultures

Arthur H. McIntosh and Karl Maramorosch
Boyce Thompson Institute, Yonkers, New York 10701

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Abstract: The present and future use of polyhedral insect viruses for biological control justifies extensive tests for their safety, not only as possible disease agents of various hosts but also as possible inducers of other virus infections, transforming factors, and causes of allergies. This paper describes the retention of an insect polyhedral virus in cultured human cells. No deleterious effects of this virus on growing cells was observed. Polyhedral inclusion bodies (PIB) and free virions of the nuclear polyhedrosis virus (NPV) of *Heliothis zea* (cotton bollworm) were studied to determine their effects on several human cell cultures. No cytopathic effect (CPE) was observed in cultures of primary human amnion (PHA), foreskin (HF), embryo (EM), lung (WI38), and leucocytes (LEU) inoculated with both PIB and virions. Cell viability studies employing HF and LEU cultures revealed no difference between controls and cultures inoculated with PIB over a 3-week period. PHA and WI38 cultures inoculated with virions and stained with hematoxylin and eosin showed no presence of inclusion bodies or other cytopathic effects. However, virus was recovered from PHA, WI38, and LEU cultures by bioassay 4 weeks after inoculation. Immunofluorescence of PHA cultures inoculated with the NPV failed to detect antigen over a 5-week period. DNA synthesis of LEU cultures was unaffected by exposure to the virus as assessed by autoradiography, nor did such cultures ever transform. PHA cultures inoculated with NPV did not show the presence of any transformed foci over a 4-month period. A neutralization test whereby antiserum could be tested for its neutralizing capacity in a bioassay test was developed.

INTRODUCTION

Although the control of insect pests by viruses is by no means a recent innovation, this method is receiving ever-increasing attention. The reasons for this probably are the apparent high degree of specificity of insect viruses, leaving other species and predators unharmed, and a desire to decrease the use of chemical insecticides wherever possible. Since there have been relatively few reports (Himeno *et al.*, 1967; Ignoffo and Rafajko, 1972) concerning the effects of insect viruses on mammalian cell cultures, the present study was initiated employing a commercially available product, *Heliothis* (cotton bollworm) nuclear polyhedrosis virus (NPV).

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MATERIALS AND METHODS

Cell cultures. Human foreskin (HF) and embryonic (EM) cultures were obtained from the Cell Culture Division, Naval Biomedical Research Laboratory, Oakland, California. WI38 diploid (lung) cell line was purchased from the American Type Culture Collection (ATCC), Rockville, Maryland. Primary human amnion (PHA)[1] and leucocyte (LEU) cultures from normal individuals were prepared in this laboratory according to well-established techniques (Chang, 1968; Chang *et al.*, 1971). Cell cultures were grown in both roller tubes (15 × 150 mm) and Leighton tubes at 35 C. Roller-tube cultures were placed on a roller drum (15 rev/h) following inoculation with virus.

Nutrient media. All cultures with the exception of leucocytes were grown in Eagle's minimal essential medium (MEM) (Eagle, 1959), containing 10% inactivated fetal bovine serum and 1 ml of 200 mM glutamine per 100 ml medium. Leucocytes were cultured in medium 199 (Morgan *et al.*, 1950), containing 20% inactivated fetal bovine serum and glutamine as described. Antibiotics were incorporated into media at concentrations of 50 units/ml penicillin and 50 μg/ml streptomycin. In addition, amphotericin at 2.5 μg/ml was included in media when cultures were inoculated with crude polyhedral inclusion bodies (PIB).

Virus. Polyhedral inclusion bodies (PIB) of *Heliothis zea* (Cotton bollworm) nuclear polyhedrosis virus (NPV) and ova were generously donated by International Minerals and Chemical Corp., Libertyville, Illinois. The commercial PIB preparation known as Viron/H contains at least 4×10^9 PIB per gram of product. Crude PIB were prepared by suspending 0.25 g of Viron/H in 25 ml of Hanks' balanced salt solution (HBSS) containing 100 units/ml penicillin, 100 μg/ml streptomycin, and 2.5 μg/ml amphotericin. The suspension was allowed to stand for 10 min, centrifuged at 500 rpm for 5 min, and the supernatant removed and recentrifuged at 2,000 rpm for 30 min. The pellet was resuspended in HBSS, suitably diluted, and PIB counted in a hemocytometer. LEU, HF, EM, and PHA cultures were inoculated with 2.74×10^5 to 1.25×10^7 PIB/ml.

Virions were released from PIB by the following method: 0.6 g of Viron/H was resuspended in 2 ml of distilled water and layered onto a 40 to 65% (w/v) linear sucrose gradient. Preparations were centrifuged for 1 hr at 24,000 rpm in a Beckman L3–40 ultracentrifuge with an SW 27 rotor at 4 C. The resulting white band 5 to 6 cm from the bottom of the meniscus was removed by aspiration. PIB from several such runs were pooled together. Residual

[1] Full-term human placentas delivered by Caesarian section were obtained through the courtesy of St. John's Riverside Hospital, Yonkers, New York.

sucrose was removed by diluting with distilled water and centrifuging at 5,000 rpm for 1 h or by dialyzing against distilled water and concentration of PIB by centrifugation. 10^8 to 10^{10} PIB were treated with an equal volume of alkali (0.05 M Na_2CO_3 + 0.05 M NaCl, pH 9.5) for 30 to 60 min. The alkali digestion was arrested by careful neutralization with 0.2 N HCl, and the suspension centrifuged at 5,000 rpm for 1 h. Examination of supernatant fluids by electron microscopy revealed the presence of bacilliform particles typical of NPV. This virus suspension was used as a source of inoculum for cell cultures.

SV40 virus was obtained from the ATCC and passed three times in primary African green monkey kidney (PAGMK) cells. Pooled fluids and cells from the last passage were frozen and thawed several times to disrupt cells and then passed through a 0.45 μm (Millipore Corp.) filter. The virus pool titered 10^6 infectious units/ml in a established African green monkey kidney cell line (CV-1). For the determination of enhancing or inhibiting effect on SV40, PHA cultures were inoculated with 0.1 ml of *Heliothis* NPV (from the digestion of 10^{10} PIB) and 3 days later challenged with 0.1 ml of 10^5 infectious units of SV40. Controls consisted of PHA cultures challenged with SV40 alone and uninoculated PHA cultures.

Immunofluorescence. PHA cultures in Leighton tubes were inoculated with 0.1 ml of virus suspension derived from the digestion of 10^9 PIB. Cultures were incubated at 35 C for 2 h, the cell sheaths washed twice with HBSS, and fresh media added. Coverslips were removed at weekly intervals for 5 weeks and prepared for immunofluorescence by an indirect fluorescent antibody method previously described (McIntosh and Chang, 1971). The fluorescent conjugate employed was goat-anti rabbit globulin (Microbiological Associates Inc., Bethesda, Maryland). A Nikon microscope with fluorescent attachment was used to examine slides.

Immunization of rabbits. Female New Zealand white rabbits weighing 6 to 7 lb were prebled and immunized using a foot-pad technique similar to that described by Gray *et al.* (1966). The challenge dose consisted of virions released from the alkali digestion of 10^8 PIB. Rabbits were bled from the marginal ear veins employing a rabbit bleeding apparatus (Bellco, Vineland, New Jersey). All sera were stored at –20 C.

Autoradiography. Each leucocyte culture was inoculated with 0.1 ml of a virus suspension obtained from the alkali digestion of 10^8 PIB. Cultures were exposed to 1 μCi/ml of thymidine-methyl-^{3}H (specific activity 6.7 Ci/mM) 24 h prior to termination of the experiment on the seventh day. Controls consisted of uninoculated cultures treated in the same manner. For autoradiography, cultures were centrifuged at 1,000 rpm for 10 min in a clinical

centrifuge and the pellet washed several times with PBS. Smears from the cell suspensions were made on clean microscopic glass slides, air dried, and dipped in liquid emulsion as previously described (McIntosh and Chang, 1971). The percentage of cells showing nuclear labeling was scored in inoculated and control cultures.

Bioassay. PIB and virus containing suspensions from inoculated cultures were tested using a sensitive neonatal-larvae-feeding technique (Ignoffo, 1966).

Neutralization test. 0.6 ml of virus suspension (from the digestion of 10^9 PIB) was mixed with 0.6 ml of antiserum (appropriately diluted) and placed at 35 C for 2 h. At the end of this period, 0.1 ml aliquots were plated onto the surface of the diet in the neonatal bioassay test. Controls consisted of pre-antiserum plus virus and postantiserum plus PIB.

Viable cell counts. The method described by Merchant *et al.* (1964) employing 0.4% erythrosin B was employed.

RESULTS

Cytopathology. Of four cultures (PHA, HF, EM, and WI38) inoculated with PIB and free virions of *Heliothis*, none showed any CPE over a 4-week period. In addition, coverslips from PHA, HF, and WI38 inoculated cultures were removed at weekly intervals and stained with hematoxylin and eosin. No inclusion bodies were observed in any of the inoculated cultures with the exception of PHA. However, this property was nontransmissible and an extensive search of control cultures showed a low proportion of cells with such inclusions in the nuclei. Inoculated HF cells were passaged three times at weekly intervals without the appearance of any cytopathic effects.

Cell viability studies. HF cultures inoculated with 2.74×10^5 and 2.74×10^6 PIB per culture gave average cell viability figures of 77% and 84% (for two experiments), respectively, as compared with 94% for control cultures at 2 weeks. Similarly, EM cultures gave values of 67% and 85% as compared with 79% for controls under the above described conditions. In addition, LEU cultures inoculated with 1.25×10^7 PIB/culture gave an average cell viability count from two experiments of 4.50×10^5 cells/culture as compared with 2.65×10^5 cells/culture for controls.

DNA synthesis. Since it is known that some vertebrate viruses can cause an increase in DNA synthesis of leucocyte cultures (Brody *et al.*, 1968), this property was examined with the *Heliothis* NPV. The average percentage of cells showing nuclear labeling, from two experiments in which 2,000 cells were examined, were 4.00% and 1.98% for inoculated cultures and 1.33% and 1.39%, respectively, for controls.

Table 1. The effect of *Heliothis zea* nuclear polyhedrosis virus on the transformation of primary human amnion cultures by SV40

Experiment	Proportion of cultures transformed		
	Control	SV40	SV40-NPV
I	0/7	4/8	8/8
II	0/4	5/7	7/7
III	0/6	6/6	7/7

Transformation. Two approaches to the study of viral transformation were employed in this investigation. The first was the examination of inoculated PHA cultures for the presence of transformed foci. The second was the determination of cell proliferation in LEU cultures inoculated with the NPV. Both PHA and LEU cultures were kept for 4 to 6 months following inoculation. A total of eight experiments were performed. No development of foci in PHA cultures nor increase in cell numbers in LEU cultures was observed.

It has been reported that superinfecting viruses may be either enhanced or inhibited by other viruses (Tsuchiya and Rouhandeh, 1971). Table 1 illustrates the results of such a study where PHA cultures were inoculated with the NPV followed by superinfection with SV40. As can be seen, only in one experiment did there appear to be an enhancing effect. There was no difference in percent of cells showing presence of T antigen in SV40 and SV40-NPV inoculated cultures. SV40 virus was also recovered from both groups of transformed cultures.

Viral persistence in cell cultures. Table 2 illustrates the recovery of *H. zea* NPV from three inoculated cultures. With the exception of WI38, mortalities at the fourth-week test period were greater than 50%. The reason for the low

Table 2. The recovery of *Heliothis zea* nuclear polyhedrosis virus from inoculated cell cultures

Culture	% Mortality[a]					
	Time of assay[b] (days)					
	0	3	7	14	24	28
Virus	100	–	–	–	–	–
PHA	–	100	89	41	63	63
Control	–	4	–	–	–	–
WI38	–	100	88	71	45	5
Control	–	–	9	–	–	–
LEU	–	100	100	90	27	53
Control	–	–	–	0	–	–

[a] 15 to 25 cotton bollworms per test were used.
[b] Assay was made on cells plus supernatant fluids.

TABLE 3. The neutralizing effect of antiserum on *Heliothis zea* nuclear polyhedrosis virus as tested in neonate cotton bollworms

Treatment	No. dead/total	% mortality
Virus[a]	8/8	100
Virus + preantiserum	8/8	100
Virus + postantiserum	0/8	0
Virus + postantiserum (1:2)	0/8	0
Virus + postantiserum (1:4)	0/7	0
Virus + postantiserum (1:8)	3/7	43
PIB[b] + postantiserum	7/7	100
Control (uninoculated)	0/10	0

[a] 0.6 ml of virus inoculum (released by digestion of 10^9 PIB) per test was employed.
[b] 0.6 ml of 10^5 PIB/ml per test was used.

mortality rate for fluids and cells from WI38 at this period is unknown. No attempt was made to titrate the virus.

Immunofluorescence. Since virus could be recovered from inoculated PHA cultures after 4 weeks, it was of interest to determine whether or not antigen could be detected in such cultures since it is possible for viral coded antigens to be synthesized without viral multiplication (Tevethia *et al.*, 1965). Coverslips were removed both from controls and from inoculated cultures at weekly intervals for 5 weeks. No foci of fluorescence were observed in inoculated or control cultures.

Neutralization test. In order to assess the potency of the antiserum prepared against the NPV of *H. zea*, a neutralization test was developed. As can be seen from Table 3, postantiserum completely neutralized the virus up to a 1:4 dilution of antiserum, whereas undiluted preantiserum failed to do so. Of interest also was the failure of postantiserum to neutralize PIB. This experiment was repeated with similar results.

DISCUSSION

Inoculation of human cell cultures with PIB and free virions of *Heliothis* NPV had no adverse effect on cell viability; neither was any CPE produced in such cultures. Furthermore, no accumulation of viral antigen in inoculated PHA cells as determined by immunofluorescence could be demonstrated over a 5-week period. *Heliothis* NPV did not transform either PHA or LEU cultures. However, in one out of three experiments *Heliothis* NPV did enhance the transformation of PHA cultures by SV40. The most likely possibilities which might explain this lack of reproducibility include differences in the genetic constitution of amnion cells which were derived from three different placentas and the presence of adventitious agents in the PHA cultures in which enhancement was demonstrated. Further studies are being conducted

with *Heliothis* NPV and other insect viruses in an attempt to elucidate this phenomenon.

The recovery of *Heliothis* NPV from mammalian cell cultures 4 weeks after inoculation represents the first report concerning the persistence of an insect virus in vertebrate cell cultures. Since culture fluids were changed at least once a week, it is unlikely that recovery of virus was due solely to extracellular virus remaining from the inoculum. Although it has been reported that *Heliothis* NPV retains approximately 50% of its infectivity after 14 days at 37 C in cell-free diluent (Ignoffo and Rafajko, 1972; Shapiro and Ignoffo, 1969), no prior information concerning the infectivity of this virus from inoculated mammalian cultures has been reported. Electron microscopic studies are in progress to determine if actual penetration of cells by the virus occurred.

The development of a neutralization test for *Heliothis* NPV whereby the potency of antiserum can be assessed should be applicable also to other insect viruses. The titer of the antiserum in this study, although low, could possibly be increased by employing a more severe course of immunization. Since it is the virions contained in the PIB which are infective, the infectivity of released virions from PIB treated with antiserum is not surprising.

These results further support the findings of Ignoffo and Rafajko (1972) concerning the nonlethal effect of *Heliothis* NPV for primate cells. However, further studies should be made before other insect viruses are employed on a large scale for biological control. The finding by Longworth *et al.* (1973) that domestic and wild animals have IgM antibodies that react with insect viruses raises some very interesting questions with regard to possible infection of higher species with these types of viruses.

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The Genus *Chitrella* in America (Pseudoscorpionida, Syarinidae)

William B. Muchmore
Department of Biology, University of Rochester, Rochester, New York 14627

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Abstract: Since the paper of Malcolm and Chamberlin (1960) on "The pseudoscorpion genus *Chitrella*," a number of new specimens have come to hand, giving further support to the idea that this genus is widely represented in the eastern United States. In 1963 the present author redescribed the tritonymph holotype of *Obisium cavicola* Packard and assigned the species to *Chitrella*.

This paper describes, for the first time, adults of *Chitrella cavicola* (Packard) and extends our knowledge of the range of that species, describes a male of *C. regina* Malcolm and Chamberlin, describes a new cavernicolous species, *C. superba*, from Virginia, and discusses the relationships of *C. transversa* (Banks) from New Mexico.

Suborder Diplosphyronida Chamberlin
Family Syarinidae Chamberlin
Subfamily Chitrellinae Beier
Genus *Chitrella* Beier

Chitra Chamberlin, 1930, p. 41.
Chitrella Beier, 1932, p. 165; Hoff, 1956, p. 20; Malcolm and Chamberlin, 1960, p. 2.

Type species: *Chitra cala* Chamberlin, 1930, p. 41.

Diagnosis (emended): Diplosphyronid pseudoscorpions with pleural membranes of abdomen longitudinally, smoothly striate; both fingers of chelicera with marginal teeth; spinneret apparently absent from movable cheliceral finger; venedens and venom duct well developed in fixed finger of chela, venom duct short; terminal tooth of movable chelal finger short and without trace of venom duct; marginal teeth of chelal fingers numerous, contiguous; trichobothria of fixed finger arranged in two more or less distinct groups, *et*, *it*, *est* and *ist* distally with *ist* at about middle of finger, and *esb*, *isb*, *eb* and *ib* proximally with *ib* clearly on dorsum of hand; *st* of movable finger nearer to *t* than to *sb*; leg I with telofemur longer than basifemur; articulation between basifemur and telofemur of leg IV slightly oblique to transverse axis; posterior genital operculum of male with one pair of small setae internally; in most species, sixth sternite of male with a median, circular area containing a number of microsetae (presumably sensory); median cribriform plate of female circular and heavily sclerotized.

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Chitrella cavicola (Packard)

(Figs. 1–4)

Obisium cavicola Packard, 1884, p. 202.
Microcreagris? cavicola, Beier, 1932, p. 157; Hoff, 1958, p. 12.
Chitrella cavicola, Muchmore, 1963, p. 11.

Heretofore this species has been known only from the holotype tritonymph from New Market Cave, Shenandoah County, Virginia. It now appears that the species may actually be widespread in the middle Atlantic states and that it is mainly an epigean, rather than a cavernicolous, form. On the basis of new material studied, the adults can be described for the first time and a more complete description of the tritonymph can be presented.

Material: Many males, females and nymphs from Fredericksburg National Military Park, Spotsylvania County, Virginia, 10 April 1969 (C. H. Alteri); one female from Lewis Mountain (2,000 feet elevation), Shenandoah National Park, Virginia, 10 April 1967 (S. Peck); several tritonymphs and one deutonymph from Big Meadows and Thorofare Mountain Overlook (about 3,500 feet elevation), Shenandoah National Park, 2 July 1963 (W. B. Muchmore); one female from Whiting's Neck Cave, Berkeley County, West Virginia, 26 March 1966 (J. Cooper).

Diagnosis (emended): Generally similar to *Chitrella cala* Chamberlin, and *C. muesebecki* Malcolm and Chamberlin, but smaller than the former and larger than the latter and with specific differences as indicated in the key.

Description of adults (based upon six mounted males and eight mounted females): Males and females indistinguishable in size and proportions. All sclerotized parts pale reddish brown. Carapace about one-third longer than broad; no epistome; no transverse furrows; two well-developed eyes on each side, anterior eyes slightly more than one ocular diameter from anterior margin and about half a diameter from posterior eyes; with about 30 vestitural setae, including, usually, six along anterior and six near posterior margin and a small seta anteroventral to each anterior eye. Abdominal tergal chaetotaxy about 6 or 7:11:11:12:13:14:15:13:13:11:5:2. Sternal chaetotaxy of males about 14:[1–1]: $(4)\frac{6}{14}(4):(4)20(4):25:\frac{4(N)4}{18}$:17:18:16:14:9:2; middle 8–10 setae on sternites 4 and 5 distinctly smaller than those more laterad; the circular area (N, according to terminology of Malcolm and Chamberlin, 1960, p. 14) on sternite 6 with variable number of clusters of microsetae; two larger setae near middle of sternite 7 are in the marginal row, not displaced anteriorly as in *C. cala* (see Fig. 1). Sternal chaetotaxy of females about 8: $(4)17(4):(4)12(4):15:\frac{2}{15}$:18:15:14:13:9:2; two small setae near middle of sternite 6 lie anterior to the marginal row.

Chelicera about 0.6 as long as carapace. Hand with five setae; fixed finger with 15–20 and movable finger with 10–15 teeth of varied sizes; no galea or silk ducts visible; serrula exterior of about 25 blades; flagellum usually of six setae, all except proximal one serrate along one margin.

Palps moderately long and slender; femur about 1.0 and chela about 1.6 times as long

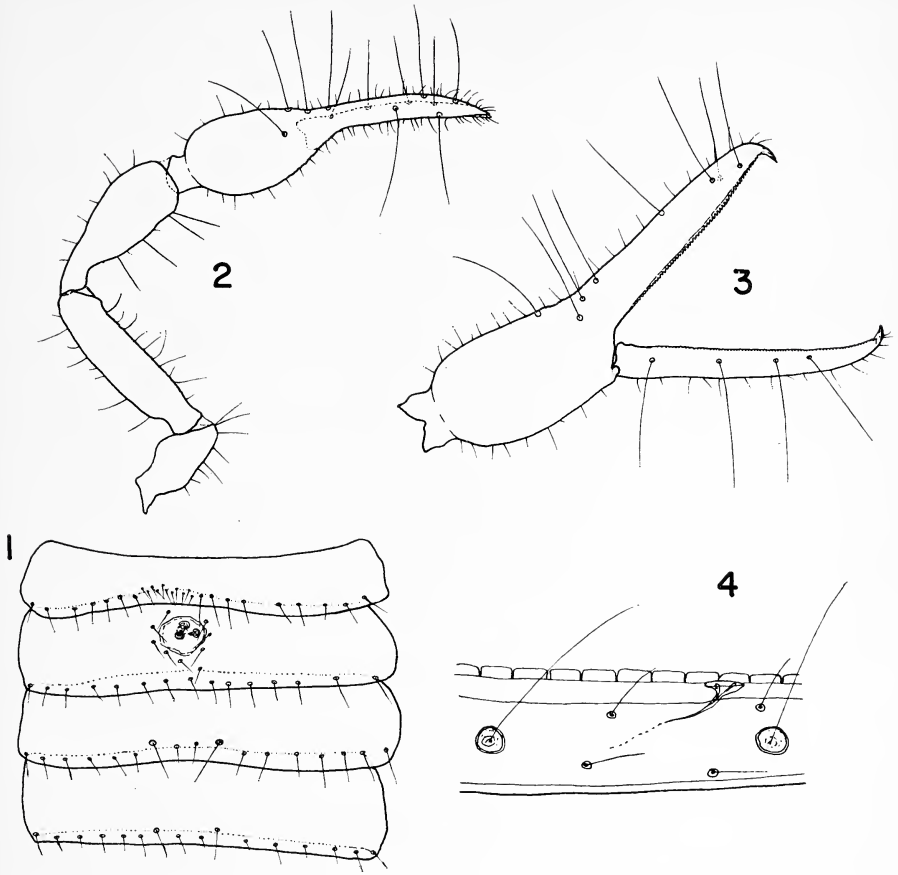


Fig. 1–4. *Chitrella cavicola* (Packard). 1. Sternites 5–8 of male. 2. Dorsal view of left palp. 3. Lateral view of right chela. 4. Part of movable finger of chela showing sensillum near dental margin (trichobothrium *st* at right, *sb* at left).

as carapace. Proportions of palpal segments as shown in Fig. 2; trochanter 2.3–2.6, femur 3.7–4.15, tibia 2.45–2.7, and chela (without pedicel) 3.5–3.7 times as long as broad; hand (without pedicel) 1.5–1.65 times as long as deep; movable finger 1.5–1.6 times as long as hand. All segments sparsely granulate, and with distinct concentrations of granules on flexor surface of femur and on chelal hand at bases of fingers. Fixed chelal finger with row of 50–59 contiguous, retroconical teeth; movable finger with 54–62 low, rounded teeth, only the distalmost four or five with cusps. Venedens and venom apparatus in fixed finger only, venom duct very short; terminal tooth of movable finger short and with no evidence of a venom duct. Positions of trichobothria as shown in Fig. 3. Movable finger with a small, rounded sensillum just external to the dental row and posterior to the level of trichobothrium *st* (Fig. 4).

Legs moderately long and slender; leg IV with entire femur 2.95–3.2 and tibia 4.8–5.3 times as long as deep. Leg IV with tactile setae on tibia about two-thirds and on meta-

tarsus about one-fourth length of segment from proximal end. Subterminal tarsal setae with 3–5 sharp rami in distal half.

Tritonymph (based on nine mounted specimens from Spotsylvania County, nine from Shenandoah National Park, and the holotype from New Market Cave): The description by Muchmore (1963, pp. 12, 13) is generally satisfactory; only a few points need clarification and some indications of variability can be given. The number of vestitural setae on the carapace varies from 27 to 31, usually with six at both anterior and posterior margins; included in this number are two setae, smaller than the rest, one just anteroventral to each anterior eye (as in the adult). Tergal chaetotaxy of a typical specimen 7:11:11:11:11:12:12:11:11:8:3:2. Sternal chaetotaxy of typical specimen 2:(3)8(3):(3)9(3):11:$\frac{2}{12}$:13:12:10:11:7:2; two small setae on sternite 6 lying close together at about the center of the sternite.

Chelicera much as described previously. However, flagellum difficult to make out accurately; apparently consisting of five setae, all but the shorter, basal one finely denticulate along one margin.

Palps much as described earlier. Proportions of segments: trochanter 2.0–2.45, femur 3.55–3.8, tibia 2.1–2.55, and chela (without pedicel) 3.3–3.7 times as long as broad; hand (without pedicel) 1.4–1.55 times as long as deep; movable finger 1.37–1.53 times as long as hand. Fixed chelal finger with 35–42 and movable finger with 40–46 contiguous teeth. Movable finger with a rounded sensillum like that found in adult, located usually at level of trichobothrium *st*.

All legs with telotarsi swollen basally, as noted earlier. Leg IV with tactile setae on tibia 0.53–0.70 and on metatarsus 0.25–0.32 length of segment from proximal end. Subterminal tarsal setae variably dentate, as in adult.

Measurements (in mm): Males and females: Body length 2.0–2.7. Carapace 0.57–0.69, ocular breadth 0.44–0.49. Chelicera 0.34–0.40 by 0.155–0.18. Palpal trochanter 0.35–0.40 by 0.14–0.17; femur 0.57–0.66 by 0.14–0.17; tibia 0.50–0.57 by 0.19–0.23; chela (without pedicel) 0.95–1.12 by 0.26–0.31; hand (without pedicel) 0.38–0.445 by 0.24–0.29; movable finger 0.59–0.68 long. Leg IV: entire femur 0.51–0.59 long; basifemur 0.19–0.22 by 0.155–0.185; telofemur 0.33–0.385 by 0.17–0.19; tibia 0.41–0.48 by 0.08–0.10; metatarsus 0.19–0.22 by 0.06–0.08; telotarsus 0.24–0.28 by 0.05–0.06.

Tritonymphs: Body length 1.54–2.29. Carapace 0.45–0.555 long. Chelicera 0.265–0.315 by 0.125–0.15. Palpal trochanter 0.23–0.30 by 0.105–0.13; femur 0.39–0.48 by 0.11–0.145; tibia 0.335–0.41 by 0.14–0.18; chela (without pedicel) 0.65–0.78 by 0.185–0.23; hand (without pedicel) 0.27–0.33 by 0.18–0.22; movable finger 0.395–0.49 long. Leg IV: entire femur 0.335–0.42 by 0.115–0.155; tibia 0.28–0.34 by 0.065–0.08; metatarsus 0.13–0.155 by 0.05–0.06; telotarsus 0.175–0.21 by 0.05–0.06.

Remarks: Although the first known specimen of *C. cavicola* was found in a cave, it now appears that the species is normally surface dwelling. The specimens from Fredericksburg, Virginia, were living in very damp litter in deciduous woodland, while those from Shenandoah National Park were found in damp leaf litter at the bases of large boulders, also in deciduous woodland. Such a moisture-loving hypogean form is probably admirably suited for entering and surviving in caves—witness the holotype and the specimen from Whiting's Neck Cave.

The sensillum on the external surface of the movable chelal finger is the same structure as that called an "accessory tooth" by Malcolm and Cham-

berlin in *C. muesebecki* (1960, p. 10). (The identity of these structures was confirmed by direct examination of the holotype of *C. muesebecki.*) It usually appears as a rounded elevation with a shallow depression at the summit in which are seen one or two sensory pegs. Similar sensilla are found on the movable finger of *C. archeri*, where there are usually two, one at a level between trichobothria *st* and *sb*, and the other between *sb* and *b*. Further, such a sensillum is present just distad of *sb* in the one specimen of *C. cala* which I have been able to examine. As noted below, these sensilla are also found in all other American species of *Chitrella*. Whether they will prove to be of taxonomic significance remains to be determined.

Chitrella regina Malcolm and Chamberlin
(Fig. 5)

Chitrella regina Malcolm and Chamberlin, 1960, p. 7.

The original diagnosis of this species is based on a single female specimen from Coffman Cave, near Frankford (*not* Frankfurt), Greenbrier County, West Virginia. The present description of a male from a neighboring cave is given as a supplement to that diagnosis.

Material: One male (WM 261.01001) collected in Higginbotham's Cave, 1½ miles WNW of Frankford, Greenbrier County, West Virginia, by Carl Krekeler on 24 July 1957.

Description of male: Quite similar to the female described by Malcolm and Chamberlin, but slightly smaller and with the following characteristics. Carapace about one-third longer than broad; with four barely discernible eyespots; chaetotaxy 6-6-4-2-4 = 22, the lateralmost setae in the second row being much reduced in size. Abdominal tergal chaetotaxy 4:6:6:8:9:8:10:10:10:7:5:2. Sternal chaetotaxy $15:[1\text{-}1]:\frac{13}{(4)13(4)}:(4)16(4):18:\frac{4(N)5}{13}:5T2T5:14:12:9:7:2$; middle six or seven setae on sternites 4 and 5 distinctly smaller than those more laterad; the circular area (N) on sternite 6 bears a single cluster of 25–30 closely set microsetae; the two tactile setae on sternite 7 are in line with the other marginal setae (Fig. 5).

Chelicera nearly two-thirds as long as carapace. Hand with five setae; fixed finger with 13 and movable finger with ten teeth; no galea or silk ducts visible; serrula exterior of 25 blades; flagellum of seven setae, all finely serrate on anterior edges.

Palp as in female; femur 1.55 and chela 2.35 times as long as carapace. Proportions of palpal segments: trochanter 2.85, femur 7.05, tibia 5.4, and chela (without pedicel) 6.15 times as long as broad; hand (without pedicel) 2.1 times as long as deep; movable finger 2.05 times as long as hand. Movable chelal finger with 114 and fixed finger with 109 marginal teeth. Movable finger with two small rounded sensilla lying between trichobothrium *sb* and the dental row. Trichobothria as in female, except that *t* is closer to *st* than is indicated in the figure by Malcolm and Chamberlin (1960, Fig. 2B, p. 8).

Legs generally similar to those of female. Leg IV with tactile setae on tibia 0.63 and on metatarsus 0.28 length of segment from proximal end. Subterminal tarsal setae with one or two small rami at midpoint and terminally.

Measurements (in mm): Body length 2.34. Carapace 0.79. Chelicera 0.49 by 0.21. Palpal trochanter 0.585 by 0.205; femur 1.23 by 0.175; tibia 1.11 by 0.205; chela (without pedicel) 1.84 by 0.30; hand (without pedicel) 0.63 by 0.30; pedicel 0.11 long; movable

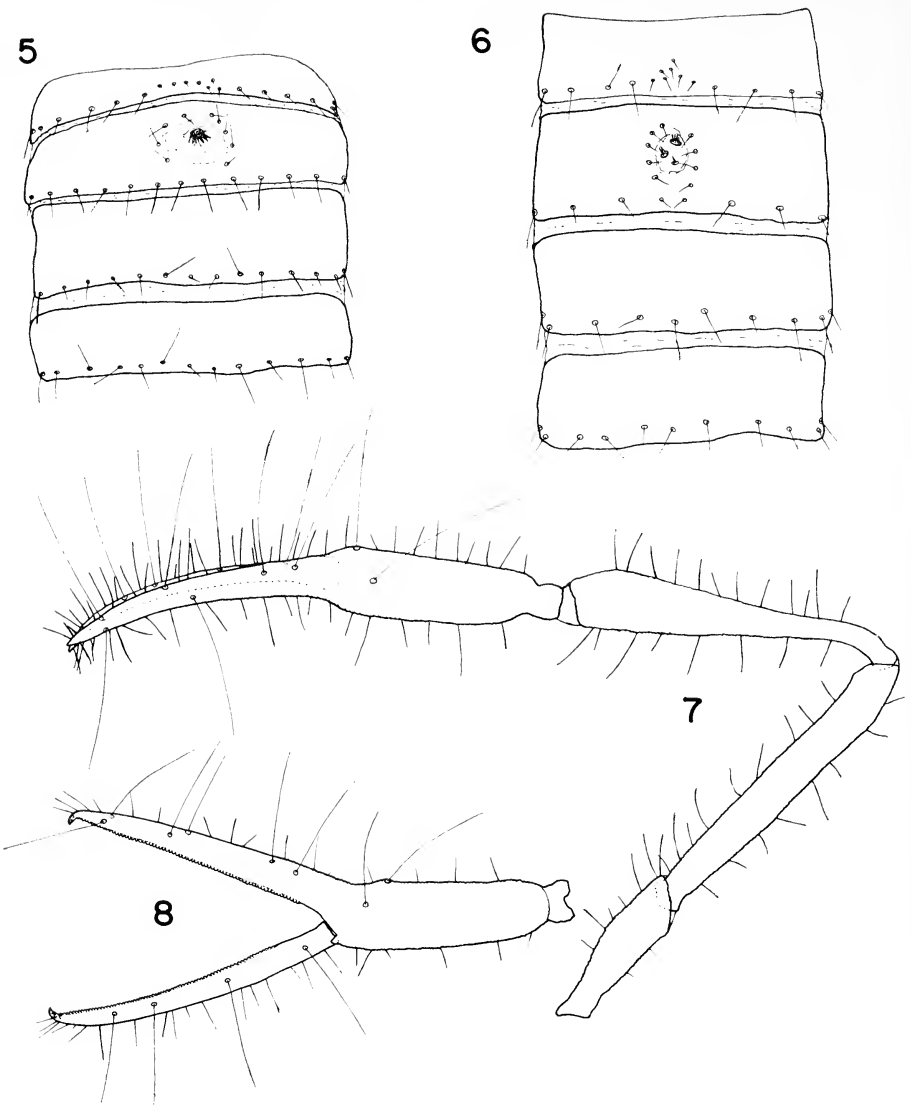


FIG. 5. *Chitrella regina* Malcolm and Chamberlin. Sternites 5–8 of male.
FIGS. 6–8. *Chitrella superba*, new species. 6. Sternites 5–8 of male. 7. Dorsal view of right palp. 8. Lateral view of left chela.

finger 1.28 long. Leg I: basifemur 0.555 by 0.115; telofemur 0.34 by 0.10; tibia 0.505 by 0.08; metatarsus 0.225 by 0.065; telotarsus 0.365 by 0.06. Leg IV: entire femur 0.913 long; basifemur 0.34 by 0.16; telofemur 0.585 by 0.16; tibia 0.78 by 0.10; metatarsus 0.315 by 0.09; telotarsus 0.465 by 0.08.

Remarks: Higginbotham's Cave, in which the present male was found,

is situated very close to Coffman Cave, the type locality of the species. It is probable that there are underground connections between the two caves through which pseudoscorpions could disperse (see Davies, 1958, p. 82).

It is interesting to find that the male of *C. regina* possesses the unique sensory area on the sixth sternite characteristic of most species of *Chitrella*.

Chitrella superba, new species
(Figs. 6–8)

Material: Holotype male (WM 279.01002) and paratype male collected in Madden's Cave, Shenandoah County, Virginia, 25 August 1958, by Thomas C. Barr, Jr. The types are deposited in the collection of the American Museum of Natural History in New York.

Diagnosis: A large, blind species with greatly attenuated appendages, generally similar to members of the European genus *Pseudoblothrus* Beier.

Description of male: Carapace about 1.6 times as long as broad, greatest breadth in "ocular" region; anterior margin smoothly rounded; surface finely reticulated; eyes completely lacking. Carapacial chaetotaxy 6-6-4-4-4 = 24, lateralmost setae in second row much reduced in size. Coxal area typical; chaetotaxy 2-12(10):6:8:4:8. Abdomen elongate; surfaces of tergites and sternites finely reticulated; pleural membranes longitudinally striate. Tergal chaetotaxy 4:6:8:8:9:9:9:9:6:5:2 (paratype with seven setae on second tergite and nine on third). Sternal chaetotaxy $13:[1\text{-}1]:\frac{7}{(4)15(4)}:(4)18(4):16:\frac{5(N)4}{9}:11:11:11:10:7:2$: Sternite 4 with 3–6 and sternite 5 with a group of 7–12 smaller setae at center of marginal row (see Fig. 6); sternite 6 of holotype with a medial, nearly circular, and slightly depressed area (N), surrounded by nine irregularly placed, large setae; just anterior to center of the area is a compact group of about 25 microsetae, behind this a pair of microsetae, and behind the pair a single, isolated microseta (paratype similar, but not identical); sternite 7 with no distinctly larger setae near middle of row.

Chelicera little more than half as long as carapace. Hand with five setae; fixed finger with 22–24 teeth, more or less alternating large and small; movable finger with 12–13 similar teeth; no evidence of galea or silk duct; serrula exterior with 30–32 blades and serrula interior with 18–20 blades; flagellum of seven setae, all finely serrate along anterior margin.

Palp very long and slender; femur about 1.61 and chela about 2.17 times as long as carapace. Proportions of palpal segments as shown in Fig. 7; trochanter 3.45–3.5, femur 7.85, tibia 5.65, and chela (without pedicel) 6.9 times as long as broad; hand (without pedicel) 3.0 times as long as deep; movable finger 1.39–1.42 times as long as hand. All surfaces heavily granulate, except chelal fingers. Fixed finger with row of about 90 teeth, those in distal third bluntly pointed, the rest low and rounded; movable finger with about 105 teeth, the distalmost 8–10 bluntly pointed, the rest low and rounded. Only fixed finger with venedens, venom duct very short. Movable finger with a single, small sensillum situated obliquely between trichobothrium *sb* and dental margin. Positions of trichobothria as shown in Fig. 8.

Legs long and slender; leg IV with femur 4.9 and tibia 7.5–7.7 times as long as deep. Fourth leg with tactile setae on tibia 0.54–0.56, on metatarsus 0.47–0.49, and on telotarsus 0.55 length of segment from proximal end. Subterminal tarsal setae with one or two prominent rami distally.

Female: Unknown.

Measurements (in mm) (first figures are for holotype, with those for paratype in parentheses): Body length 4.15 (3.97). Carapace 1.16 (1.15) long, "ocular" breadth 0.75 (0.69). Abdomen 2.99 (2.82) long by 1.09 (0.99) broad. Chelicera 0.64 (0.61) long by 0.29 (0.28) broad; movable finger 0.42 (0.40) long. Palpal trochanter 0.92 (0.93) by 0.26 (0.27); femur 1.89 (1.83) by 0.24 (0.23); tibia 1.82 (1.77) by 0.32 (0.31); chela 2.51 (2.51) by 0.37 (0.37); hand 1.09 (1.09) by 0.37 (0.37); pedicel 0.12 (0.12) by 0.25 (0.24); movable finger 1.55 (1.52) long. Leg I: basifemur 0.86 (0.85) by 0.16 (0.15); telofemur 0.48 (0.46) by 0.13 (0.12); tibia 0.72 (0.73) by 0.11 (0.10); metatarsus 0.38 (0.37) by 0.09 (0.09); telotarsus 0.48 (0.49) by 0.08. Leg IV: entire femur 1.28 (1.26) long; basifemur 0.41 (0.41) by 0.26 (0.26); telofemur 0.90 (0.88) by 0.26 (0.26); tibia 1.04 (1.01) by 0.14 (0.13); metatarsus 0.48 (0.45) by 0.10 (0.10); telotarsus 0.60 (0.58) by 0.08 (0.09).

Etymology: This species is named *superba* because of its magnificent size.

Remarks: If this species had been found in Europe it would certainly have been placed in the genus *Pseudoblothrus* Beier. However, its presence in eastern United States together with its obvious close similarity to other American species of *Chitrella* mandates its inclusion in the latter genus. Vachon (1969) has already pointed out the difficulty of distinguishing between the genera *Chitrella* and *Pseudoblothrus* on the basis of characters commonly used. The possibility that the genera are synonymous must be seriously considered, but a final decision in the matter can be reached only after detailed comparative study of American and European forms.

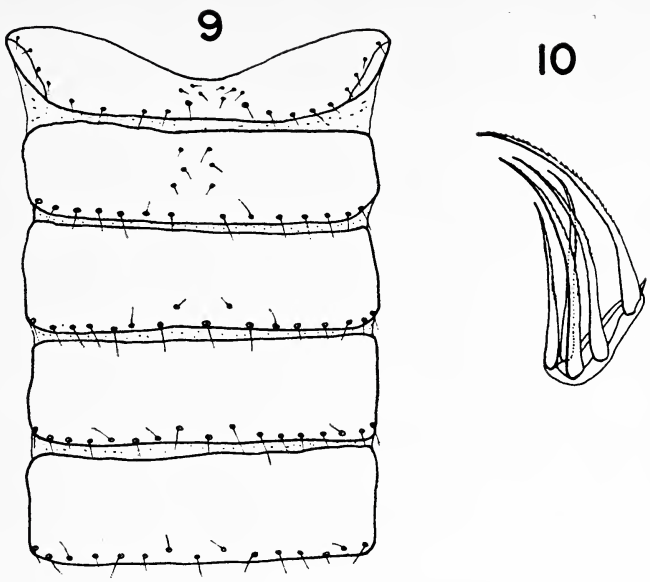
Chitrella transversa (Banks)
(Figs. 9 and 10)

Obisium transversum Banks, 1909, p. 307.
Chitrella transversa, Hoff, 1956, p. 21; 1961, p. 434.

Hoff (1956, 1961) has redescribed and discussed this species in considerable detail, using material from New Mexico and Colorado, though he did not examine the type specimen of *Obisium transversum* in the Museum of Comparative Zoology (see 1956, p. 21). The holotype, a female, has subsequently been mounted on a microscope slide and examined carefully by the present author. In all respects it falls within the ranges of measurements of Hoff's specimens; there is no doubt that all of these are conspecific.

While Hoff has described most features of *C. transversa* adequately, there are several aspects of its morphology that need clarification in the light of recent study of other species in the genus.

Reexamination of the abdominal sternites of a number of specimens from both New Mexico and Colorado have confirmed the observation of Hoff that there is nothing on the sixth sternite of males comparable to the circular sensory or glandular area found in *C. cala* and other species. On the other hand, the sternal chaetotaxy of *C. transversa* males has some peculiarities of its own, as shown in Fig. 9: on sternite 4 there is a group of smaller setae near the middle as in other species; sternite 5 is unique, however, in having several (4 to 7) smaller setae near the middle, situated well anterior to the marginal row; sternite 6 usually has one or two small setae near the middle, slightly anterior to the marginal row; on sternite 7 two larger setae near the middle are essentially part of



Figs. 9 and 10. *Chitrella transversa* (Banks). 9. Sternites 4–8 of male. 10. Flagellum of chelicera.

the marginal row. Such an arrangement of sternal setae is quite similar to that described for *Pseudoblothrus thiebaudi* Vachon (1969, p. 388). This observation makes even more intriguing the question of the relationship between species presently assigned to *Chitrella* and *Pseudoblothrus*. However, as noted above, a resolution of the problem must await further study and comparison of both American and European material.

Like other species of *Chitrella, C. transversa* has a small sensillum on the exterior surface of the movable chelal finger. In this case, the organ is usually located posterior to trichobothrium *sb* and at some distance from the dental margin.

The cheliceral flagellum consists of five setae, subequal in length and all finely serrate along the distal margin; the distalmost of these is heavier than the others and distinctly separated from them at the insertion (Fig. 10). The form and arrangement of these flagellar setae appear to be unique in the genus, but confirmation of this opinion must await further critical study of favorable material.

Key to species of *Chitrella*

1. Sixth sternite of male with circular central area containing patches of microsetae (it is assumed that *C. muesebecki* belongs here, even though the male is as yet unknown 2

   Sixth sternite of male without a specialized area containing microsetae; known from New Mexico and Colorado ..... *C. transversa* (Banks)

2. Modified for cave dwelling: eyes absent; relatively large size, with length of palpal femur 0.75 mm or greater; attenuation of appendages, with length/breadth ratio of palpal femur 4.4 or greater 3

   Not so modified: with four corneate eyes; length of palpal femur usually less than 0.70 mm; length/breadth ratio of palpal femur less than 4.2 5

3. Appendages moderately attenuated, with length/breadth ratio of palpal femur about 4.5 and of chela about 4.0; known from caves in Grundy and Smith Counties, Tennessee ..... *C. archeri* Malcolm and Chamberlin
   Appendages greatly attenuated, with length/breadth ratio of palpal femur and chela both greater than 6.0 4
4. Length of palpal femur greater than 1.8 mm, with length/breadth ratio greater than 7.5; known from a cave in Shenandoah County, Virginia ..... *C. superba*, new species
   Length of palpal femur about 1.2 mm, with length/breadth ratio 7.1 or less; known from caves in Greenbrier County, West Virginia ..... *C. regina* Malcolm and Chamberlin
5. Carapace heavily sclerotized and with distinct transverse furrow; movable chelal finger usually less than 1.4 times as long as hand; seventh sternite of both sexes with a median pair of prominent setae in large areoles set anterior to the marginal row; known from California and Utah ..... *C. cala* Chamberlin
   Carapace lightly sclerotized, with little or no evidence of transverse furrow; movable chelal finger 1.5 or more times as long as hand; seventh sternite without a prominent pair of setae set anterior to the marginal row 6
6. Smaller species, with palpal femur about 0.5 mm and chela about 0.85 mm in length; sensillum on movable chelal finger distal to level of trichobothrium *t*; known from Roane County, Tennessee ..... *C. muesebecki* Malcolm and Chamberlin
   Larger species, with palpal femur greater than 0.55 mm and chela greater than 0.95 mm in length; sensillum on movable chelal finger proximal to level of trichobothrium *st*; known from several localities in Virginia and from Berkeley County, West Virginia ..... *C. cavicola* (Packard)

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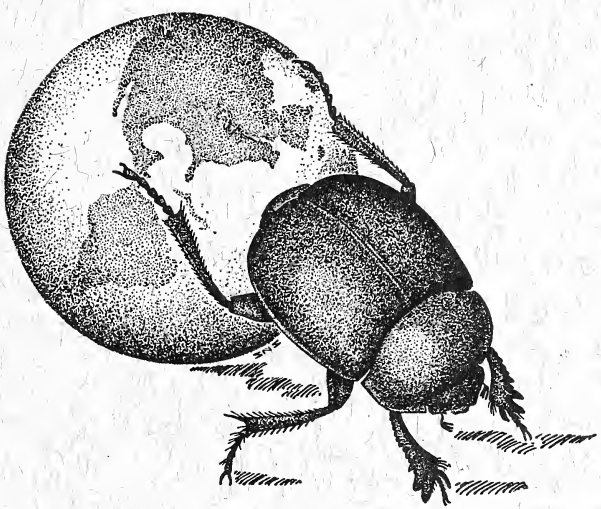

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CONTENTS

The Possible Use of *Bacillus thuringiensis* Plus Chitinase Formulation for the Control of Spruce Budworm Outbreaks

W. A. SMIRNOFF

LAURENTIAN FOREST RESEARCH CENTER, DEPARTMENT OF THE ENVIRONMENT, CANADIAN FORESTRY SERVICE, STE. FOY, QUEBEC, CANADA

RECEIVED FOR PUBLICATION MAY 31, 1973

Abstract: Ten thousand acres of a balsam fir forest severely infested by *Choristoneura fumiferana* Clemens was treated with a *Bacillus thuringiensis* + chitinase formulation by means of Avenger aircraft. In the 70% of the territory that was properly sprayed mortality averaged 88% and foliage protection 70% as determined by visual observations. The results of this experiment were sufficiently good to recommend the use of *B. thuringiensis* + chitinase formulation for the control of spruce budworm outbreaks.

Infection of larvae of the most serious defoliator of conifers in Canada, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae) by *Bacillus thuringiensis* Berliner is characterized by a typical septicemia enterotoxinosis. It was also observed that disease development and mortality produced by the bacteria were faster when spores of the bacillus penetrate into the hemolymph through the gut wall, and this penetration seems easier when the insect supports a tolerant infection by microsporidian (Protozoa) (Smirnoff, 1963). The results of laboratory tests revealed that hydrolysis of the chitin layer covering the gut walls of larvae by the enzyme chitinase increased considerably the pathogenicity of *B. thuringiensis* in larvae of *C. fumiferana* (Smirnoff, 1971, 1973).

During the spring of 1971, the *B. thuringiensis* + chitinase formulation was tested on two 100-acre plots of balsam fir severely infested by *C. fumiferana*. The results obtained were good, 93% averaged mortality was registered in the plot treated with *B. thuringiensis* + chitinase and 85% average mortality in the plot treated with *B. thuringiensis* alone. Foliage protection resulting from the treatment was particularly good: 76% of the current year's shoots were preserved in the plot treated with *B. thuringiensis* + chitinase and only 35% in the plot treated with *B. thuringiensis* alone.

However, it was found that in order to obtain definitive information on potential use of *B. thuringiensis* for control of spruce budworm outbreaks, it was necessary to resort to large-scale aerial applications using commercial equipment. Thus, in 1972, 10,000 acres of balsam fir forest severely infested by the spruce budworm were treated in the lower St. Lawrence Valley, Quebec, Canada. The present paper reports on the results obtained and discusses

the possibilities offered by *B. thuringiensis* for the control of spruce budworm outbreaks.

MATERIALS AND METHODS

During the spring of 1972, 10,000 acres of a homogeneous balsam fir stand that was severely infested by the spruce budworm were chosen for the tests. This stand was producing up to 15 cords of pulpwood per acre. Control plots were established 2 miles from the treated plots in a balsam fir stand of the same type. The larval population in the treated plots was 18.6 larvae per 18 in. branch tip, and there were 18.9 larvae per 18 in. branch tip in the control plots.

Spraying was done by means of 3 Avenger aircraft, each of which carried 650 US gallons of spray material. The aircraft were equipped with boom and nozzles and guided by Cessna pointers as commonly used for application of chemical insecticides. However, it was the first time that *B. thuringiensis* was sprayed by means of the commercial method. Spraying was done between June 4 and 7 when 5.98% of the larvae were in the second instar, 71.70% in the third instar, 21.57% in the fourth instar, and 0.75% in the fifth instar. The formulation per acre was:

Thuricide HPC concentrate	0.5 gal (US)
Polyglycol 400	0.5 gal (US)
Chevron spray sticker	0.16 oz (US)
Water	1 gal (US)
Chitinase (980 nephelemetric units)	10 mg

Spray rate was 2 gallons per acre.

Assessments of results in the field were made using the following techniques:

1. Kromekote cards (4 × 4 in.) to check deposit.
2. One hundred millimeter petri dishes with nutrient agar culture medium to check deposit.
3. Portable 9′ × 3′ cloth tables on iron stands to determine the number of fallen larvae and quantity of frass.
4. Electrostatic bacterial air sampler to determine the presence of *B. thuringiensis* spores in the air.
5. Small particle detector to determine the quantity of solid particles in the atmosphere.
6. The method of the 18-in. branch tip cut at midtree crown was used to determine larval population before and after spraying.

The same techniques were used in the control plots.

Twenty-five sample plots were selected at random throughout the area.

At each plot 5 co-dominant balsam fir trees were selected at 2-chain intervals, the first sample tree being at least 3 chains from the edge of the forest. Nine sample plots to serve as controls were made in a similarly infected stand 5 miles distant from the sprayed areas. Interfering trees and shrubs were cleared from around the sample trees to ensure even spray coverage. Numbered floor tiles were placed in the cleared area near each sample tree. Larval-drop tables, measuring 30 square feet, were placed under the crown of two trees in each plot to collect falling insects and to provide information on the progress of the disease in the budworm population and its possible effect on associated insects.

The microscopical examination and biochemical analyses required to determine the perturbation provoked by *B. thuringiensis* on the metabolism of larvae were performed in a field station.

RESULTS

Measurement of spray deposit revealed that only 70% of the area had been treated properly. The number of gallons per acre (GPA) measured by the droplet count varied between 0.0045 and 1.3237 GPA. Only the areas of the territory which received over 0.4 GPA were considered to have received a sufficient quantity of deposit. The quantity of *B. thuringiensis* colonies per square centimeter of culture medium varied between 21 and 113 col/cm^2, and counts over 50 col/cm^2 were considered as a good deposit. The deposit was lower than that obtained with the Micronair sprayers which equipped the Stearman aircraft during the 1971 experiment. In general, it was found that the boom and nozzle attachments were not able to give the high-quality deposit given by the Miconair system, a higher-deposit volume being in the larger drop-size categories.

Mortality of larvae in buds was 49.81% seven days after spraying. During the same period, an average of 105 larvae had fallen on each cloth table. The larval mortality in plots that received a sufficient amount of deposit averaged 88.2% (between 84 and 93%). Pupal mortality averaged 33.9%.

The survival of parasites was made evident by the presence of several healthy pupae of Tachiniidae on cloth tables. Similar to the 1971 operation, spores survived in the air of treated plots up to 15 days after spraying, and no particles remained in the air after spraying, indicating that *B. thuringiensis* treatments are not a source of pollution.

From visual observations it was estimated that some 70% of the current year's foliage was protected in the treated area compared to no protection in the control area. By using a statistical method proposed in 1972 by the Conservation Branch, Department of Lands and Forests, Quebec, and the Department of Entomology, Faculty of Forestry, Laval University, it was established that 47% of the foliage in the treated area and 12% in the control

area remained on the trees. Although these figures seem rather low, they compare advantageously with those obtained when spraying with the chemical insecticide fenitrothion.

Five to six hundred larvae were weighed and measured periodically in treated and control plots. The results obtained revealed a reduction in the weight and length of treated larvae, and this is not unusual since it was observed that treated larvae stop feeding a few days after spraying for the following ten-day period. For example: Measurements of the weight of larvae in treated plots were .0059, .0176, and .0497 gram compared to .0073, .0410, and .0579 gram for larvae from the control, a 56% decrease. On the same days, the length of larvae from treated plots was 6.55, 10.22, and 13.91 millimeters compared to 6.92, 13.94, and 14.16 millimeters for larvae from control plots, a 26% decrease. The weight of pupae was 6.3 grams in treated plots and 7.8 grams in control plots. Fifteen days after spraying the surviving larvae started feeding again and a higher defoliation, which was still considerably lower than that in control plots, was observed.

Studies on the enzymatic activities in the hemolymph of infected living larvae and healthy larvae revealed that the larval metabolism is greatly modified during infection. The activity of the glutamic-oxaloacetic transaminase (GOT) and glutamic-pyruvic transaminase (GPT) did not vary; the activity of the dehydrogenases was greatly reduced [isocitrate dehydrogenase (ICDH) —from 603 to 186 mU/ml*] and that of the phosphatases increased (alkaline phosphatase—from 200 to 490 mU/ml). Furthermore, the infection provoked a strong decrease, from 4.8 to 2.7%, in the lipid reserves of the organism and a strong elevation of the rate of chloride in the hemolymph (from 36.0 to 100.5 mEq/1†). In infected pupae, and increase of transaminase activity (GOT—up to 32 mU/g) and a decrease of the dehydrogenase (from 38.8 to 11.2 mU/g) were observed. The activity of the phosphatases remained elevated (alkaline phosphatase: 185 mU/g compared to 120 mU/g in the control). In healthy pupae, a strong cholinesterase activity (49.0 mU/g) was observed, whereas it diminishes to 17.5 mU/g in infected pupae. Besides, the rate of lipids decreased by half during infection, from 5.3 to 2.9% (Smirnoff and Valéro, 1972).

The estimation of egg masses made in August revealed that in more than half of the sample points in the territory sprayed with Thuricide the number of egg masses per 100 square foot of foliage for 5 branches was under 640 masses, indicating a low defoliation in 1973. Throughout the control area the number of egg masses for 5 branches always exceeded 935 masses—an indication probably of a high defoliation in 1973.

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* 1 mU/ml or g $= \frac{1 \text{ mU mole converted substract}}{1 \text{ min} \times 1 \text{ ml or g}}$

† mEq/l = milliequivalent/liter

DISCUSSION

In Maine, Dr. J. B. Dimond, professor at the University of Maine, tested several formulations of *Bacillus thuringiensis* against the spruce budworm. In a personal communication he confirmed that only sprayings with *B. thuringiensis* + the same concentration of chitinase that we used in our tests gave good foliage protection.

Special attention should be paid to determine why Plot 1 sprayed in 1971 with *B. thuringiensis* + chitinase was practically not affected by the insect this year and why the egg count carried out in the fall of 1972 indicates a low population for 1973. Is it possible that *B. thuringiensis* treatments are able to maintain their effects on the population the following year? Does a reserve of bacterial material remain in the biotope the year following a mass introduction of bacteria? These important questions are now being studied.

It was concluded from the 1972 application of *B. thuringiensis* on 10,000 acres that this bacterial insecticide offers strong possibilities for its use in the control of spruce budworm outbreaks.

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Ecological Characteristics of the New York State Butterfly Fauna (Lepidoptera)

Arthur M. Shapiro
Department of Zoology, University of California, Davis, California 95616

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Abstract: "Niche breadth" as reflected by occurrence in nine ecological regions of New York State is examined by family for the 142 species of butterflies recorded in the state fauna. Species/genus ratios are also examined by families and regions. Data on voltinism and immigration are presented. It is concluded that "niche breadth" is smallest in the Lycaenidae and Hesperiidae and that the ecological distribution of species in these families in the regions with the largest faunas (excluding immigrants) tends to increase the species/genus ratio.

INTRODUCTION

New York State is one of the best-collected and most thoroughly documented areas for butterflies in the United States. The fauna has recently been reviewed in detail (Shapiro, in press). A total of 142 species has been recorded for the state. This is a sufficiently large fauna for ecologically significant information to be extracted from its composition and distribution.

ECOGEOGRAPHIC DISTRIBUTION AND "NICHE BREADTH"

The ecological geography of New York is complex. Thompson (1966) presents various regional classifications of the state based on climate, landforms, vegetation, etc. A convenient summation of these only partially concordant classifications is the division of the state into nine ecogeographic regions based broadly on physiography (Shapiro, in press) (Fig. 1). Each region includes a variety of habitats; relative areas of the regions may be estimated from the figure. The occurrence of each butterfly species in each region has been tabulated (presented in full in Shapiro, *ibid.*). The number of regions in which a species occurs may be taken as a crude index of its "niche breadth," at least insofar as its New York range is concerned. Table 1 gives the occurrence by number of regions of species grouped into five major "families" (sens. lat.). Separate tabulations are given with and without species which occur in New York only as immigrants; these have a significant impact on the overall pattern. The sources and seasonal characteristics of immigration into New York are discussed in Shapiro (*ibid.*).

These data are not strictly comparable with previously published distributions

Acknowledgments: Drs. George W. Salt and E. W. Jameson, Jr., reviewed aspects of this study. The data on which it is based were obtained from many sources credited in Shapiro, in press.

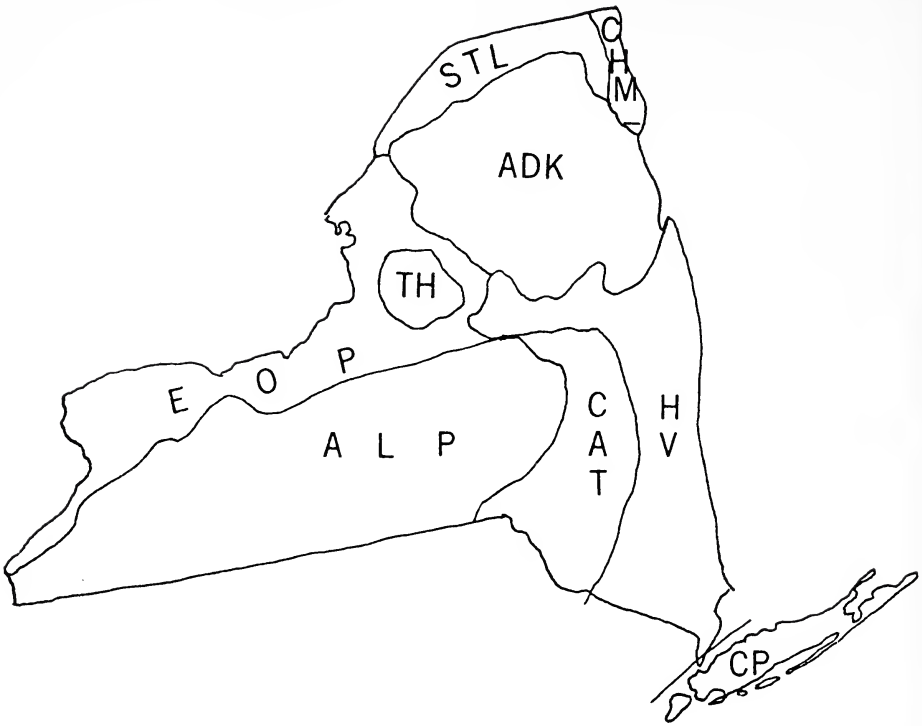

FIG. 1. Ecogeographic regions of New York. Abbreviations: CP, Coastal Plain; HV, Hudson Valley; CAT, Catskill Mts.; ALP, Allegheny Plateau; ADK, Adirondack Mts.; TH, Tug Hill Plateau; EOP, Erie-Ontario Plain; STL, St. Lawrence Valley; CHM, Champlain Valley.

of "niche breadth," based on measurements such as occurrence by habitat types (several examples in Williams, 1964). Such distributions typically give a more-or-less U-shaped graph when number of species is plotted against the measure of breadth. The New York data give a trimodal plot reminiscent of that derived by Williams (1964) from the data of Emmel and Emmel (1962) on the butterfly fauna of Donner Pass, California. There, "niche breadth" is based on occurrence in ten habitats of four general types.

Table 1 also includes the mean number of regions/species on a family-by-family basis. Comparison of the tables with and without immigrants demonstrates the role of these species in lowering the average "niche breadth" of species in the families with especially large numbers of immigrants. In the resident fauna, the Lycaenidae and Hesperiidae appear to have especially narrow niches.

In Table 2, the characteristics of the regional faunas are examined in terms of "niche breadth" of the component species (as expressed by number of regions

Table 1*a*. Number of species in each butterfly family occurring in different numbers of ecogeographic regions in New York, including immigrant species.

Family	Number of regions									Total # of species	Mean # of regions/ species	% of species found in all 9 regions
	1	2	3	4	5	6	7	8	9			
Nymphalidae	6	1	0	6	5	3	1	3	15	40	5.0	37.5
Lycaenidae	6	1	4	3	4	1	3	2	5	29	4.8	17.1
Pieridae	3	4	1	1	2	0	0	0	3	14	3.9	21.4
Papilionidae	1	0	0	2	2	0	0	0	2	7	5.3	28.6
Hesperiidae	9	6	5	8	8	4	2	1	9	52	4.5	19.2
Total # of species:	25	12	10	20	21	8	6	6	34	142	4.9	24.0

of occurrence and by voltinism) and the role of immigration both from outside the state and from outside the region (including out-of-state). Of all of these bases, the Coastal Plain has the most distinctive fauna. This single region, moreover, contributes sixteen species not found in any other region and has the largest fauna of any region, with 83.8 percent of the total New York fauna although it has an area comparable to Tug Hill, with only half as many species in a very severe climate.

Tables 3 and 4 demonstrate the degree of faunal relationship among all possible pairs of regions. In Table 4, this is quantified as the percentage of each given regional fauna shared with each of the others, and also the percentage of each other regional fauna found in it. A more complex matrix showing the consistency of co-occurrence of species in regions has also been prepared. Very similar patterns are obtained when various suggested formulae for faunal affinity (Long, 1963) are substituted for these simple percentages. Such formulae attempt to combine the two components of faunal resemblance given in Table 4.

On a regional basis species distributions must be interpreted as a continuum rather than as a set of discrete associations, but a strong tendency toward as-

Table 1*b*. Same, excluding immigrant species.

Family	Number of regions									Total # of species	Mean # of regions/ species	% of species found in all 9 regions
	1	2	3	4	5	6	7	8	9			
Nymphalidae	3	1	0	4	5	3	1	3	13	33	6.4	39.4
Lycaenidae	4	1	4	3	4	1	3	2	5	27	5.1	18.9
Pieridae	0	2	1	1	1	0	0	0	3	8	5.4	37.5
Papilionidae	0	0	0	2	2	0	0	0	2	6	6.0	33.3
Hesperiidae	3	5	3	8	8	4	2	1	9	43	5.1	20.9
Total # of species:	10	9	8	18	20	8	6	6	32	117	5.6	27.4

TABLE 2. Ecological characteristics of the regional faunas. Regional abbreviations are as in Figure 1.

	Region								
	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
Total species recorded	119	106	81	107	57	46	94	52	48
% recorded from $\geqslant 5$ regions in N.Y.	56.2%	68.0	90.1	71.0	89.9	73.9	77.7	90.4	100%
% recorded from $\leqslant 2$ regions in N.Y.	22.7%	7.5	1.2	3.7	5.3	4.3	4.3	4.0	0%
% immigrant from out-of-state	18.9%	8.5	3.7	9.3	3.5	4.3	9.6	4.0	4.1%
% immigrant from out-of-region (includes out-of-state)	24.4%	12.3	6.2	15.0	3.5	6.5	11.7	7.5	4.1%
% univoltine	38.9%	44.3	55.5	57.0	60.0	63.0	56.4	60.0	60.4%

sociations could be expected on a habitat basis. The Coastal Plain and Hudson Valley can be considered "southern" regions and Tug Hill and the Adirondacks "northern," with intergradation through the others, especially the Allegheny Plateau and Erie-Ontario Plain. The peak in the 4 to 5 region range reflects this; both "northern" and "southern" species are able to occupy that many regions, but a sixth carries either one too far into unfavorable environment for successful occupation to occur.

SPECIES-TO-GENUS RATIOS

The ratio of the number of species to number of genera in a fauna or flora has been taken as a measure of intrageneric competition by various writers, but its interpretation has been inconsistent and often controversial (cf. Williams, 1964; Elton, 1946). The New York data are of special interest since species-to-genus ratios can be obtained not only for the entire state but for the regions

TABLE 3. Number of species shared by pairs of regions in New York.

Region	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
CP	(119)	98	67	94	45	39	84	45	44
HV		(106)	74	99	44	39	87	47	47
CAT			(81)	81	53	44	74	48	47
ALP				(107)	49	44	80	49	48
ADK					(57)	44	48	45	43
TH						(46)	41	39	36
EOP							(94)	48	47
STL								(52)	42
CHM									(48)

Table 4. Relationships of the regional faunas. Above the diagonal: Percentage of the fauna in the diagonal recorded in each other fauna (read across the columns to the right). Below the diagonal: Percentage of each other fauna recorded in the fauna in the diagonal (read down the rows from the diagonal).

Region	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
CP	(100)	82.4	56.3	79.0	37.8	32.8	70.6	37.8	37.0
HV	92.4	(100)	70.0	93.4	42.5	37.0	82.1	44.3	44.3
CAT	82.7	91.3	(100)	100.0	65.4	54.3	91.3	59.3	58.0
ALP	90.3	92.5	75.7	(100)	45.8	41.1	74.7	45.8	44.9
ADK	78.9	77.2	93.0	86.0	(100)	77.2	84.2	78.9	75.4
TH	85.0	85.0	95.7	95.7	95.7	(100)	89.1	84.8	78.2
EOP	89.8	92.5	78.7	85.1	51.1	43.6	(100)	51.6	50.0
STL	86.5	90.4	92.3	94.0	86.5	75.0	92.3	(100)	80.7
CHM	91.7	97.9	97.9	100.0	89.5	75.8	97.9	87.5	(100)

and thus can be related to the overall faunal richness and its environmental component. The butterfly fauna of New York corresponds well to a logarithmic series (Table 5), suggesting that its classification is internally reasonably consistent and can also be compared with other faunas. Table 6 gives the regional and total species-to-genus ratios with and without immigrants. There is a broad correlation of large faunas with larger numbers of species per genus. This correlation is partly obscured where large numbers of immigrant species are included, since most of them are the only representatives of their genera in the fauna. These data suggest in a very general sense that more congeners can coexist in areas with milder climates, i.e., that finer subdivision of the environment into minimally competitive niches can be achieved. This statement agrees with most current ecological thought.

In Table 1 there was a strong suggestion that "niche breadth" is different in the butterfly families, and when species-to-genus ratios are examined on a per-family basis they support this inference. In Table 7, the number of genera

Table 5. Genera and species in the New York fauna and their fit to a logarithmic series.

Species/genus	Observed	Number of species calculated from log series
1	39	38.3
2	14	13.4
3	4	8.9
4	6	6.7
5	5 ($\sum_{1}^{5} = 68.0$)	5.4 ($\sum_{1}^{5} = 72.7$)
6	1	4.5
7	0	3.8
8	1	3.4
	70	84.4

Total: 142 species in 70 genera.

TABLE 6. Species/genus ratios of the New York regional faunas.

Region	Including immigrants			Excluding immigrants		
	Total # of species	Total genera	Species/ genus	Total # of species	Total genera	Species/ genus
CP	119	63	1.90	97	48	2.02
HV	106	55	1.93	98	48	2.04
CAT	81	39	2.08	78	37	2.11
ALP	107	54	2.00	98	47	2.09
ADK	57	31	1.84	55	30	1.83
TH	46	28	1.67	44	27	1.62
EOP	94	48	1.96	86	42	2.05
STL	52	32	1.62	50	31	1.61
CHM	48	29	1.66	46	28	1.70
	142	70	2.03	117	54	2.18

containing one to eight species is given on a family basis. In the New York fauna, the Lycaenidae and especially the Hesperiidae have many monotypic genera. On the other hand, only two genera have more than five species, and these are both Hesperiidae-*Polites*, with six (one immigrant), and *Erynnis*, with eight (seven sympatric on the Coastal Plain); and the Lycaenids have two of seventeen genera with more than three species (*Satyrium, Incisalia*) and the Hesperiids five of 25 (*Erynnis, Hesperia, Polites, Poanes, Euphyes*), accounting for more than half of the thirteen such genera (out of 70). Also, congeners in the Lycaenidae and Hesperiidae tend to be sympatric while those in Nymphalidae and Pieridae tend to replace one another geographically.

The role played by the Hesperiidae in the New York fauna, of a large, dominant family (52 of 142 species, 36.7 percent) of specialized species, corresponds to that of the Lycaenidae in the Sierra Nevada (28 of 74 species, 37.8 percent at Donner Pass, Emmel and Emmel, 1962; 49 of 134 species, 36.5 percent, Yosemite, Garth and Tilden, 1963), and to the Plebeiinae and Satyrinae in various Palaearctic faunas. The roles of the Lycaenidae and Hesperiidae are effectively reversed in New York and at Donner Pass: New York Lycaenidae number 29 (20.4 percent) and Donner Pass Hesperiidae ten (13.5 percent). The

TABLE 7. Number of genera with one to eight species, by families, in the New York fauna.

Family	Number of species							
	1	2	3	4	5	6	7	8
Nymphalidae	8	5	3	2	1	0	0	0
Lycaenidae	12	2	1	0	2	0	0	0
Papilionidae	2	0	0	0	1	0	0	0
Pieridae	2	2	0	2	0	0	0	0
Hesperiidae	15	5	0	2	1	1	0	1
Total:	39	14	4	6	5	1	0	1

Table 8. Number of species per family and region in the New York fauna.

Family	Region								
	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
Nymphalidae	31	31	29	33	26	20	31	20	21
Lycaenidae	23	31	17	23	12	7	17	10	10
Papilionidae	7	6	4	6	2	2	6	2	2
Pieridae	10	7	5	8	5	4	8	6	3
Hesperiidae	48	41	26	37	12	13	32	14	12
Total:	119	106	81	107	57	46	94	52	48

role of the Nymphalidae in the two localities is the same (New York, 40/142, 28.2 percent; Donner Pass, 23/74, 31.1 percent).

Table 8 gives the number of species per family in each region. As might be expected, the numbers of Hesperiidae and Lycaenidae drop rapidly in the regions with small faunas, while the number of Nymphalidae remains high and the relative importance of the family increases in the smaller regional faunas. Note in Table 1 that both the mean number of regions occupied/species and the percentage of all species found in all nine regions are highest in this family, also indicating broad adaptation.

HOST SPECIALIZATION

One measure of "niche breadth" not yet mentioned is specialization to the larval host plant. Data on this point are only partial. Ideally, the hosts for each species should be recorded in each region. In practice, each species has been classified into one of three categories on the basis of its recorded hosts state wide. No records not actually from New York have been considered. The categories are: "monophagous," recorded on only one plant genus; "oligophagous," recorded on two or more genera in the same plant family; and "polyphagous," recorded on two or more plant families. This classification, based on plant taxonomy, pays no attention to the chemistry of host-insect relationships, although in those cases where it is known it seems to control host selection, and although it often cuts across wide taxonomic boundaries. The chemistry of host selection is understood only for three or four New York butterflies.

In Table 9, these data are presented on a regional basis for all species for which satisfactory host data are available. Overall, oligophagy is the commonest condition, but in the regions with the largest faunas monophagy is nearly as frequent or more so, indicating a high incidence of specialization. In the regions with small faunas, the relative dominance of oligophagy increases. There is little increase in polyphagy, which occurs in few species in New York state (these are nearly all of very wide distribution).

Most specialization patterns are not dramatically different among the butter-

TABLE 9. Distribution of monophagy (M), oligophagy (O), and polyphagy (P) by families and species in each region.

Region	Family	M	O	P	Region	Family	M	O	P
CP	Nymph.	10	10	6	ALP	Nymph.	11	11	6
	Lycaen.	11	6	3		Lycaen.	10	6	4
	Pap.	2	1	3		Pap.	2	1	3
	Pier.	2	5	0		Pier.	3	4	0
	Hesp.	17	16	2		Hesp.	12	15	2
	Total:	42	38	14		Total:	38	37	15
	%:	44.4	41.7	14.9		%:	42.2	41.1	16.7
HV	Nymph.	9	11	6	ADK	Nymph.	9	9	3
	Lycaen.	9	6	4		Lycaen.	6	2	2
	Pap.	2	1	3		Pap.	0	1	1
	Pier.	2	5	0		Pier.	1	4	0
	Hesp.	13	16	2		Hesp.	1	6	1
	Total:	35	39	15		Total:	17	22	7
	%:	39.3	43.9	16.8		%:	37.0	47.8	15.2
CAT	Nymph.	9	11	5	TH	Nymph.	8	7	3
	Lycaen.	6	5	3		Lycaen.	4	1	2
	Pap.	0	1	3		Pap.	0	1	1
	Pier.	2	3	0		Pier.	1	3	0
	Hesp.	6	12	1		Hesp.	1	7	1
	Total:	23	32	12		Total	14	19	7
	%:	34.3	47.7	18.0		%:	35.0	47.5	17.5
EOP	Nymph.	10	11	6	STL	Nymph.	7	9	3
	Lycaen.	7	5	3		Lycaen.	8	1	2
	Pap.	2	1	3		Pap.	0	1	1
	Pier.	2	4	0		Pier.	2	4	0
	Hesp.	8	14	2		Hesp.	0	9	1
	Total:	29	35	14		Total:	17	24	7
	%:	37.2	44.8	18.0		%:	35.4	49.9	14.7
CHM	Nymph.	9	10	3	State-wide	Nymph.	11	11	6
	Lycaen.	5	2	2		Lycaen.	12	6	4
	Pap.	0	1	1		Pap.	2	1	3
	Pier.	0	3	0		Pier.	4	6	0
	Hesp.	0	8	1		Hesp.	18	17	2
	Total:	14	22	7		Total:	47	41	15
	%:	32.5	51.2	16.3		%:	45.6	39.8	14.6

fly families in New York. The Nymphalidae have a surprisingly large number of monophagous species, but most of these feed on widespread and common plant genera. The small Papilionid and Pierid faunas are consistent across the state. In the Lycaenidae and Hesperiidae, oligophagy often involves several alternate or seasonal hosts, none of which is especially common or widespread. Indeed, the narrowness of some butterfly niches may be defined by the low probability of finding two or more required host species close together.

CONCLUSION

One of the central problems of community ecology is the nature of the factors determining species diversity. Interspecific competition is one of these factors, acting in ecological time through competitive exclusion and in evolutionary time through character displacement. The data on New York State butterflies support the familiar gradients of species richness associated with latitude and climate, and, at the same time, they suggest strongly that the adaptive responses of different families to these conditions have produced different patterns of resource allocation and niche differentiation.

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An Annotated List of the Siphonaptera of Connecticut

DONALD H. MILLER
DEPARTMENT OF SCIENCE, LYNDON STATE COLLEGE, LYNDONVILLE, VERMONT

AND

ALLEN H. BENTON
DEPARTMENT OF BIOLOGY, STATE UNIVERSITY COLLEGE, FREDONIA, NEW YORK 14063

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Abstract: In previous papers, eleven species of fleas have been reported from Connecticut. The present list, consisting largely of specimens collected by the senior author in Windham and Tolland counties, adds eleven species to those previously recorded from the state. The additional species include: *Atyphloceras bishopi* Jordan, *Catallagia borealis* Ewing, *Tamiophila grandis* (Rothschild), *Nearctopsylla genalis genalis* (Baker), *Stenoponia americana* (Baker), *Rhadinopsylla orama* Smit, *Megabothris asio asio* (Baker), *Orchopeas leucopus* (Baker), *Peromyscopsylla hamifer hamifer* (Rothschild), *Peromyscopsylla hesperomys hesperomys* (Baker), and *Peromyscopsylla scotti* I. Fox. A hypothetical list of twenty species is appended.

Although publications have appeared listing the fleas of several neighboring states (e.g., Geary, 1959; Mathewson and Hyland, 1964; Osgood, 1964), no separate list of Connecticut fleas has been published, and records of fleas are few. Fox (1940) gave records of only seven species from the state. Fuller (1943) added two more, and Main (1970) brought the list to eleven. Since the New York list is nearly fifty species, the Vermont list thirty-three, and the Rhode Island list eighteen, it is evident that these lists are very incomplete.

During 1963 to 1966 the senior author collected 803 fleas from mammals in Tolland and Windham counties. These specimens were prepared and identified by the junior author. The junior author was privileged also to examine specimens in the collection of the Archbold Biological Station, Lake Placid, Florida, which had been collected in Connecticut by Dr. John Mackiewicz. We are grateful to Dr. James N. Layne for the opportunity to include these specimens in the present list.

The collections here reviewed include eleven species previously unrecorded from Connecticut, thus doubling the number of flea species known from the state. We include also a hypothetical list, including twenty additional species which have been taken in states bordering Connecticut from hosts which occur within the state. The total expected state list thus approximates forty species.

Nomenclature of the Siphonaptera follows Hopkins and Rothschild (1953 et seq.). Mammalian nomenclature follows Hall and Kelson (1959).

FAMILY PULICIDAE

Cediopsylla simplex (Baker)
Counties: Litchfield, Middlesex (Main); Oxford (Mackiewicz); Windham
Hosts: *Sylvilagus floridanus*;* occurs also on *S. transitionalis** and *Lepus americanus** and occasionally on their predators and ecological associates

Ctenocephalides canis (Curtis)
Counties: Hartford (Main)
Hosts: *Canis familiaris*;* also occurs on wild foxes

Ctenocephalides felis felis (Bouche)
Counties: Fairfield, Hartford, New Haven, Tolland, Windham (Main)
Hosts: *Canis familiaris*;* *Felis domestica*;* also occurs on wild predators and will bite man freely.

FAMILY HYSTRICHOPSYLLIDAE

Atyphloceras bishopi Jordan
Counties: Tolland, Windham
Hosts: *Microtus pennsylvanicus;** *Clethrionomys gapperi; Synaptomys cooperi; Blarina brevicauda*

Catallagia borealis Ewing
County: Windham
Hosts: *Clethrionomys gapperi;** *Synaptomys cooperi*

Tamiophila grandis (Rothschild)
County: Windham
Host: *Mustela* sp. This is a parasite of the chipmunk, *Tamias striatus*, of which the weasel is a predator.

Epitedia wenmanni wenmanni (Rothschild)

Epitedia wenmanni testor (Rothschild)

Southern New England is within the area of intergradation between these two forms. Our collection includes both subspecies, and three males show intergradation.

Rhadinopsylla orama Smit

Specimens of this species are very rare in collections. It is usually taken from microtines, especially *Microtus pennsylvanicus* and *M. pinetorum*. A single female was collected by John Mackiewicz at Waterbury, June 9, 1952.
County: New Haven
Host: *Microtus pinetorum*

Ctenophthalmus pseudagyrtes pseudagyrtes Baker
Counties: Hartford, New Haven (Main), Tolland, Windham
Hosts: *Blarina brevicauda, Sorex cinereus, Sorex fumeus, Scalopus aquaticus, Peromyscus leucopus, Clethrionomys gapperi, Microtus pennsylvanicus, Microtus pinetorum, Napeozapus insignis*

Doratopsylla blarinae C. Fox
Counties: Hartford, Windham (Main), Tolland
Hosts: *Blarina brevicauda,** *Peromyscus leucopus, Microtus pinetorum*

Nearctopsylla genalis genalis (Baker)
County: Tolland
Hosts: *Condylura cristata, Blarina brevicauda*

Stenoponia americana (Baker)
Counties: New Haven, Tolland

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* True hosts, where known with some assurance, are marked with an asterisk.

Hosts: *Blarina brevicauda, Peromyscus leucopus, Microtus pennsylvanicus, Clethrionomys gapperi*

FAMILY CERATOPHYLLIDAE

Ceratophyllus gallinae (Schrank)
Counties: Fairfield, Hartford, New Haven, Windham (Main)
Hosts: A variety of birds, including domestic chickens

Ceratophyllus idius Jordan and Rothschild
County: Windham (Main)
Host: *Iridoprocne bicolor**

Megabothris asio asio (Baker)
Counties: Tolland, Windham
Hosts: *Microtus pennsylvanicus,** *Microtus pinetorum, Clethrionomys gapperi, Mustela frenata, Condylura cristata*

Orchopeas howardii howardii (Baker)
Counties: New Haven (Main), Tolland, Windham
Hosts: *Sciurus carolinensis,** *Glaucomys volans, Clethrionomys gapperi*

Orchopeas leucopus (Baker)
Counties: Tolland, Windham
Hosts: *Peromyscus leucopus,** *Clethrionomys gapperi*

Oropsylla arctomys arctomys (Baker)
Counties: Fairfield, Litchfield, Middlesex, New London, Tolland
Hosts: *Marmota monax,** *Urocyon cinereoargenteus*

FAMILY LEPTOPSYLLIDAE

Peromyscopsylla hamifer hamifer (Rothschild)
County: Tolland
Hosts: *Microtus pennsylvanicus, Condylura cristata*

Peromyscopsylla hesperomys hesperomys (Baker)
Counties: Tolland, Windham
Hosts: *Peromyscus leucopus,** *Clethrionomys gapperi*

Peromyscopsylla scotti I. Fox
County: Tolland
Host: *Peromyscus leucopus**

FAMILY ISCHNOPSYLLIDAE

Myodopsylla insignis (Rothschild)
Counties: Hartford, Litchfield, New Haven
Host: *Myotis* sp.*

HYPOTHETICAL LIST

The following species have been taken in adjacent states, from hosts known to occur in Connecticut.

FAMILY PULICIDAE

Pulex irritans (Linnaeus)—on humans and mammals associated with houses
Xenopsylla cheopis (Rothschild)—on rats, *Rattus* spp.

FAMILY VERMIPSYLLIDAE

Chaetopsylla lotoris (Stewart)—on carnivores

FAMILY HYSTRICHOPSYLLIDAE

Conorhinopsylla stanfordi Stewart—on *Glaucomys* spp.
Hystrichopsylla tahavuana Jordan—on moles and shrews
Epitedia faceta (Rothschild)—on *Glaucomys* spp.
Corrodopsylla hamiltoni (Traub)—on *Cryptotis parva*
Corrodopsylla curvata curvata (Rothschild)—on *Sorex* spp.

FAMILY CERATOPHYLLIDAE

Ceratophyllus celsus celsus Jordan—in swallow nests
Ceratophyllus diffinis Jordan—in nests of ground-nesting or low-nesting birds
Ceratophyllus riparius riparius Jordan and Rothschild—in nests of *Riparia riparia.*
Megabothris acerbus (Jordan)—on *Tamias striatus*
Megabothris quirini (Rothschild)—on *Clethrionomys gapperi*
Monopsyllus vison vison (Baker)—on *Tamiasciurus hudsonicus*
Nosopsyllus fasciatus (Bosc)—on *Rattus norvegicus*
Opisodasys pseudarctomys (Baker)—on *Glaucomys* spp.

FAMILY LEPTOPSYLLIDAE

Leptopsylla segnis (Schonherr)—on *Mus musculus*
Odontopsyllus multispinosus (Baker)—on *Sylvilagus* spp. and *Lepus* spp.
Peromyscopsylla catatina (Jordan)—on *Clethrionomys gapperi*

FAMILY ISCHNOPSYLLIDAE

Nycteridopsylla chapini Jordan—on *Eptesicus fuscus*

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Notes on the Life Cycle and Natural History of Butterflies of El Salvador
II A.—*Epiphile adrasta adrasta* (Nymphalidae-Catonephelinae)

ALBERTO MUYSHONDT
101 AVENIDA NORTE #322, SAN SALVADOR, EL SALVADOR

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Abstract: The life cycle of *Epiphile adrasta adrasta* Hewitson (Nymphalidae-Catonephelinae) and its natural history were studied in several localities of El Salvador during a period of two years. Special attention was given to the description of the life-cycle stages, time spent in the different stages of the metamorphosis, foodplants during the larval period, and behavior of the early stages and adults. The apparent correlation between the Catonephelinae and Callicorinae is discussed, emphasizing the paradoxical behavior of the species at times suggesting palatability and at times unpalatability to predators.

INTRODUCTION

This is the second article of a second series describing what my sons and I have found in relation to the life cycle and natural history of butterflies belonging to the Catonephelinae found in El Salvador, Central America.

The purpose of these articles is to present the life cycle and observations on the early stages of behavior and to record the foodplants of the local species of *Rhopalocera* that according to the available literature have been studied only partially or not at all in the past; we hope thus to alleviate the task of the experts in taxonomy, who in many cases have had only the adult morphological characteristics on which to base their groupings. As a result of the present situation, there is no uniformity of consensus on how to group the families, "as this depends upon each writer's viewpoint" (Klots, personal communication). Thus, what for one modern author is Heliconiidae (Klots, 1960), for another is Heliconiini (Ehrlich and Ehrlich, 1961). It is not surprising therefore to find in relatively recent publications statements such as this: "The Nymphalinae" [which for other authors means Nymphalidae] "have not been the subject of a modern revision (which is sorely needed) and thus the tribal arrangement used below is, in many places, quite arbitrary ..." (Ehrlich and Ehrlich, 1961).

Acknowledgments: We are greatly indebted to Dr. Alexander B. Klots for his unfailing guidance and encouragement of our observations and for his help in the preparation of our manuscripts. We thank also Drs. Frederick D. Rindge for determining the specimens sent to him and S. D. Steinhauser for giving us free access to his technical library. The senior member of the Muyshondt family gives due credit to his sons for their valuable help in the fieldwork and to their mother for putting up with it!

In order to determine the species described in this article we submitted specimens of the adults to the American Museum of Natural History, where Drs. Alexander B. Klots and Frederick H. Rindge kindly gave their valuable assistance. Specimens of the early stages have been placed with the museum, where they are available to students of the group.

In an earlier article dealing with the life cycle and natural history of *Prepona omphale ocatavia* Frühstorfer (Muyshondt, 1973a), a description of the country and its climatic zones was given in order to establish a clear idea of the habitat of the species described.

Adults of *Epiphile adrasta adrasta* Hewitson frequent wooded ravines and creeks where second-growth plant communities are found, usually in the proximity of coffee plantations, which can be considered manmade forests, (about the only forests left in the country), at altitudes ranging from about 500 m to 1500 m of elevation.

Late in July 1970, some eggs were found on the underside of the leaves of an unidentified vine. In early September the adults emerged and we were amazed to find two different kinds of butterflies, subsequently determined to be males and females of *Epiphile adrasta adrasta* (we had the same surprise with adults of *Catonephele numilia esite* Felder). Since that time we have reared this species from egg to adult a number of times, from the beginning of the rainy season to mid-dry season (June to March). The eggs and larvae have been kept in individual transparent plastic bags, and photographs as well as measurements have been made of every stage. We kept records of the time spent on each stage of development. The bags were at all times at ambient light and temperature conditions.

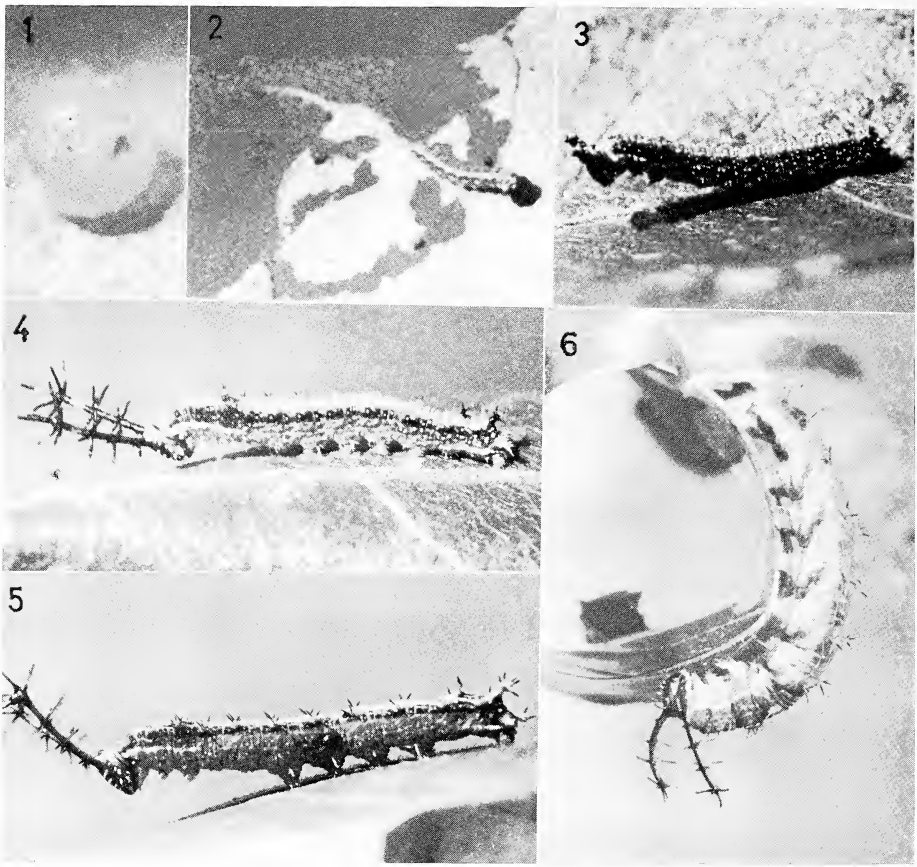
LIFE-CYCLE STAGES

Egg. Pure white when recently deposited, turning to gray before hatching. Shape a truncated cone, with convex micropyle surrounded by a crown of nine rounded prominences, from which inconspicuous white ribs originate, reaching vertically the base of the egg. About 1 mm long and laterally at widest point. They hatch in 5 days.

First instar larva. Head dark brown, naked, roundish, about same thickness as body. Body green dorsally, yellowish subspiracularly, with two dorsal rows of small tubercules. About 1.7 mm when recently hatched and 4.1 mm when ready to molt. Lasts 3–4 days.

Second instar larva. Head dark brown with short thick horns ended by a rosette of tiny spines on apex of epicrania. Body greenish brown with a thin yellowish stripe subspiracularly. Many transversal rings of clear tiny tubercules all along the body, and two subdorsal rows of tiny forked spines from second thoracic segment caudad, seventh and eighth abdominal with an additional spine at meson. Measures 7 to 8 mm long before molting in 4 days.

Third instar larva. Head brown with long horns on epicranial apex and small thin spines at lateral margins of epicrania. The horns bear three tranversal rows of spines each,



FIGS. 1–6. *Epiphile adrasta adrasta* Hewitson.

FIG. 1. Egg. About 1 mm.

FIG. 2. First instar larva, about 3 mm. Prolonged vein at left. Pellet of frass stuck to its body.

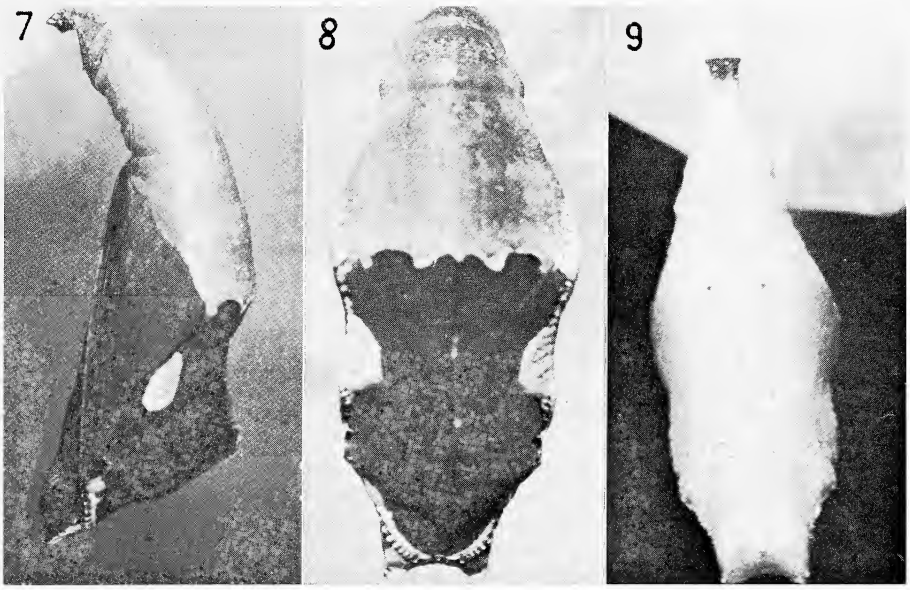
FIG. 3. Second instar larva in typical attitude. About 8 mm.

FIG. 4. Third instar larva in straight attitude. About 1.2 cm.

FIG. 5. Fourth instar larva in raised attitude. About 2 cm.

FIG. 6. Fifth instar larva, about 3 cm.

the first basally, the second at the middle, and the last one distally. Body yellowish brown dorsally with thin black line at meson; then longitudinal dark brown band supraspiracularly, then green down to ventral zone. The whole body with tiny tubercules and a pair of short forked spines on each segment, as in second instar the ones on third thoracic segment and the spines on meson of seventh and eighth abdominal segments being now more prominent. The caudal spines are directed posterad. There is a noticeable light seta at the base of each leg and proleg. On the third thoracic segment there is a black dorsal spot surrounded by a dark brown area and the spines grow at each side of this dark zone. It grows to 1.2 cm in 4 days.



FIGS. 7–9. *Epiphile adrasta adrasta* Hewitson.

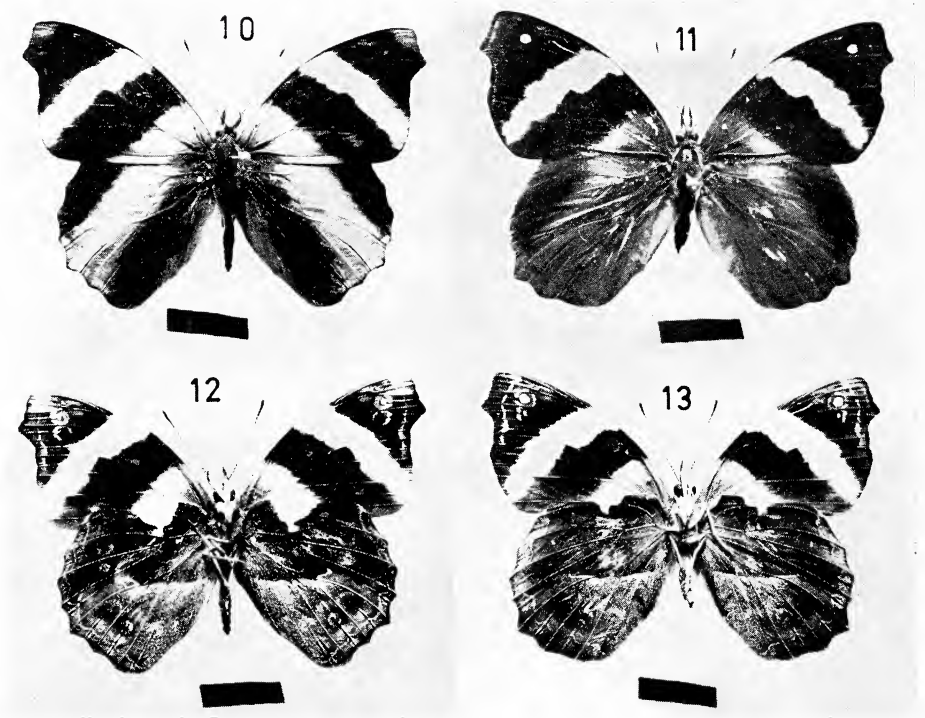
FIG. 7. Pupa, lateral view.
FIG. 8. Pupa, dorsal view.
FIG. 9. Pupa, ventral view, about 2 cm long.

Fourth instar larva. Head as in third stadium, with bigger lateral spines and epicranial horns that are now more or less incurved caudad and have grown tiny setae on the stem and spines. Body as in third instar but darker dorsally, mostly at thoracic and caudal segments. Spines orange with black forks, except those of the first abdominal segment which have yellow forks, contrasting against dark dorsal color. A slight transverse hump dorsally on third thoracic segment. Median spine on eighth abdominal segment very prominent now. Measures 1.8 or 2 cm before molting in 6–7 days.

Fifth instar larva. Head brown with reddish tinge, and light lateral margins of epicrania, with thin whitish spines surrounding the head and a light triangular spot at the frons. Body all green with yellow longitudinal stripe at sides of thoracic segments, thin yellow lines parallel to meson dorsally, and laterally irregular pattern of thin yellow lines. Slanting lateral zones of whitish green. Base of spines and spiracula yellowish-orange. It grows to 2.8 or 3 cm in 9–11 days.

Prepupa. Body becomes all green, short and thick, 1.8 cm long, and lasts 1 day.

Pupa. Abdomen thickens gradually from green cremaster to wing cases (widest point laterally) then tapers gradually to bifid head. Dorsal emargination at thorax where it joins abdomen, followed by thoracic projection strongly keeled (thickest point dorsoventrally). Abdomen light green with tiny yellowish spiracula. Wing cases darker green ventrally. Thorax still darker green dorsally. Brown lining bordering wing cases laterally and separation between abdomen and thorax dorsally. Edge of dorsal thoracic keel brown also. A silver patch laterally about mid-wingcase, and a silver lining bordering the head



FIGS. 10–13. *Epiphile adrasta adrasta* Hewitson.

FIG. 10. Male, dorsal view.
FIG. 11. Female, dorsal view.
FIG. 12. Male, ventral view.
FIG. 13. Female, ventral view.
Black bar measures 1 cm long.

dorsally, and dorsal portion of the antennae. Cremaster with flat surface armed with crochets. Measures 1.8 cm to 2.1 cm long, .9 cm laterally at widest point, and .7 cm dorsoventrally at widest point. Duration 8–9 days.

Adults. Wing shape the same in both sexes: forewing with projected angle at apex, then a short concavity followed by a long convexity to tornus; inner margin straight. Hind wing rounded with sinuose outer margin.

Drastic difference in dorsal colors between males and females.

Males: Forewing dorsally with small dark brown triangle basally, then an orange band covering up to ¼ costal margin down to mid-inner margin, then a dark brown band, parallel to the preceding one, covering up to mid-costal margin to tornus, followed by a second orange band, parallel to the others, covering up to ¾ costal margin to mid-outer margin. The rest of the forewing dark brown except for a small orange spot apically. Hind wing dark brown basally followed by an orange band from mid-costal margin to outer angle. The rest dark brown.

Females: Forewing a dark orange basally, slightly lighter at inner margin, then a pale yellow band from ¾ costal margin narrowing as it reaches outer margin just above tornus. The rest dark brown with a small round white spot subapically. Hind wing dark orange except for a dark brown area parallel to outer margin covering from mid-costal margin to close to outer angle.

Ventral wing coloration almost the same in both sexes; forewing a paler version of the male dorsal forewing, showing in addition two small spots subapically: The upper one is gray; the inferior, very dark brown. Hind wing is reddish brown with a row of inconspicuous eyes alongside the outer margin and a small triangular spot about mid-costal margin (bigger in males than in females).

The body is brown above, cream underneath; eyes brown and antennae orange tipped.

Females are usually larger than males, averaging 4.8 cm from tip to tip of the spread front wings in females, 4.6 cm in males. Time spent in the complete metamorphosis varies from 40 to 45 days, the females being slightly slower than the males.

NATURAL HISTORY

Eggs and larvae of *Epiphile adrasta adrasta* have been found on several species of Sapindaceae vines belonging to the genera *Paullinia, Serjania, Urvillea,* and *Cardiospermum,* with a definite predilection for *Paullinia fuscescens,* H.B.K.

P. fuscescens is a scandent plant with persistent, shiny, glabrous, rather thick bi-ternate leaves with lance-oblong leaflets from 6 to 15 cm long, sparsely serrate-dentate; its inflorescence consists of axillar racemes of tiny whitish flowers that produce trilobed hard capsules, bearing one seed in each section; the seeds are shiny black, and are half covered by a spongy white arillum. The young stems of the plant are squarish, rounded when mature.

Most vines belonging to the Sapindaceae, in particular the ones belonging to the genera *Paullinia* and *Serjania,* are reputed to possess "narcotic poisonous properties and some of them are employed for stupefying fish" (Standley, 1923). A local common name for this species is "Barbasco cuadrado." The noun barbasco is widely used for plants having fish-stupefying properties.

The eggs of *E. adrasta adrasta* are deposited singly on the undersides of mature leaves.

Upon emerging the tiny larvae eat the upper part of the eggshell and at times part of the walls, move later to the edge of the leaf, and nibble around a vein, baring it. To this vein they attach, by means of silk, pellets of frass that are rescued with their mouthparts at the moment they are expelled from the anus. Soon the vein seems to project beyond the leaf limits. This "vein" is used during the first, second, and sometimes the third stadia as a resting place by the larvae, which keep the head usually pointing outward. They only abandon the vein for feeding purposes, and after that is done they crawl back to it. While in the vein or even on top of a leaf, the young larvae sometimes are seen holding on with the prolegs only, the anterior part of the body being slightly raised. It happens at times that the whole leaf where the vein was

bared is consumed during these stadia; when that happens a new vein is treated the same way and with the same materials in another leaf. First and second-stadia larvae are seen with excreta pellets stuck to their body.

Fourth and fifth instar larvae (sometimes third instar also) wander about the plant, usually on the upper surface of the leaves. They can stay motionless for long periods of time, adopting three peculiar attitudes: one as described for the earlier instars, or straight, holding to the leaf with legs and prolegs, or the S-shaped one. In the last two cases the head is bent forward so that the horns are parallel to the supporting surface. When touched, the larvae strike with their horns with a side or back movement of the body, depending on their stance. If more than one larva happen to meet on the same leaf (which seldom occurs because of the amount of leaf surface available compared with their much smaller number), one might get punctured by the other. When ready to pupate, the larvae clean their digestive tracts by expelling an amount of green liquid mixed with excreta and weaving a silken pad on top of a leaf or on a twig, and affixing thereon their anal prolegs. They stay there straight, parallel to the supporting surface, not hanging in the usual manner of many butterflies.

The pupae, due to the flat surface on their cremaster, stand at an angle in relation to a supporting object, even when they seem to hang from it, which can be checked by turning the object at various angles: The pupae maintain the same relative position. Shortly before the adult emerges, the pupa turns dark gray. Similar to other species in the same group, the pupae of *E. a. adrasta* can emit a creaking sound when molested by wriggling sideways or moving like an accordion.

The adults emerge from the pupa shell very rapidly and find a place from which to hang and expand their wings. This process takes about 15 minutes and they are then ready to fly. In the process they expel an amount of reddish meconium.

Males and females of *E. adrasta adrasta* are swift flyers. The females are seen more often because they fly slowly and at low levels when looking for the foodplant on which to oviposit. The female alights under a mature leaf of the foodplant and deposits one egg on the underside of it. Several eggs are laid on a single vine, but never more than one egg on the same leaf. Oviposition occurs from late in the morning to early in the afternoon.

The adults of this species are not flower visitors, but feed greedily on rotten fruits and animal excrements on the ground and on the sap from tree-trunk wounds. When feeding, the adults lose their habitual alertness and are then easily netted.

We have collected eggs and larvae of *Epiphile adrasta adrasta* mostly from August to February. During the several years we have been rearing this spe-

cies in our insectarium and observing the larvae in the fields, we have not found a case of parasitism or witnessed a case of predation. The only cause of mortality in lab has been a diarrhea causing a softening of the body that is followed by bursting of the skin and death. In the fields we have found small larvae desiccated during the dry season.

DISCUSSION

J. Röber, writing in Seitz (1914), credits Müller (no reference is given of the publication) for a good description of fifth instar larva and pupa of *Epiphile orea* Hübner, and reports the foodplants for the genus *Epiphile* in Brazil to be *Paullinia seminuda* Rod. and *Serjania meridionalis* Cambes.

As stated in our article on the life cycle of *Catonephele numilia esite* Felder (Muyshondt, 1973b), the genus *Epiphile* is grouped by Ebert (1969) with the genera *Catonephele*, *Cybdelis*, *Myscelia*, and *Temenis*, under the Catonephelinae subfamily of the Nymphalidae. We include in the same group the genera *Pseudonica* and *Pyrrhogyra*, the latter being perhaps an intermediate between the Catonephelinae and the closely related subfamily Callicorinae, which encompasses the genera *Callicore*, *Diaethria*, *Paulogramma*, and *Catagramma*, because the eggs of that species are more like those of Callicorinae and the larvae more like those of Catonephelinae. It is true that there are striking similarities between the larvae and the pupae of both groups, that their respective behavior is almost the same during their early stages and that the two groups have enough adult characteristics in common to cause some authors to place species belonging to either one (*Myscelia* spp., *Diaethria* spp.) and other species not so closely related (*Eunica* spp., *Mestra* spp., *Hamadryas* spp., and *Biblis* spp.) in a single tribe, the Ergolini (Ehrlich and Ehrlich, 1961). Another point of contact between the two groups is the common use of foodplants belonging to the Sapindaceae. In our experience the only two exceptions to that are: *Catonephele numilia esite* and *C. nyctimus* Westwood, being the only two local species which feed on Euphorbiaceae. Our experience in these groups consists in having reared from egg to adult, in addition to the species described in this article, *C. numilia esite*, *Temenis laothöe liberia* Fabricius, *Pseudonica flavilla canthara* Doubleday, *Pyrrhogyra hipsenor* Godman and Salvin, *Diaethria astala* Guérin and *Catagramma titania* Salvin, plus others belonging to the two groups studied only partially. We hope to be able to present the life cycles of all these species to expose the evident similarities, not only morphological but behavioral as well during their early stages.

Epiphile adrasta adrasta larvae, feeding on plants known to contain narcotic/poisonous properties, would be expected to be unpalatable to predators and therefore to have the gaudy coloration associated with that condition,

and move about in the open. In fact the first and second instar larvae of this species seem to rely on crypsis for their defense rather than on the presumable protection derived from the foodplant. The larvae during these two stadia keep themselves motionless on the bared vein of the leaf, imitating portions of leaf tissue still adhering to it. But then, from third stadium on, the larvae expose themselves on the upper surface of the leaves and even if their colors could not be considered gaudy, they are readily spotted on the plant. Contrary to *C. numilia esite* larvae, which are practically covered by a shield of long forked spines, the larvae of *E. a. adrasta* have only two dorsal rows of very short forked spines, whose mechanical value for protection against predators would be minimal. Probably chemical protection provided by plant juices has made unnecessary the mechanical protection that would be supplied by a profusion of spines that might, indeed, become a handicap to larvae moving among masses of small leaves in their foodplants. The pupae, which are at times on tops of leaves and at times on the stems of the plant, disrupt their potentially protective green coloration by the shiny silver lining and conspicuous silver spot on the head and thoracic parts. From these facts we deduce that the noxious components extracted by the larvae from their foodplants must reach a certain degree of concentration in the body of the larvae (two first instars) to become efficient as predator deterrents.

The adults also could be expected to be chemically protected by the foodplant derivatives, but even if they are so protected, they do not rely solely on that for their survival; they also exploit their fast and erratic flight, combining it with the flash-and-hide effect obtained from the contrast between their brilliant dorsal colors and the dull brown color of the hindwings, which almost completely cover the forewings when at rest.

As in *C. numilia esite*, the drastic sexual dimorphism existing in *E. a. adrasta* is extremely puzzling, as no individual of either sex imitates any other of the local butterflies traditionally considered to be protected, thus eliminating the would-be logical explanation of a Müllerian mimicry case. If any benefit is derived by this species from this sexual dimorphism it has not yet been determined.

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Notes on the Life Cycle and Natural History of Butterflies of El Salvador III A.—*Temenis laothöe liberia* Fabricius (Nymphalidae-Catonephelinae)

ALBERTO MUYSHONDT
101 AVENIDA NORTE #322, SAN SALVADOR, EL SALVADOR

RECEIVED FOR PUBLICATION JULY 18, 1973

Abstract: For the first time a complete description, including photographs, of the life cycle of *Temenis laothöe liberia* Fabricius is presented, as well as a record of the foodplants in Central America. Behavior during early and adult stages is described and compared with behavior of closely related species. The findings are discussed with relation to the possibility that this species is protected against predators as a result of the poisonous properties of its foodplants.

This is the third article of a series dealing with what my sons and I have found in relation to the life cycles and natural history of the local butterflies belonging to the Catonephelinae, a group of the Nymphalidae. Another series has been presented elsewhere describing the life cycle with notes on the natural history of some of the local Charaxinae. The purpose of these articles is to present information on tropical butterflies, mostly of the family Nymphalidae, of which there is only exiguous knowledge in the literature. The papers will provide the experts with new elements that hopefully will help them in the sorely needed revision of the Nymphalidae, which are grouped by many authors on the basis of the broad characteristic that both adult sexes have the prothoracic legs much atrophied. Similarly, the actual Papilionidae and Pieridae were grouped not long ago under one family, Papilionidae, on the bases that adults of both sexes have six ambulatory legs and the pupae are secured not only by the cremaster but also by a girdle (Holland 1914). Simultaneous with the presentation of the articles, complete series of preserved specimens of the early stages of the species described have been sent to museums where they are available to students of those groups.

Our greatest difficulty has been the actual determination of the species because we are dependent on old publications (Seitz 1924), which, although they represent a formidable step in the knowledge of tropical American fauna and

Acknowledgments: We are greatly obliged to Drs. Alexander B. Klots and Frederick H. Rindge of the American Museum of Natural History for their sustained guidance and counsel in our studies and the identifications of the materials submitted to them. We thank them also for reading and criticizing our manuscript. We are also grateful to Miguel Serrano, El Centro El Salvador–Estados Unidos, who gave free access to reference publications and to Victor Hellebuyck who helped the younger members of the family in the fieldwork.

therefore deserve due credit, refer to many species by names that have since been changed. To overcome this handicap, Drs. Alexander B. Klots and Frederick H. Rindge of the American Museum of Natural History have made the determination of the species mentioned in this article. For future verifications of identifications, specimens have been placed in the museum.

When describing the life cycle of *Prepona omphale octavia* Frühstorfer (Muyshondt 1973a), a short description of the country is included, with pertinent information regarding its climatic conditions, altitudes, and vegetation, to familiarize the reader with the habitats of the species described.

The adults of *Temenis laothöe liberia* Fabricius, like its close relative *Epiphile adrasta adrasta* Hewitson, favor wooded ravines and creeks in the vicinity of coffee plantations. The ravines and creeks harbor the remains of the wild flora of El Salvador, consisting of second-growth plant communities where the wild vines used as food by the larvae are quite abundant. This species ranges from about 500 to 1500 m. altitude.

Shortly after our finding, in 1970, the eggs of *Epiphile adrasta adrasta* (Muyshondt 1973c), we found on the same plant other eggs resembling them so much that we expected the new ones to belong to a closely related species. After a time we obtained from these eggs orange-colored butterflies, later determined as *Temenis laothöe liberia*, thus confirming our expectations.

The eggs collected at that time and the larvae that hatched from them were kept until pupation in transparent plastic bags under ambient lighting and temperature conditions. The pupae were transferred to a wooden box with wide openings covered by mosquito netting and maintained until the adults emerged. Photographs were taken of every stage and records of developmental time and measurements were kept. Specimens of early stages were preserved in alcohol and have been sent to the American Museum of Natural History, New York City.

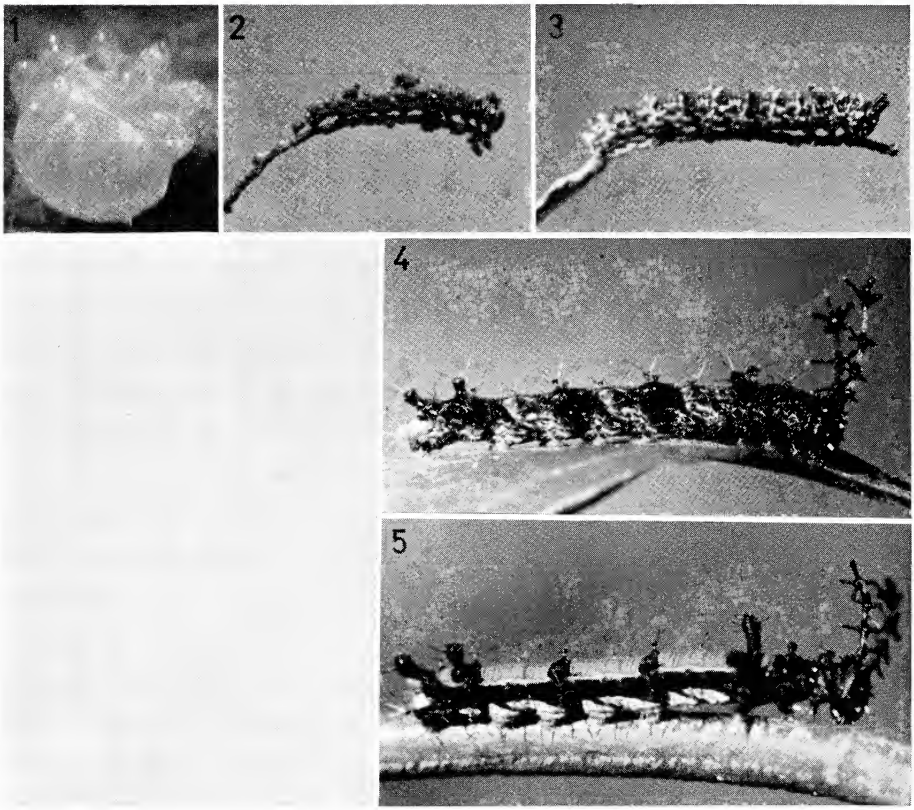
Since that occasion we have reared this species from egg to adult a number of times, during different months of the year, obtaining about the same results.

LIFE CYCLE STAGES

Egg. White, truncated, cone-shaped. Surrounding the micropylar zone, there are nine thick prominences, from which inconspicuous white ribs originate that reach the base of the egg. It measures about 1 mm. longitudinally and laterally at widest point. The eggs hatch in 5 days.

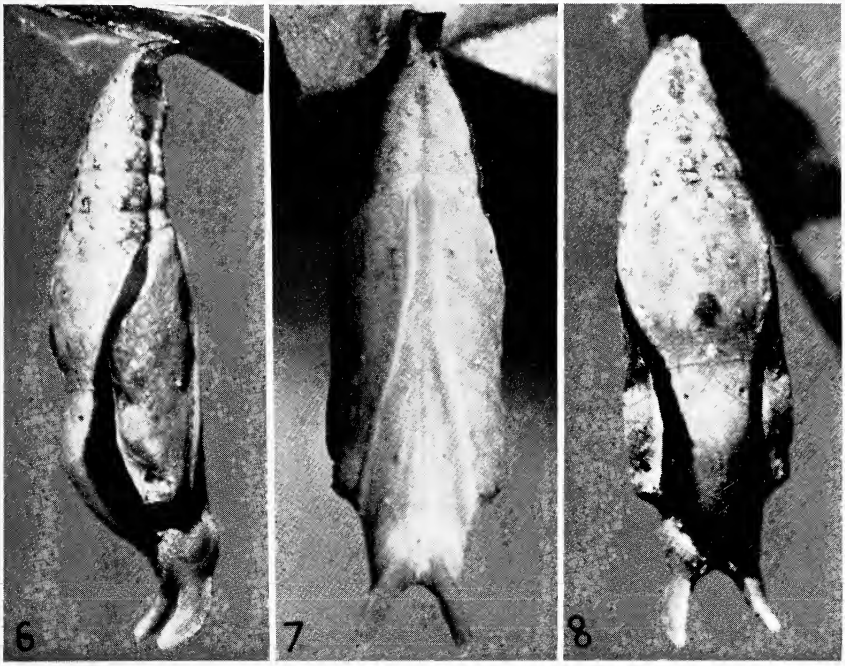
First instar larva. Head dark brown, naked, roundish. Body naked, about the same width as head, dark brown mottled with lighter tiny tubercules. About 1.8 mm. long upon emerging and 4 mm. when ready to moult in 6 days.

Second instar larva. Head dark brown with thick and short horns at apex of epicrania. Horns and sides of head with tiny spines of lighter color. Body brown with transversal rows of short forked spines, the rows being alternately dark brown and light brown in the segments. Measures about 7 mm. when ready to moult in 3 to 6 days.



FIGS. 1 to 5. *Temenis laothöe liberia.* Fabricius. 1. Egg, about 1 mm. 2. First instar larva, about 3.8 mm. Notice frass pellets stuck to the body. 3. Second instar larva, about 6 mm. 4. Fourth instar larva, about 1.5 cm. 5. Fifth instar larva, about 3 cm. Notice enlarged spines on third thoracic segment and 7th and 8th abdominal segments.

Third instar larva. Head very dark brown with long slender horns at apex of epicrania. The horns bear three transversal rows of spines, one basad, one at the middle, and the last at the tip. Spines scattered on the head, mostly at sides. Body very dark brown with longer forked spines, brown basally, light brown distally. The spines are located in the following order, as seen laterally: on first thoracic segment (T-1), two simple spines on the shield, one forked spine supraspiracularly, and one simple spine subspiracularly. On T-2 and T-3, one prominent forked spine subdorsally, one smaller forked spine supraspiracularly, and one simple spine subspiracularly. On first abdominal segment (A-1), one forked spine subdorsally, one forked spine subspiracularly. From A-2 to A-6, one forked spine subdorsally, one forked spine supraspiracularly, one forked spine subspiracularly, and one simple spine supraventrally. On A-7 and A-8, one prominent forked spine at meson, one forked spine subdorsally, one forked spine supraspiracularly, and one forked spine subspiracularly. On A-9, one forked spine directed caudad supraspiracularly. Measures 1.1 cm. before moulting in 4 to 7 days.



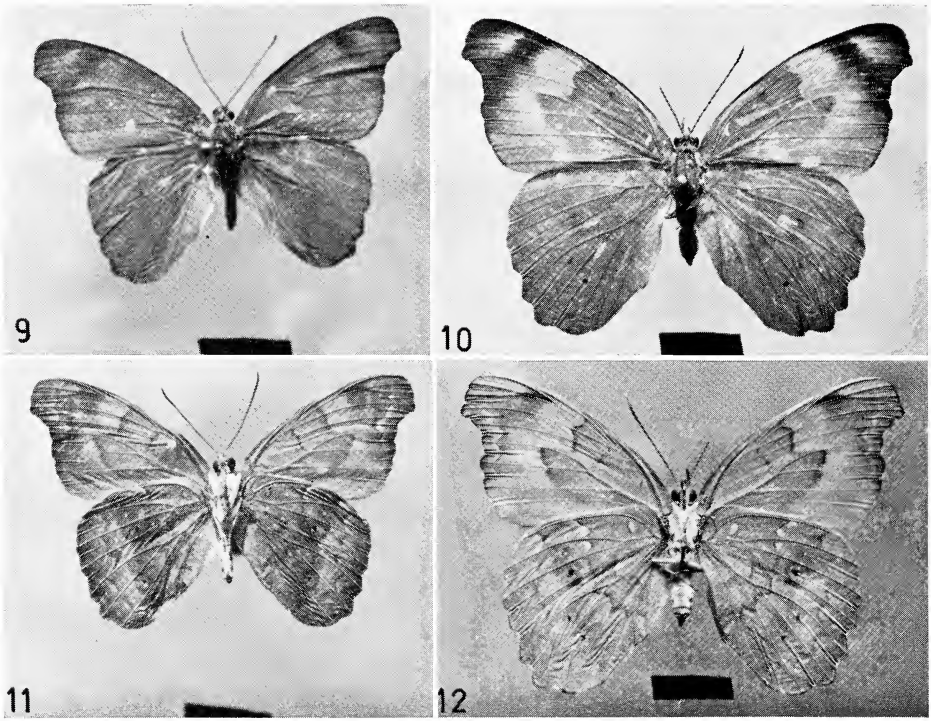
FIGS. 6 to 8. *Temenis laothöe liberia*. 6. Pupa lateral aspect. 7. Pupa ventral aspect. 8. Pupa dorsal aspect.

Fourth instar larva. Head as in third instar with longer horns, slightly incurvated posterad, with lighter color between rosettes of spines. The apical rosette has the spines blunted and swollen at the tip. Spines at sides of head long and slender; spines on frons short, stubby, and whitish. Body lighter brown than in third instar, with segments alternately brown and light brown (A-2, A-4, and A-6). Subdorsal spines on T-3 and the median spine on A-7 and A-8 swollen and clubbed with a crown of fine spines around the tip. Some spines have a metallic blue pinaculum. Measures 1.8 cm. before moulting in 5 to 6 days.

Fifth instar larva. Head as in fourth instar but with longer, thicker horns whose shafts are covered by visible but minute sharp tubercules between the rosettes of spines. Body shows a drastic change of color: It is now mostly green from A-1 caudad, with a longitudinal dark brown band spiracularly, originating from dark brown thoracic segments, terminating around A-8. From this band arise several dorsal transversal stripes on A-3, A-5, and A-7, and diagonal infiltrations into ventral area, the stripes and infiltrations of the same dark brown color. Subdorsal spines on T-3 and median spines on A-7 and A-8 long and greatly thickened and clubbed, covered by tiny sharp tubercules, with a crown of spines distally. It grows to about 3 cm. in 5 to 8 days.

Prepupa. No color changes, but the larva shortens and thickens considerably. Lasts one day.

Pupa. Long and slender. Abdomen thickens gradually from flat cremaster to wingcases which are the widest and thickest point laterally and dorsoventrally, then tapers gradually to bifid head, which terminates in two prolongations flat and slightly incurved dorsad.



FIGS. 9 to 12. *Temenis laothöe liberia*. 9. Male, dorsal aspect. 10. Female, dorsal aspect. 11. Male, ventral aspect. 12. Female, ventral aspect. Black bar 1 cm.

General color light green with dark green lining dorsally along wingcases and along the cephalic prolongations. Sparse brown spots along abdominal meson and spiracular zone. Measures about 2.5 cm. long, 0.8 cm. laterally and dorsoventrally, at widest point. Duration nine days.

Adults. Very little sexual dimorphism in this species. Both sexes have the same shape and about the same color. Forewing with a projecting angle at apex of front wings, followed by a concavity to vein M3, then a slight convexity to tornus; inner margin straight. Hind wing rounded with sinuose outer margin and a fold at inner margin.

Wings dorsally orange of various shades, darker at apex of front wings, more so in females. Wings ventrally dull orange of various shades, with some inconspicuous "eyes" in the hindwings, again more noticeable in females. Body orange dorsally, whitish ventrally; eyes brown, proboscis orange, as well as the antennae, which show whitish rings between segments. The females are noticeably larger than males: 5.4 cm. in females, 4 cm. in males between apex of spread front wings.

Total developmental time for this species varies from 38 to 48 days, that of females being slightly longer than of males.

NATURAL HISTORY

The females of *Temenis laothöe liberia* oviposit, usually from 1000 to 1500 hrs, on various wild vines of the Sapindaceae family, belonging to the genera

Paullinia, *Serjania*, *Urvillea* and *Cardiospermum*, with a definite preference for *Paullinia fuscescens* H.B.K.

Paullinia fuscescens is a scandent plant with biternate, winged-petiolated, lustrous, glabrate, and persistent leaves composed of sparsely serrate-dentate leaflets, from 3 to 7 cm. long. The inflorescence is axilar, pedunculate, with small whitish flowers that produce reddish, three-angled, thick-skinned capsules that open when mature, revealing up to three black seeds, half covered by a spongy, white arillum.

Many vines belonging to the Sapindaceae are used in the tropics by the natives to stun fish in streams and lakes. They are known locally under the common name of "barbasco." Wells (1857) gives a description of a fishing party in Honduras, which poured a decoction of a Sapindaceae vine (possibly a *Paullinia*) into the stream of Almendares River in Olancho. Standley (1923) says about *Paullinia*: "The crushed plants of various species of *Paullinia* and related genera are often thrown in streams to stupefy fish." And he says about *Serjania* (alternate foodplant for *Temenis l. liberia*): "All the species are believed to possess narcotic poisonous properties of varying intensity, and some of them are employed for stupefying fish." Standley and Calderon (1941) say about *Paullinia fuscescens*: "Los tallos estrupados son puestos en el agua como un estupefaciente para entorpecer los peces." ("The crushed stems are placed in water as a narcotic to anesthetize the fish.")

The females of *T. laothöe liberia* oviposit their eggs on the underside of mature leaves of the foodplants, one on each leaf, not in clusters. When two or more eggs are found on the same leaf, more than one female has oviposited.

Recently emerged larvae eat the top of the eggshell and at times parts of the walls but always leave at least a recognizable portion of the eggshell. Soon after emerging the larvae move to the edge or the tip of the leaf, nibble around the end of a vein, and affix to the bared vein pellets of frass stuck with silk, until the vein seems to project beyond the leaf limits. To do this, the larvae bend the body until they can grab with their months the pellet as it is expelled from the anus and proceed to place it on the bared vein. At times they affix the pellets to their own body. First and second instar larvae stay on the bared vein most of the time, often holding to it with only the prolegs, the anterior part of the body slightly raised. They leave their resting place only to feed, usually at dawn or at dusk. From third instar stage on, the larvae abandon their vein and stay on tops of leaves, at times with the anterior part of the body raised; they adopt two typical attitudes, one S-shaped, the other straight, but in both cases the head is bent forward so that the horns are parallel to the leaf surface. When crawling to another place, larvae move their heads from side to side, laying footholds of silk with the spinnerets on the leaves. When prodded with a sharp object the larvae strike viciously with their horns, a behavior which also occurs when two larvae meet on the same leaf. At time of pupation, the

larvae weave a silken mat over or under a leaf or a twig and affix their anal prolegs thereon. The larvae shorten and thicken considerably. In the process they expel an amount of liquid mixed with excrements to clean their digestive tract. The larvae do not hang as most do, but keep parallel to the supporting surface.

The pupae are usually hidden among the abundant leaves of their foodplant, but some of them are found over the uppermost leaves. Due to the flat surface of their cremaster they practically "stand" on the supporting surface. When disturbed they wriggle or move vigorously in an accordion-like manner, producing an audible creaking sound that is similar to the one emitted by cerambicid beetles.

Adults emerge from the pupa shell rapidly and find an appropriate place from which to hang until their wings are rigid, meanwhile ejecting a reddish-brown meconium. The adults of *T. laothöe liberia* dwell on treetops, returning to the ground to feed on fermenting fruits or vertebrate excrements. Females are often seen flying at lower levels in search of the foodplant for the purpose of ovipositing. Males show a marked territorial-defense behavior. Recently emerged females we have dissected did not have eggs in their abdomen.

We have reared this species a number of times during the rainy and part of the dry season (June to February) and up to the present never have found any cases of parasitism.

DISCUSSION

Seitz (1914) describes the larva and the pupa of the genus *Temenis* Hübner as follows: "The larvae are green with a cordiform head bearing two long horns furnished with rosettes of accessory spines; the dorsal spines are reduced in number, somewhat irregular, those on the 3rd. and 11th. segment thickened in the shape of a clavola; the pupa is green with fine red markings and two points on the head." Unfortunately, no mention of the foodplant is made.

The genus *Temenis*, if judged by the close morphological similarities existent in the respective early stages, is very closely related to the genera *Catonephele, Epiphile, Pseudonica, Pyrrhogyra*, and, according to Ebert (1969), to the genera *Cybdelis* and *Myscelia*, which he groups under the Catonephelinae. This group on the other hand seems to be very closely related to Ebert's grouping of Callicorinae (which comprises the genera *Callicore, Diaethria, Paulogramma,* to which we add *Catagramma*). Seitz calls the Catonephelinae, Group G.: Epicaliidi and the Callicorinae; Group H: Catagrammidi. Some modern authors lump the two groups, with other genera not so closely related (*Mestra, Hamadryas, Biblis*), under the tribe Ergolini (Ehrlich and Ehrlich, 1961) or under the subfamily Ergolinae (Klots, 1960), but they warn that the present status of the classification within the Nymphalidae is confused and the groupings in many instances are arbitrary. We use Ebert's system because it seems more in

accordance with reality, based on what modern authors state (Ford, 1945; Brower, Brower, and Collins, 1963; Crane, 1957), that morphological and behavioral characteristics in the early stages are as important as wing venation and structure of the genitalia in the adults for accurately establishing the phylogenetic relationship of the genera. Comparing the photographs and descriptions of the early stages and behavior in our presentation of *Catonephele numilia esite* Felder and of *Epiphile adrasta adrasta* (Muyshondt, 1973b and c), the reason for preferring Ebert's classification is evident, as will also be our opinion regarding the close affinity of the Catonephelinae with the Callicorinae when the future article on *Diaethria astala* Guérin will be presented.

T. laothöe liberia, like most Catonephelinae and Callicorinae, feed exclusively during the larval stage on plants belonging to the Sapindaceae. The only exceptions found so far are *Catonephele numilia esite* and *C. nyctimus* Westwood, which feed on Euphorbiaceae; but Röber (1915) says: "According to Müller the following is to be said [referring to the genus *Myscelia*], about the early stages: Foodplant of *M. orsis* is *Daleschampia triphylla* Lam" (*Daleschampia* is another Euphorbiaceae), and about *Callicore meridionalis*: "The larva lives on *Trema micrantha* Dell." *Trema micrantha* (an Ulmaceae) abounds in El Salvador in the same localities as the Sapindaceae, but so far no Callicorinae have been found there, so this may be a case of misidentification of the plant or an instance when a larva ready to pupate was collected on that plant by Müller after it had abandoned a Sapindaceae vine.

T. laothöe liberia prefers *Paullinia fuscescens* but also uses several species of the genera *Serjania, Urvillea*, and *Cardiospermum*. Most, if not all, of these plants are reputed to contain noxious substances; therefore, it would be expected than an animal feeding on them would accumulate in its body sufficient poisonous material to cause it to be avoided by predators. It is generally accepted that Lepidoptera protected by toxic components of their food plants have evolved gaudy and showy warning coloration in all stages combined with fluttery flight of the adults. In this way, they avoid automatic rush attacks by predators. Contradictory to this, the larvae of *T. laothöe liberia* seem to depend on crypsis for their survival. First and second instars remain motionless through the day on their prolonged vein, looking very much like remnants of leaf tissue on it. They move away from the vein only to feed at dawn or at dusk, minimizing the chances of being perceived. During the subsequent stadia the larvae favor the upper surface of the leaves where the third and fourth instar larvae, owing to their dark brown color, can be taken for bird excrement, mostly when they assume the S attitude. The fifth instar larvae are hard to notice because their shape is concealed by the cryptical combination of green and dark brown colors. The pupae also have an effective camouflaging combination of different shades of green to dissolve their contours among the shady leaves.

Conversely this species seems to be losing the mechanical defense against predators that the horns armed with sharp accessory spines provide *Catonephele numilia esite,* because in *T. laothöe liberia* the accessory spines are found to be thick and blunt. This alteration may indicate an evolutionary deterioration of mechanical defenses as a result of the defensive superiority of unpalatability from the noxious components of their foodplant. The orange coloration of the adults also points in this direction: instead of the flash-and-hide effect related species derive from their brilliant dorsal colors contrasted with the dull brown of their underwings (*C. n. esite, C. nyctimus, Epiphile a. adrasta,* etc.), *Temenis laothöe liberia* (and *Pseudonica flavilla canthara* Doubleday) are orange all over, making them very conspicuous against the green background of the leaves. But it is true that their flight is still faster than the species traditionally considered distasteful (*Danaus plexippus, Heliconius petiveranus, Battus polydamas,* etc.). Another characteristic this species has lost is the puzzling sexual dimorphism other Catonephelinae (*C. numilia, C. nyctimus,* and *E. adrasta*) exhibit, even if the benefit that dimorphism represents in their case is not clear, as neither sex imitates any of the local protected species, thus eliminating the logical explanation of a Müllerian mimicry.

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Notes on the Life Cycle and Natural History of Butterflies of El Salvador. IV A.—*Pseudonica flavilla canthara* (Nymphalidae-Catonephelinae)

ALBERTO MUYSHONDT
101 AVENIDA NORTE #322, SAN SALVADOR, EL SALVADOR

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Abstract: This is the first description of the life cycle of the genus *Pseudonica* and the first photographs of the species *P. flavilla canthara* Doubleday ever published. For a period of two years eggs and larvae of this species were collected in the neighborhood of San Salvador to study developmental time and behavior during the early stages. The foodplant is recorded for Central America, and an account of larval mortality causes is given. The possible unpalatability to predators is suggested as deduced from the color and behavior of the adults and from the properties of the components of the foodplant.

Acknowledgments: We are greatly indebted to Dr. Alexander B. Klots for generously dedicating part of his time to advise us in relation to our studies, for reading our manuscripts, and for giving helpful criticism. We thank S. Steinhauser for the identification of this species and M. Serrano for giving us access to his technical library.

INTRODUCTION

Through the present series of articles my sons and I are giving our observations on the life cycle and behavior of the early stages of local butterflies belonging to the genera grouped by Ebert (1969) in the subfamily Catonephelinae of the Nymphalidae.

Not much has been published in relation to the majority of the Rhopalocera inhabiting the American tropics, after the monumental works *Biologia Centrali-Americana* (Godman and Salvin, 1879–1901) and *Macrolepidoptera of the World* (Seitz, 1913–24); these works unfortunately presented only incomplete information, if any, about the early stages and the foodplants of many groups, among which we count the Catonephelinae (incorporated in Seitz's Epicaliidae). Besides, according to Klots (1960), both works contain many names that have been changed since their publication and thus there are many errors in the names.

Owing to the lack of the necessary data, some groupings, (especially within the Nymphalidae) have been tentatively, and at times arbitrarily, made solely on the basis of the known morphological characteristics of the adults. It is our hope that our contribution will help to fill the enormous information gap existent, supplying taxonomists with some new elements that, together with data from other nature students, will eventually permit them to effect the sorely needed revision of the Nymphalidae.

It is generally accepted by modern authors that any classification must take into consideration, in addition to the sexual structures and wing venation of the adults, the morphological characteristics and behavior of the early stages. Some authors rightly recognize even the value of foodplant associations as a taxonomic tool in butterfly classification (Downey, 1963).

The determination of the species and subspecies in this article was effected by S. Steinhauser, and specimens of the early stages and adults have been placed in The American Museum of Natural History, New York, where they are available to students of the group.

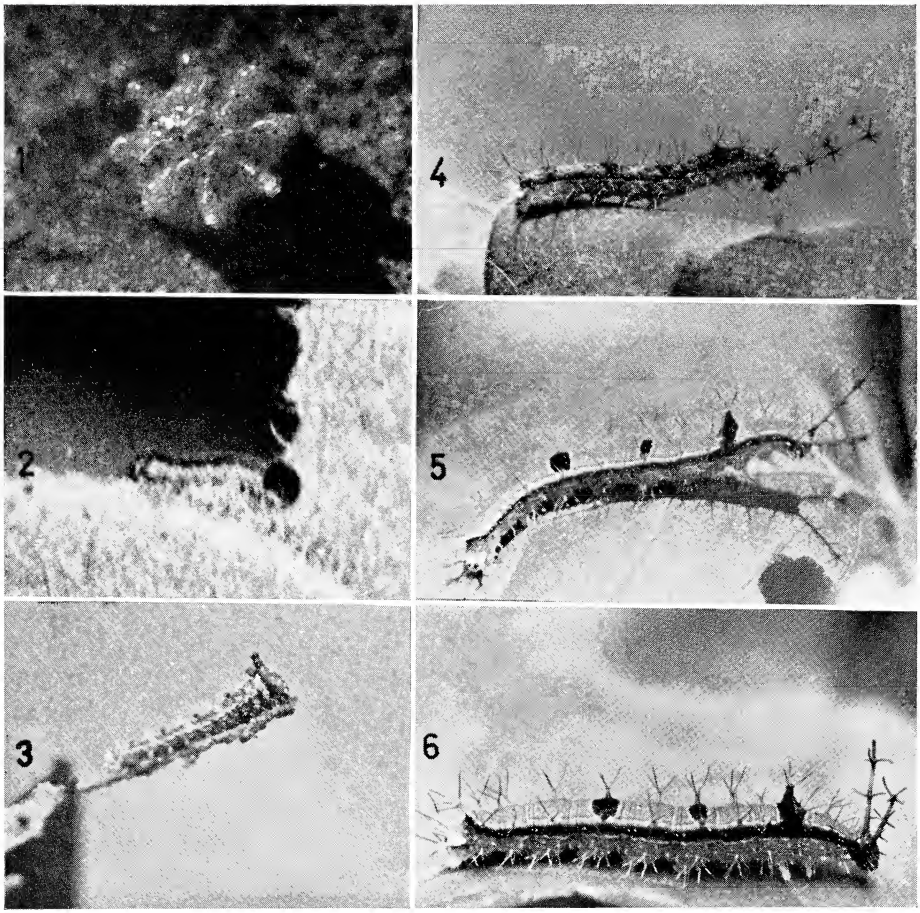
Like most local Catonephelinae, the adults of *Pseudonica flavilla canthara* Doubleday frequent coffee plantations bordered by wooded ravines or creeks, where the foodplants of the larvae are found. Coffee plantations in El Salvador are manmade forests that have been brought about by the local technique of planting the coffee trees under a canopy of shade trees (mostly *Inga* spp.), with sparse fruit trees scattered within (resulting from seeds dropped by workers) supplying food not only to butterfly adults but to birds and small mammals. Coffee plantations cover extensive areas ranging from 500 m to about 2000 m altitude, mostly in the mountainous part of the country. Thus they have a tremendous influence not only on El Salvador's economy for the value of its coffee crop, but on its ecology, as they are about the only woods left in that small, overpopulated country, whose land is under intensive cultivation. Coffee plantations function therefore as a kind of artificial sanctuary for a good part of the local wild fauna.

At the beginning of the rainy season in 1972, we found some eggs, a number of eggshells, and first instar larvae on a Sapindaceae shrub in a ravine near San Salvador. They were put as usual in individual bags of clear plastic. Photographs of every stage were made until the adults emerged. Records of the time spent in development and measures of each instar were kept. Specimens of the early stages were preserved in alcohol to be sent to a museum.

The eggs were so similar to those of *Temenis laothöe liberia* Fabricius, that at first we thought they were of that species, but when the larvae moulted into third instar we realized that we had a species that we had not bred before. During the first days of June the butterflies emerged; they were determined as *Pseudonica flavilla canthara*, another of the Catonephelinae. We have reared the species several times since, with about the same results.

LIFE CYCLE STAGES

Egg. White when recently oviposited, darkening before hatching. Shape a truncated cone with eight rounded prominences around the micropylar area; from each prominence a white, inconspicuous rib originates, descending to the base of the egg. The rounded dome of the micropyle shows eight triangular panels around the central circular depression. Around 1 mm long and in diameter. Hatches in five to six days.



FIGS. 1 to 6. *Pseudonica flavilla canthara* Doubleday 1. Egg, seen from above, about 1 mm. 2. First instar larva, 1.6 mm. 3. Second instar larva on bared vein, about 5 mm. 4. Third instar larva in characteristic attitude, about 1.3 cm. 5. Fourth instar larva, about 2 cm. 6. Fifth instar larva, 2.6 cm.

First instar larva. Head rounded, dark brown and naked. Body cylindrical, naked, greenish brown. About 1.6 mm when recently emerged, growing to about 3.5 mm before moulting in five to six days.

Second instar larva. Head brown with sparse, tiny, whitish tubercules, and stubby horn on each apex of the epicrania. Body greenish brown with short forked spines alternately dark brown and greenish brown. Grows to about 5.5 mm before moulting, three to five days.

Third instar larva. Head dark brown with long, slender light brown horns (about four times as long as the head), bearing three rosettes of accessory black spines. Spines of varying lengths on lateral and superior margin of head. Body greenish brown with dark brown zones dorsally across second and third thoracic segments and third and fifth abdominal segments. A dark stripe runs supraspiracularly from first thoracic segment along the entire

body, ending around eighth abdominal segment. Body spines arranged in the following order, as seen laterally: first thoracic segment (T-1) is armed with four simple spines: one subdorsally, one supraspiracularly, one subspiracularly and one just above the leg. T-2 and T-3 with one prominent forked spine subdorsally and one smaller forked spine subspiracularly. Subdorsal spine on T-3 noticeably bigger than the rest, and five-branched. First abdominal segment (A-1) with one small forked spine subdorsally and one small forked spine subspiracularly. From A-2 to A-6, one prominent three-branched spine subdorsally and one smaller forked spine supraspiracularly. A-7 and A-8 have in addition one forked spine at the meson, the one on A-8 thicker and four-branched. A-9 with one lateral four-branched spine, deflected posterad. Pinacula of spines on A-4 and A-6 light brown, the rest dark brown. Spiracula small and light brown colored, except those on T-1 and A-8 which are darker and larger. Grows to 1 cm (not including the horns) in four to five days.

Fourth instar larva. Head brown with small reddish spots on frons. Horns longer now, measuring about 0.5 cm. Body mostly green with supraspiracular dark brown stripe, bordered above by a thin pinkish line, running the length of the body. Very conspicuous transverse dark brown bands across T-3, A-3, and A-5 dorsally. Subdorsal spines on T-3, median spine on A-8, and lateral spine on A-9 swollen and prominent. Grows to 1.5 cm, not counting the horns, in six to seven days.

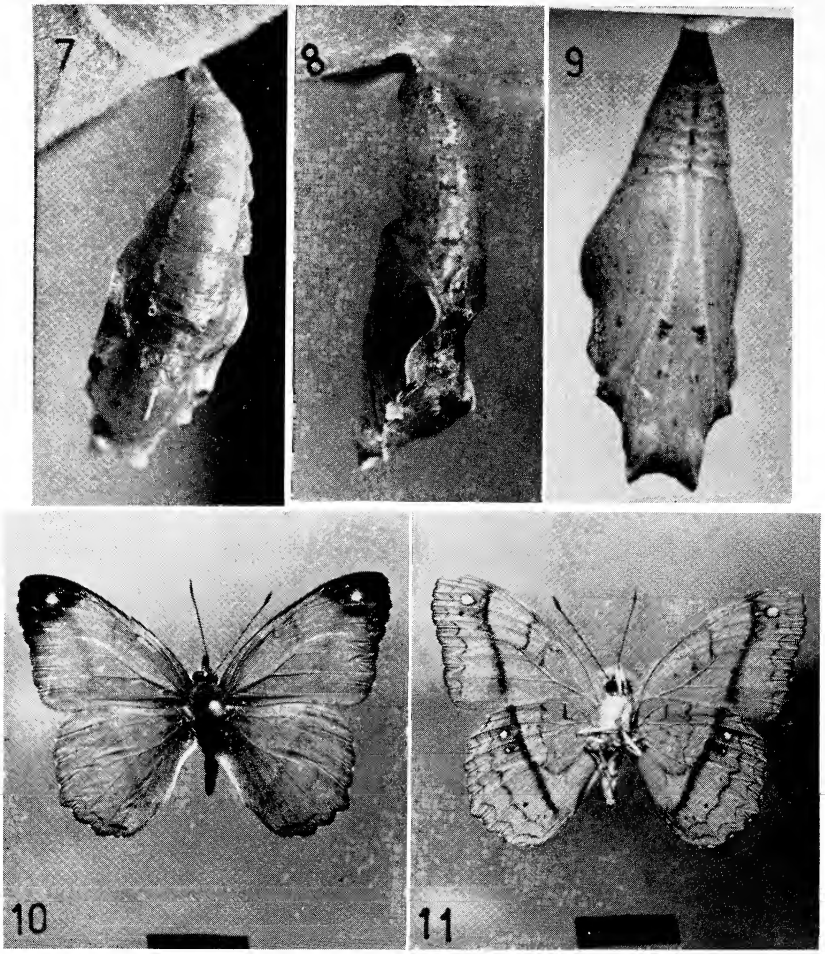
Fifth instar larva. Head dark brown with orange areas on frontal, adfrontal, and lower lateral margins of head. Ocelli black on a dark brown area. Horns dark brown at the base and at the rosettes of accessory spines, orange in between. Slender spines on lateral border of head and four white spines on frontal area: two near the ocelli, two near the bases of the horns. Body mostly green as in fourth instar with same color pattern but with stronger colors. Subdorsal spines on T-3 and median spine on A-8 much longer and thicker than the rest. Grows 2.4–2.8 cm in five to eight days.

Prepupa. Same as fifth instar, but shorter and thicker. One day.

Pupa. Mostly green with profusion of brown speckles all over, with subdorsal rows of brown round spots over abdomen and thorax; spiracula inconspicuous light brown. Abdomen thickens gradually from brown and flat cremaster to wingcases which show a lateral border of light brown color, then tapers gradually to bifid head. A dorsal indentation separating abdomen from thorax, which has a brown lined keeled dorsal hump. Measures 1.5 to 1.8 cm long. Lasts seven to nine days.

Adults. No marked sexual dimorphism in this species. Forewings with rounded apex, straight outer and inner margins. Hindwings rounded without any projections. Predominating color dorsally a bright orange with brown apical area on forewing, where a small round orange dot is located, and a marginal row of small groups of white scales placed on each vein terminal on both fore and hindwing; a faint brown, broken submarginal line on hindwing. Ventrally dull yellowish orange with a marked brownish band running from subapical costal margin of forewing to mid-inner of hindwing, bordered distally by a serrate, thinner, brownish line on forewing and two serrate lines on hindwing; two subapical dots on the front wing, one white above and one smaller dark brown below; on the hindwing two white spots surrounded by dark blue lining, located distally from the superior end of the dark band, and three tiny blue and white stains near anal angle. Body dark orange dorsally, white ventrally; eyes and antennae dark brown, the latter with white rings between segments. Adults measure about 3.5 cm from tip to tip of spread forewings, being the smallest species among the local Catonephelinae.

Total developmental time varies from 37 to 46 days.



FIGS. 7 to 11. *Pseudonica flavilla canthara* Doubleday 7. Pupa, dorsal view, 1.8 cm long. 8. Pupa, lateral view. 9. Pupa, ventral view. 10. Adult, dorsal view. Black bar = 1 cm. 11. Adult, ventral view.

NATURAL HISTORY

The females of *Pseudonica f. canthara* deposit their eggs usually on the underside of mature leaves of the foodplants in the thickest part of the foliage. One egg is oviposited per leaf, on its central area.

The tiny larvae upon hatching eat the upper part of the eggshell and at times part of the walls also. After a time the larvae move to the border of the leaf and bare a vein by eating around it. This bared vein is prolonged with frass pellets affixed to it with silk and is used as a resting place during the first and second instars. The larvae leave the vein only to feed, which is done usually at dusk

and at dawn. From the third stadium on, the larvae crawl about the plant, mostly on top of the leaves, where they stay motionless for long periods of time. Like most Catonephelinae, the larvae of *P. f. canthara* hold to the leaf with the prolegs, raise the anterior part of the body and bend the head ventrad, keeping the horns parallel to the surface of the leaf. Also like other Catonephelinae, the larvae of this species show a strong solitary mode of behavior, and whenever two larvae happen to meet on the same leaf, they strike each other with their sharp horns. The results of such encounters are usually fatal to one or both larvae. If a larva in fourth or fifth instar is prodded with a thin object it reacts in a similar manner, striking viciously with its horns. When ready to pupate the larvae weave a pad of silk on a leaf or stem and hold to it with their anal prolegs after clearing their intestines by expelling a green liquid mixed with excrements. The prepupal larvae do not hang as most Nymphalidae do, but keep their bodies parallel to the surface on which they are fastened, often on the upper surface of a leaf.

The pupae, consequently, do not hang either, but practically stand at an angle on the leaf or stem, due to the flatness of the cremaster. As in other Catonephelinae, the pupae of *P. f. canthara* can emit an audible sound when disturbed, which is the result of an accordion-like movement. The pupae are not always found on the foodplant; they are at times on any neighboring thick-leaved shrub or tree.

The adults emerge from the pupashell rapidly and find a place from which to hang while their wings become rigid. Meanwhile they eject an amount of reddish meconium.

The adults of *P. f. canthara* are often seen flying around treetops and coming to the ground to feed on fallen fruits or excrements. After their long feeding sessions they fly to a low bush where they are seen motionless except for an occasional flapping of their wings. They are the slowest of the local Catonephelinae. Females ready to oviposit fly close to the ground while searching for the foodplants, usually between 0930 and 1500 hr.

Roughly 25 percent of the larvae we have reared succumbed to tachinid fly parasitism. Specimens of the flies were sent to the United States Department of Agriculture where they have been determined by C. W. Sabrosky to be "Gen. sp." Another common cause of mortality among the larvae, both in our insectarium and in the fields, has been a disease which causes diarrhea and softening of the body tissues, ending invariably in death. This phenomenon is most commonly connected with too much dampness or wetness of the food or in the rearing container (Klots, personal communication). This species is never abundant in this country.

The plant most used by the larvae, *Cardiospermum halicacabum* L., and all the alternate foodplants (*Paullinia* and *Serjania* spp.) we have found to the present belong to the Sapindaceae.

Cardiospermum halicacabum is a somewhat scandent plant which presents a remarkable polymorphism that has resulted in many synonyms in the literature: *C. corindum* L., *C. pubescens* Lag. Gen. and Sp., *C. coluteoides* H. B. K., *C. hispidum* H. B. K., *C. molle* H. B. K., *C. microcarpum* H. B. K., and possibly others, to cite Standley (1923). It has biternate leaves, with coarsely toothed or lobed leaflets of great variation in size (2 cm to 10 cm long), glabrous at times, or densely pubescent; the small whitish flowers grow on an axillary, racemose, pedunculate inflorescence. The peculiar fruit is an inflated, thin-skinned globe formed of three sections, and contains black seeds with a white arillum. According to Standley (1923) the roots of this plant "are said to have diuretic and sudorific properties," and Beille (1909) states: "plante riche en Saponine; racines émétiques."

C. halicacabum and the other Sapindaceae vines used by the larvae of *P. flavilla canthara* as food are commonly found between 400 and 1500 m of altitude, in or beside ravines and riverbeds that harbor what is left of the wild vegetation in El Salvador, second-growth plant communities.

DISCUSSION

As far as we have been able to learn, this is the first description of the life cycle of the genus *Pseudonica* and the first record of its foodplant ever published.

This species, *P. flavilla canthara*, belonging to the Catonephelinae, shows naturally many characteristics that closely resemble those of other related species (*Catonephele numilia esite* Felder, Muyshondt 1973*a*, *Epiphile adrasta adrasta* Hewitson, Muyshondt 1973*b*, *Temenis laothöe liberia* Fabricius, Muyshondt 1973*c*), such as the shapes of the eggs, the larvae, and the pupae. Consequently it has also striking similarities with the genera belonging to the closely related Callicorinae.

It is not surprising, therefore, to find that the behavior of this species during its early stages is almost identical with that of the early stages of the species already mentioned, so that a description of the habits of this species would be repetitious. We emphasize only the fact that the early stages exploit, as do the others, a cryptical strategy as means of defense against predation. The evident morphological and behavioral similarities seem to confirm therefore the correctness of Ebert's grouping.

Even though the behavior of the early stages of all the local Catonephelinae we have studied until now is based on crypsis for defense against predation, seeming to suggest palatability to predators, we strongly suspect that most of them, if not all (in particular the species that feed on *Sapindaceae*), are actually unpalatable as this family of plants includes many species known to contain poisonous or narcotic components (*Paullinia* spp., *Serjania* spp.) and others that are rich in saponins (*Cardiospermum* spp., *Sapindus saponaria* L.). Saponins are listed by Brower and Brower (1964) among the poisonous glyco-

sides, along with the cyanogetic glycosides, the cardiac glycosides, and the alkaloids. They say about saponins: "Saponins are another special class of glycosides in which the aglycone [sic] is either a triterpenoid alcohol or a spiroketal steroid." It seems logical that the larvae that feed on plants containing deleterious compounds would derive from such compounds an effective protection against predators.

That is commonly accepted to be the case in many species of the families Danaidae, Heliconiidae, Papilionidae, and Ithomiidae. These butterflies advertize their repellent condition by showy colors and lazy flights. There are other butterflies that are suspected of being unpalatable, although no experiments to support this suspicion have yet been carried out; these butterflies include *Morpho polyphemus polyphemus* Dbl. and Hew. (Young and Muyshondt, 1973), *Anaea* (*Consul*) *fabius* Cramer (Muyshondt, 1973*d*), and others, belonging to the Morphidae and Nymphalidae that feed on plants known to possess poisonous and/or bitter components (*Paullinia pinnata* L. and several species of Piperaceae, respectively) during the larval stages and whose adults have the flashing colors and the somewhat lazy flight connected with unpalatability. Our suspicion is sustained by the same characteristics in the cases of at least three Catonephelinae: *Pseudonica flavilla canthara*, *Temenis laothöe liberia*, and *Pyrrhogyra hypsenor* Godman and Salvin (manuscript in preparation), which are the ones within the family that have gaudy colors both dorsally and ventrally and have adopted a slower flight than is usual in the other Catonephelinae. *Pyrrhogyra hypsenor* larvae have, in addition, a very visible color combination. The latter feeds mostly on *Paullinia pinnata* which is one of the most toxic Sapindaceae, according to several authors (Baillon, 1874; Beille, 1909; Standley, 1923).

Pseudonica f. canthara and *Pyrrhogyra hypsenor* are subject to heavy parasitism by tachinid flies, which keeps the population of both species in check. The protection they seem to derive from their foodplant would tend to cause a superabundance of individuals if there were not a natural factor to keep balance. It is to be noticed that, according to some authors and our own experience, a similar phenomenon occurs in most of the local species classically considered protected by the noxious properties of their foodplants, such as *Danaus plexippus, D. eresimus, D. gilippus* (Danaidae), *Heliconius petiveranus, H. charitonius, H. telchinia* (Heliconiidae), *Battus polydamas, Parides arcas, P. photinus* (Papilionidae), *Dircenna klugii* (Ithomiidae), and even in other species suspected to be protected against predators for the same reason, such as *Morpho polyphemus* (Morphidae), *Anaea* (*Consul*) *fabius, A.* (*C.*) *electra, A.* (*Memphis*) *eurypyle confusa, A.* (*M.*) *pithyusa* (Charaxinae). All of these are heavily parasitized by tachinid flies.

That fact might be an effective survival strategy developed by the tachinid flies of taking advantage of the antipredator qualities derived from the food-

plants by their phytophagous hosts to insure their own safety during the larval stage.

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Diagnoses of New Species of *Gigantodax* Enderlein (Simuliidae, Diptera) from the Northern Andes

Pedro Wygodzinsky
The American Museum of Natural History, New York

Received for Publication September 19, 1973

Abstract: The paper contains the descriptions of five new species of *Gigantodax* from high elevations in the northern Andes.

The need for names to be used in research now in progress is motivating me to offer diagnoses of five new species of the black fly genus *Gigantodax* from the northern Andes. Detailed descriptions, biological and distributional data of these species, together with discussions of their systematic position will be contained in a monograph of the genus *Gigantodax* now in preparation.

The work leading to this paper was supported by the National Science Foundation (Grants GB-5852 and GB-8783). Dr. F. Christian Thompson most graciously listened to the problems connected with work on this and other papers on black flies, and often dispensed thoughtful advice; I am grateful to him.

All specimens mentioned were collected by P. and B. Wygodzinsky and are deposited in The American Museum of Natural History. Drawings are by Matthew Cormons and the author.

Gigantodax **corniculatum,** n. sp.

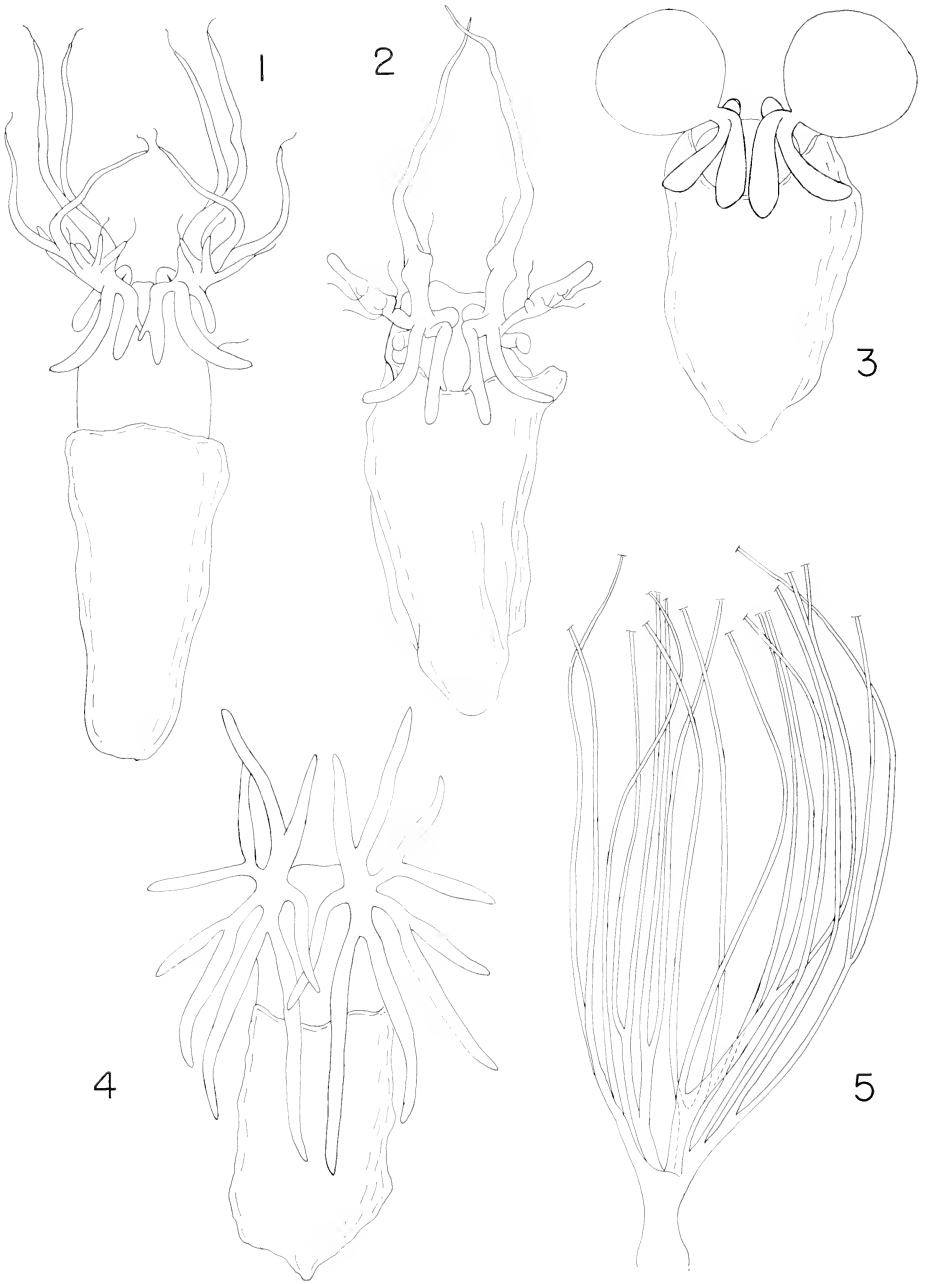
Figure 1

General color of scutum of male orange red, of female light orange brown. Wing length of male 4.1–4.2, of female 4.6–4.8 mm. R_1 with spinelike setae. Calcipala distinctly longer than half the length of second tarsomere.

Cocoon of pupa short, covering abdomen but leaving most of thorax exposed. Facial trichomes delicate, spinelike. Platelets well developed, minutely tuberculate, irregularly arranged. Gills (Fig. 1) composed each of five main tubular arms (two dorsal, one lateral, one anterior and one ventral), simple or variously branched, with a total of thirteen branches. Outer dorsal arm and ventral arm undivided. Inner dorsal arm with a short secondary branch mesad on apical half of arm. Lateral arm with a cluster of four short and two long branches. Anterior arm with one short and two long forwardly directed branches. Dorsal and ventral arms of almost uniform diameter, rounded apically; branches of lateral and anterior arms narrowing to a point apically, with terminal short caducous respiratory filaments. Surface of gills rugose-reticulate.

Maximum observed length of larva 8 mm. Third antennal segment longer than first and second combined. Mandibles with seven to eight marginal serrations.

Material examined: Venezuela: Mérida: near Apartaderos-Santo Domingo road, 3,400 m., Feb. 16–26, 1968 (one male, holotype; one female, allotype; eight males, eleven females, paratypes; all with associated pupal skins), numerous pupae and larvae.



FIGS. 1–5. Pupae of new species of *Gigantodax*, dorsal view. 1. *G. corniculatum*. 2. *G. cervicorne*. 3. *G. impossibile*. 4. *G. bettyae*. 5. *G. ortizi*.

Gigantodax corniculatum, named for the antlerlike gills of the pupa, is closely related to *G. cervicorne* described below, but can be distinguished from it by its slightly larger size and details of the structure of the gills of the pupa.

Gigantodax **cervicorne,** n. sp.

Figure 2

General color of scutum of male orange red, of female light orange brown. Wing length of male 4.0–4.1 mm., of female 3.9–4.2 mm. R_1 with spinelike setae present. Calcipala distinctly longer than half the length of second tarsomere.

Cocoon of pupa short, covering abdomen but leaving most of thorax exposed. Facial trichomes hairlike. Platelets well developed, minutely tuberculate, irregularly arranged. Gills (Fig. 2) composed each of five tubular arms: two dorsal, one lateral, one anterior, and one ventral. Outer dorsal arm and ventral arm simple. Inner dorsal arm with short mesad projection on distal third. Lateral arm clubshaped, with five, more or less prominent, projections on thickened portion. Anterior arm the longest, somewhat thickened subbasally and with two protrusions; apical portion slender. Caducous respiratory filaments arising from projections mentioned. Surface of gills rugose-reticulate.

Maximum observed length of larva 8.3 mm. Third antennal segment approximately as long as first and second combined. Mandibles with seven to eleven marginal serrations.

Material examined: Colombia: Cundinamarca: 2 km. SE of Alban, 2,400 m., Aug. 6, 1967, and Aug. 24, 1969 (1 male, holotype; one female, allotype; eighteen males, thirty-three females, paratypes; all with associated pupal skins), numerous pupae and larvae. I have examined material of this species from other localities in Colombia, Ecuador, and Venezuela.

Gigantodax cervicorne is named for the similarity of the gills of its pupae to deer antlers. The shape of the gill suffices to distinguish this species from any other in the genus.

Gigantodax **impossibile,** n. sp.

Figure 3

General color of scutum of male orange red, of female light orange brown; abdomen piceous in both sexes. Wing length of male 3.9–4.2 mm., of female 4.4 mm. R_1 with spinelike setae present. Calcipala distinctly longer than half the length of second tarsomere.

Cocoon of pupa covering most of body, leaving only head and gills exposed. Facial trichomes stout, spinelike. Platelets well developed, minutely tuberculate, irregularly arranged. Each gill (Fig. 3) consisting of two dorsal and one ventral short, thick, tubular branch with rounded apex, and one anterolaterally directed globular element, the latter coarsely rugose-reticulate on apical half; a few scattered caducous short respiratory filaments on globular portion of gill.

Maximum observed length of larva 8.5 mm. Third antennal segment shorter than first and second combined. Mandibles with seven to nine marginal serrations.

Material examined: Venezuela: Mérida: near Apartaderos-Santo Domingo road, 3,400 m., Feb. 16–26, 1968 (one male, holotype; one female, allotype; seven males, three females, paratypes; all with their associated pupal skin), numerous pupae and larvae.

Gigantodax impossibile differs from all known species of the genus by the unique gills; the specific name alludes to the unbelievable shape of these gills.

Gigantodax **bettyae,** n. sp.

Figure 4

General color of scutum of male chestnut brown, of female light brown; abdomen piceous in both sexes. Wing length of male 3.5–3.7 mm., of female 3.8–4.3 mm. R_1 with spinelike setae present. Calcipala distinctly longer than half the length of second tarsomere, almost attaining its apex.

Cocoon of pupa short, only covering its abdomen. Facial trichomes minute, in shape of very delicate hairs. Platelets very faint, smooth. Gills (Fig. 4) large, each composed of nine thick tubular, apically narrowed branches. Eight branches arising in pairs from short basal trunks, the dorsalmost branch single. Gill branches distally with short cuticular processes; each branch apically with caducous respiratory filament (not shown in drawing).

Maximum observed length of larva 8.5 mm. Third antennal segment longer than first and second combined. Mandibles with seven to nine marginal serrations.

Material examined: Venezuela: Mérida: SW of Mucuruba, 2350 m., Feb. 9–26, 1968 (one male, holotype; one female, allotype; seventeen males, eleven females, paratypes; all with associated pupal skins), numerous pupae and larvae.

Gigantodax bettyae is named for my wife in recognition of her able assistance in black fly collecting. The structure of the gills of the pupa of this species is sufficient to distinguish it from any other species of the genus.

Gigantodax **ortizi,** n. sp.

Figure 5

General color of scutum of male dark chestnut brown, of female lighter brown with faint grayish tinge; abdomen piceous in both sexes. Wing length of male approximately 3.6 mm., of female 3.7–3.9 mm. R_1 with spinelike setae present. Calcipala distinctly longer than half the length of tarsomere, almost attaining its apex.

Cocoon of pupa completely covering body, leaving only gills partially or entirely exposed. Facial trichomes slender, spinelike. Platelets well developed, minutely tuberculate, arranged in distinctive groups, on thorax frequently in circles. Each gill (Fig. 5) consisting of eighteen threadlike forwardly directed branches forming a tight bundle. Branches arising three or four in number from each of five main stems, inserted on a short basal trunk.

Maximum observed length of larva 7 mm. Third antennal segment longer than first and second combined. Mandibles with five to six marginal serrations.

Material examined: Venezuela: Mérida: near Apartaderos-Santo Domingo road, 3,400–3,500 m., Feb. 16–26, 1968 (one male, holotype; one female, allotype; two males, four females, paratypes; all with associated pupal skins), numerous pupae and larvae.

Gigantodax ortizi is named for Dr. Ignacio Ortiz, the Venezuelan entomologist, in recognition of his active interest in my work. The species differs from comparable ones by details of the structure of its gills, and mainly by the distinctively grouped platelets of the thorax of the pupae.

BOOK REVIEWS

An Illustrated Catalog of the Neotropical Arctiinae Types in the United States National Museum (Lepidoptera, Arctiidae). Part II. Smithsonian Contributions to Zoology, No. 128, pp. iii + 160, 106 pls. Superintendent of Documents, Washington, D. C. $2.86.

This is one of the enormous routine jobs that occasionally must be done in order to lay a firm nomenclatural basis for taxonomic work in any group. Such spadework is often very dull and tiresome; but when thoroughly and meticulously done, as is the case here, it opens the way for sound systematic research as nothing else can. A total of 174 types of Dognin, Druce, Dyar, Henry Edwards, Schaus and Strand were verified and studied. The whole specimens and their genitalia are figured. Type designations are cited, and lectotypes designated when necessary. Nomenclatural changes are made when advisable, and there are some synonymic notes. The complete bibliography, which corrects some earlier misapprehensions, is extremely valuable.

Alexander B. Klots
The American Museum of Natural History

Army Ants. A Study in Social Organization. T. C. Schneirla. 1971. Edited by Howard R. Topoff. W. H. Freeman, San Francisco. xx + 349 pp. $12.00.

Dr. Schneirla's unique contribution is that he observed the army ants as an animal behaviorist and comparative psychologist and at the same time studied the biology of the individuals in the colony. This book demonstrates how such a methodology can expand our understanding of biological phenomena.

The first chapter tells of the early reports of army ants, and it reviews recent past knowledge about them. The author expresses his dissatisfaction with previous simplistic explanations of the behavior of army ants and his interest in undertaking a systematic study of their social behavior. The second chapter is a general survey of the army ant colony and the activities of the individuals of the colony. The later chapters abundantly discuss the activities mentioned. They explore the bivouacs and the emigrations, the broods, the functional cycles and nomadism, the roles of the queen, males and young queens, as well as colony divisions and the establishment of new colonies. A special chapter is devoted to surface-raiding species of the widely ranging Old World doryline, *Aenictus*, and the final chapter is a correlating and summarizing one, The Doryline Colony as an Adaptive System.

Two aspects of Dr. Schneirla's research make it particularly noteworthy. First, his system of marking queens made it possible for him to have some queens and their colonies under surveillance, intermittently, over a period of five years. This system of marking queens combined with his long field trips, extending over several months, allowed him to recheck his previous observations and to refine his conclusions. Second, his search for the key to an understanding of the functional doryline cycle, once he had clarified the nomadic-statary cycle and species-typical differences in the New World genera of *Eciton* and *Neivamyrmex*, led him to a further study of the primitive Old World genus *Aenictus*. Despite reported variations in the doryline genera of different environments, Dr. Schneirla concluded that the nomadic-statary cycle is dominant.

Extensive footnotes supplement the text. They support the textual material and provide bibliographic references related to the topics under discussion. There are many excellent photographs and numerous explanatory diagrams.

It was indeed fortunate that Dr. Howard Topoff was able to see this manuscript through its final stages. He had started working with Dr. Schneirla when he was an undergraduate, and he was Dr. Schneirla's last doctoral student. After receiving his Ph.D., he continued at the American Museum of Natural History as a research associate and as a coworker with Dr. Schneirla in the doryline studies. Because of his close association with the progress of Dr. Schneirla's research and his own participation in this work, he was the ideal editor for this posthumous book.

This book will be a standard reference for a long time. It is a must for all present myrmecologists, insect behaviorists, and animal behaviorists. It is a source book of information and of ideas for investigation. It would be excellent introductory reading for graduate students as they prepare to undertake a field problem.

JAMES FORBES

ENTOMOLOGICA AMERICANA

Entomologica Americana is published by the New York Entomological Society for papers too long to be included in the *Journal*, generally over 30 printed pages. Since it is published irregularly, subscription is by volume, not by year, and costs $9.00 per volume. Subscription orders should be addressed to Publication Business Manager, New York Entomological Society, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. Future issues will include the following:

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1974. The Orthotylinae and Phylinae (Hemiptera: Miridae) of South Africa, with a phylogenetic analysis of the ant mimetic tribes of the two subfamilies for the world, by Randall T. Schuh. Pages 1–332.

Volume 48

1974. Revision of the genus *Euschistus* in Middle America (Hemiptera, Pentatomidae, Pentatomini), by L. H. Rolston. No. 1, pages 1–102.

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1969. A revision of the genus *Leptoglossus* Guerin (Hemiptera: Coreidae), by Richard Charles Allen. No. 2, pages 35–140, price $3.50

1970. A taxonomic and biological study of species of Attagenini (Coleoptera: Dermestidae) in the United States and Canada, by Richard S. Beal, Jr. No. 3, pages 141–235, price $3.50

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1973. Review of the genus *Sterphus* Philippi (Diptera: Syrphidae). Part I, by F. Christian Thompson. No. 2, pages 185–240, price $3.50

INDEX TO SCIENTIFIC NAMES OF ANIMALS AND PLANTS
VOLUME LXXXI

Generic names begin with capital letters. New genera, species, subspecies, and varieties are printed in italics. The following articles are not indexed: "Second Addition to the Supplemental List of Macrolepidoptera of New Jersey," by Joseph Muller, pp. 66–71; "An Annotated List of the Siphonaptera of Connecticut," by Donald H. Miller & Allen H. Benton, pp. 210–213.

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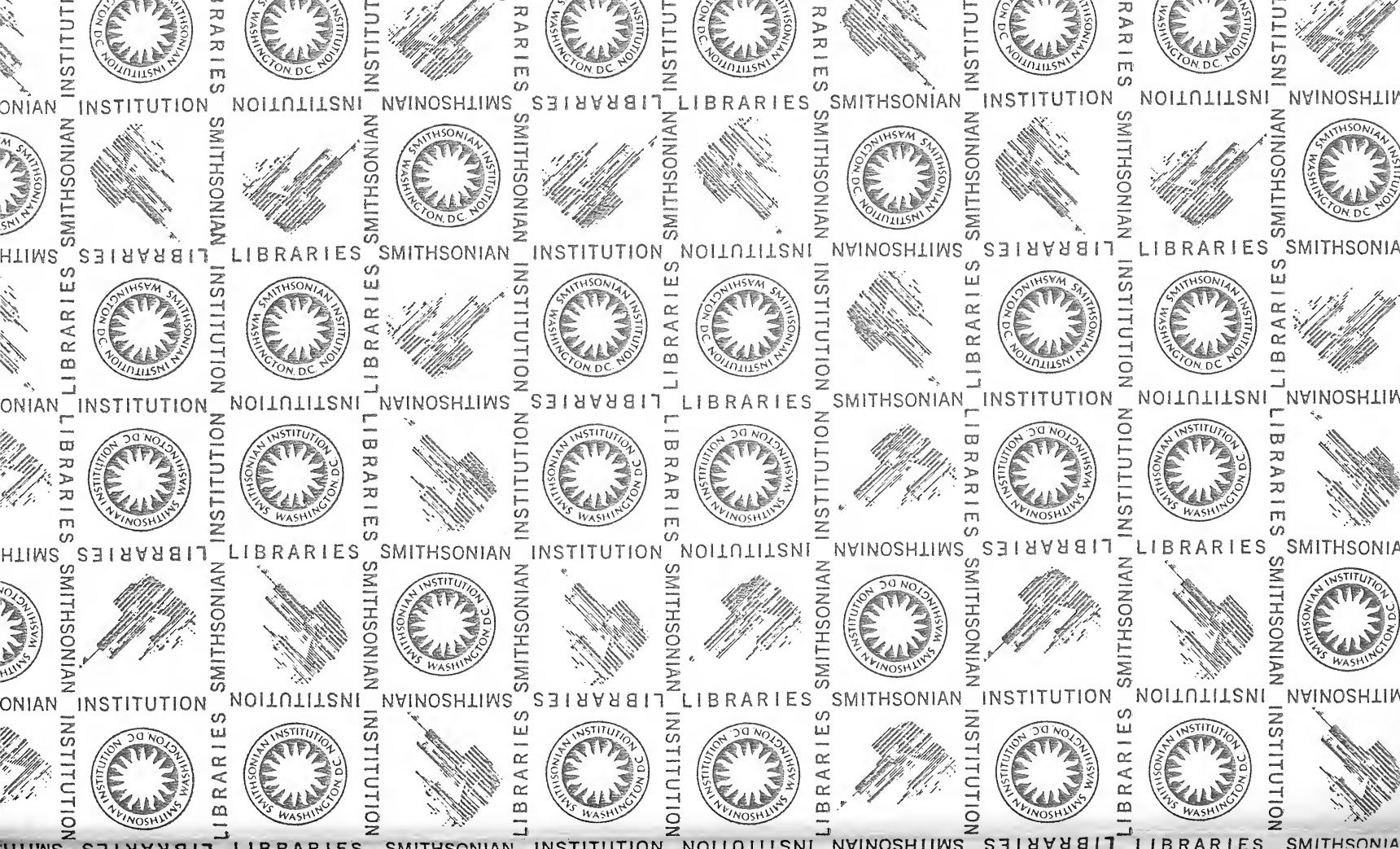
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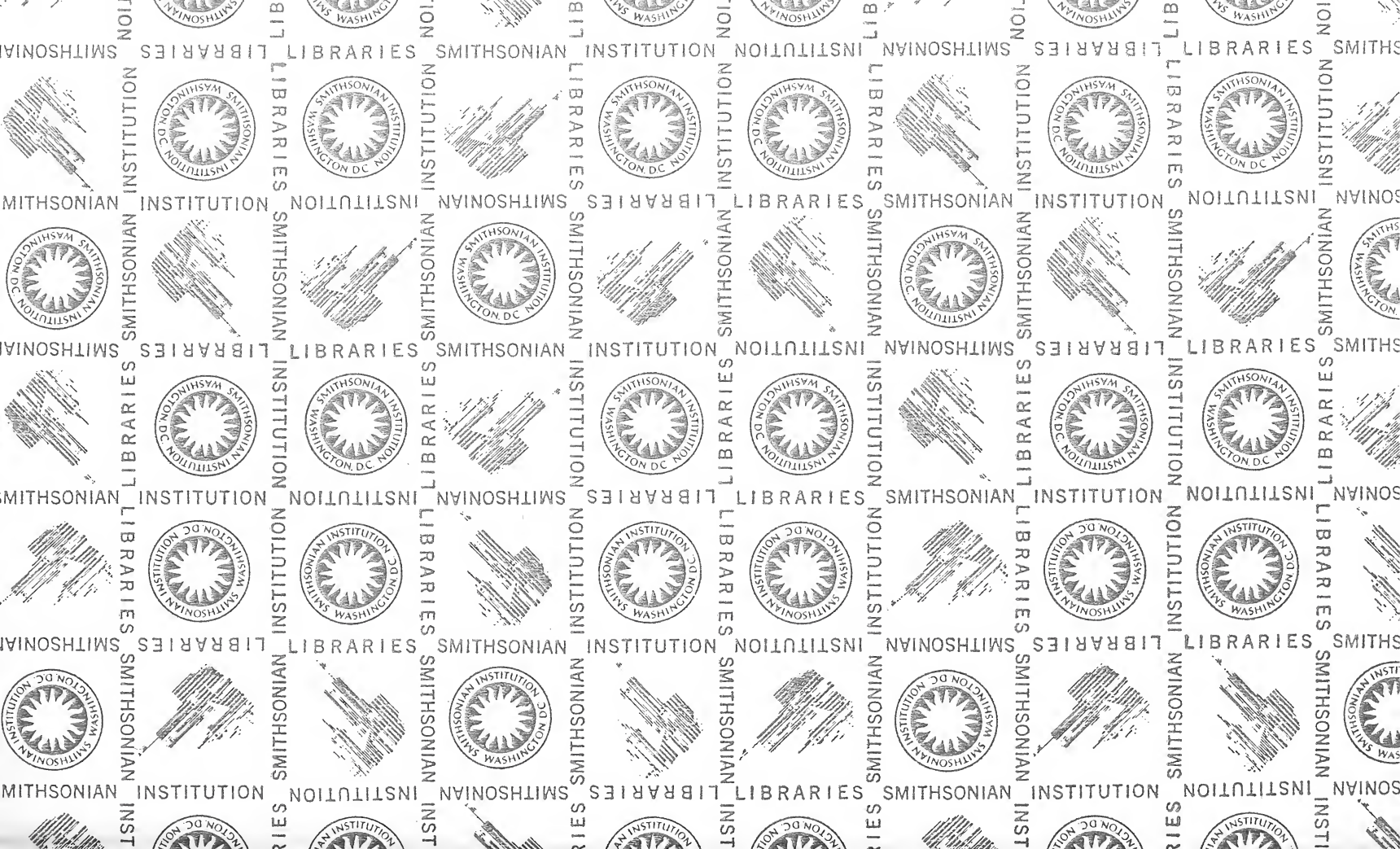
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