

THE BIOLOGY OF BLISTER BEETLES OF  
THE VITTATA GROUP OF THE GENUS  
*EPICAUTA* (COLEOPTERA, MELOIDAE)

CHERYL LYNN ADAMS AND RICHARD B. SELANDER

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## ABSTRACT

The Vittata Group of the genus *Epicauta* contains 31 species. Seven of these are confined to North America; one ranges from Central America to central South America; the rest are confined to South America. All the species from North America (*Epicauta vittata*, *E. occidentalis*, *E. temexa*, *E. abadona*, *E. tamara*, *E. vitticollis*, and *E. unilineata*) and three of those from southern South America (*Epicauta monachica*, *E. luteolineata*, and *E. leopardina*) are compared in detail with respect to ecology, behavior, and reproductive biology (courtship, copulation, oviposition, and development and hatching of eggs). Field and laboratory studies establish a high degree of uniformity among the species of the group in all

characters except those of male courtship behavior. Differences in courtship behavior are especially marked between sympatric species. Little of the variation among taxa in biological characters is explicable on the basis of variation in the physical environment of the taxa. The group is formally defined and a diagnostic key to the species occurring in North America is presented. Species accounts giving synonymy, locality records, and (for the North American species) analyses of geographic variation are presented. New species in the group are *Epicauta temexa*, *E. tamara*, *E. aragua*, and *E. apure*. *Epicauta kraussi* var. *purpureiceps* is given species status as *Epicauta purpureiceps*.

## INTRODUCTION

The Vittata Group of the meloid genus *Epicauta* Dejean is a previously unrecognized New World taxon containing 31 species. Included among these are the familiar striped blister beetles of the eastern and central United States and northern Argentina, several of which have long been known as pests of potatoes, alfalfa, and numerous other crops. Seven of the species are confined to the North American continent; one ranges from Central America to central South America; the rest are confined to the South American continent.

In the present paper the seven species endemic to North America and three species from southern South America are considered in detail with respect to ecology, behavior, and reproductive biology. The approach to these subjects is highly comparative, since two of the principal objectives of our study are to elucidate the ecological and behavioral differences involved in coexistence of species of the group in a given geographical region and to obtain an extensive and sound set of measurements of specific characteristics on which to base systematic and phylogenetic analyses. We attempt to determine the factors that determine the particular pattern of geographic variation exhibited by the species of the Vittata Group and, in particular, the degree of geographic overlap or

sympatry of the species. Whether differences between sympatric species are lacking or are less marked in allopatric species and whether ecological correlations of biological characters help explain distributional differences between species are questions that prompted us to undertake this study. The systematic portion of the work includes a formal definition of the group, a diagnostic key to the species occurring on the North American continent, and species accounts providing synonymy, locality records, and (for the North American species) analyses of geographic variation. For the North American species this treatment amounts to a taxonomic revision in the traditional sense. Of necessity, the treatment of the South American representatives of the group is, from the systematic viewpoint, limited and highly preliminary.

Sequels to this work now in preparation consider the postembryonic ontogeny of the 10 species given detailed treatment here and the comparative anatomy and identification of the larvae of these and several other species of the Vittata Group. Additional studies of ecology, behavior, and systematics of the group in South America are in progress or in the planning stage. At the completion of the project information from all studies will be incorporated in a

numerical taxonomic analysis of considerable proportion that we hope will permit us to draw reliable conclusions regarding the evolutionary history of the group and the contemporary factors determining its form and distribution.

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#### MATERIALS AND METHODS

**SPECIES STUDIED:** The species of the Vittata Group treated in detail in this study are *Epicauta vittata*, *E. occidentalis*, *E. temexa*, *E. abadona*, *E. tamara*, *E. vitticollis*, *E. uni-*



*lineata*, *E. monachica*, *E. luteolineata*, and *E. leopardina*. The last three of these are South American in distribution, the others are North American. Within *E. vittata* we have recognized and studied two subspecies or geographical races (the typical and lemniscate races), bringing the total number of taxa treated to 11. In addition, we have studied several other species of the group in greater or lesser detail; however, the results of these additional studies came too late for inclusion in the present work.

**SOURCE OF MATERIAL:** The treatment of intraspecific and interspecific anatomical variation in the adult stage and the distributional relationships of the taxa is based on examination of preserved material from a large number of institutional and private collections, as acknowledged in the introduction to this work, supplemented by large collections of each of the taxa from one or more localities made by us in the course of the study.

For behavioral studies we used both adults collected in the field and adults reared in the laboratory. Fieldwork in support of the study involved numerous trips in Illinois and neighboring states, as well as major trips to the southern United States (South Carolina, Florida, Mississippi, Tennessee, and Texas), Mexico (Sinaloa and Veracruz), and Argentina (primarily in the state of Santiago del Estero). Information regarding the source of field-caught, live material and its use in the study is summarized in table 1. The number of individuals obtained from a locality varied considerably. From most of the localities we obtained a minimum of 100 individuals, although rarely did we maintain such numbers for an extended period of time.

As outlined below, extensive use was made in quantitative behavioral studies of adults of the various taxa reared in the laboratory from eggs produced by field-caught females. Information on the source of the field-caught parental stocks involved in these rearings is also included in table 1. Several hundred adults were reared in the course of the study.

**USE OF FIELD-CAUGHT MATERIAL:** Adults from the field were our primary source of qualitative information on behavior. Some of this information was obtained in the field, but

the bulk came from the observation of the behavior in groups of caged, field-caught individuals. On first encountering a species in the field we invariably made detailed descriptions of feeding, sexual, and other behavior, and took several hundred feet of motion pictures of these activities. As it turned out, we never experienced a failure of transporting samples to the laboratory, and our preliminary studies were generally supplemented by extensive periods of observations and filming in the laboratory. In addition, field-caught adults were used in tests of feeding preferences, tests of homospesific and heterospesific sexual interactions, and, in the case of *E. vittata*, a hybridization experiment involving the two races. Samples of field-caught females were also used for ovariole counts. Finally, as mentioned above, eggs used in rearings were provided by field-caught females. Most of the field-caught material was preserved, after death, for anatomical study.

As a general rule, both in the field and laboratory, field-caught adults were maintained in sexually mixed groups of five to 20 individuals per cage. Commonly we used type B cages (see below) for this purpose. Once in the laboratory, field-caught adults were maintained in the manner described below for reared adults, except that the former were generally caged in groups.

**USE OF REARED ADULTS:** Measurements of longevity in the adult stage and all quantitative records of reproductive behavior were made on the basis of systematic, daily recordings of reared adults maintained in what we refer to as the *paired situation*. Aspects of reproductive behavior studied in this manner include courtship and copulatory behavior, the ontogeny and patterning of courtship behavior and copulation during adult life, the patterning of oviposition and its relationship to courtship and copulation, fecundity, hatching time of eggs, and the relationship of number and size of eggs to female body size. Note that reference to age or longevity of individuals in these studies is always to the number of days in the adult stage.

On emerging as an adult, a reared individual destined for assignment to the paired situation was isolated in a type C cage (see below), where it was kept throughout its adult life ex-

TABLE 1  
Source of Field-caught Adults and Their Use in the Study

Species, locality, date	Note number	Usage						
		Feeding		Sexual Behavior			Rearing number	Ovariole counts
		Obs.	Tests	Obs.	Films	Tests		
<i>E. vittata</i> (typical race)								
Buncombe and West Vienna, Johnson Co., Illinois, Sept. 1, 1970	10/11-70	—	—	X	—	—	24	—
Natchez Trace State Park, Henderson Co., Tennessee, Sept. 2, 1970	—	—	—	X	—	—	—	—
Dorsey, Itawamba Co., Mississippi, Sept. 3, 1970	—	—	—	X	—	—	—	—
Skyline, Lee Co., Mississippi, Sept. 3, 1970	15-70	—	—	X	—	—	24	—
Omega, Marion Co., Illinois, Sept. 11, 1970	30-70	—	—	X	—	—	—	—
Henderson Co., Tennessee, June 27-30, 1971	1-71	X	X	—	—	—	—	X
Ferne Clyffe State Park and Goreville, Johnson Co., Illinois, June 8-9, 1972	126-72	X	—	—	—	—	—	—
7 mi. W. Golconda, Pope Co., Illinois, July 9, 1972	127-72	X	X	—	—	—	—	—
Cowling, Wabash Co., Illinois, Aug. 27, 1972	—	X	—	—	—	—	—	—
Sidney, Champaign Co., Illinois, Sept. 16, 1972	—	X	—	—	—	—	—	—
Johnson, Pope, and Saline counties, Illinois, July 21-23, 1973	1-73	X	X	—	—	—	44	—
Mason State Forest, Mason Co., Illinois, Aug. 3-5, 1973	—	X	—	—	—	—	—	—
<i>E. vittata</i> (lemniscate race)								
4 mi. SW Jacksonboro, Colleton Co., South Carolina, Sept. 14-17, 1973	—	X	—	—	—	—	—	—
Walterboro, Colleton Co., South Carolina, Sept. 14-17, 1973	3-73	X	—	X	X	X	46	—
<i>E. occidentalis</i>								
Ferne Clyffe State Park, Johnson Co., and Jonesboro, Union Co., Illinois, July 1-3, 1970	1-70	X	—	—	—	—	Pre	—



TABLE 1 — (Continued)

Species, locality, date	Note number	Usage							
		Feeding		Sexual Behavior			Rearing number	Ovariolo counts	
		Obs.	Tests	Obs.	Films	Tests			
Buncombe and West Vienna, Johnson Co., Illinois, Sept. 1, 1970	13/18-70	—	—	X	—	—	23	—	
Natchez Trace State Park, Henderson Co., Tennessee, Sept. 2, 1970	—	—	—	X	—	—	—	—	
Dorsey, Itawamba Co., Mississippi, Sept. 3, 1970	19-70	—	—	—	—	—	23	—	
Skyline, Lee Co., Mississippi, Sept. 3, 1970	14-70	—	—	—	—	—	23	—	
Omega, Marion Co., Illinois, Sept. 11, 1970	31-70	X	—	X	—	—	—	—	
Henderson Co., Tennessee, June 27-30, 1971	2-71	X	X	—	—	—	—	X	
Ferne Clyffe State Park, Johnson Co., Illinois, July 8-9, 1972	125-72	X	X	—	—	—	—	—	
7 mi. W Golconda, Pope Co., Illinois, July 9, 1972	128-72	X	X	—	—	—	—	—	
Johnson, Pope and Saline counties, Illinois, July 21-23, 1973	2-73	X	X	—	—	—	45	—	
<i>E. temexa</i>									
Apodaca, Nuevo León, Mexico, Aug. 21, 1962	—	—	—	X	—	—	—	X	
Pearsall, Frio Co., Texas, Oct. 7-8, 1971	43-71	X	—	X	X	X	—	—	
Dilley, Frio Co., Texas, Oct. 7-8, 1971	44-71	X	—	X	X	—	25 <sup>a</sup>	—	
Beeville, Bee Co., and Berclair-Goliad, Goliad Co., Texas, Oct. 9-10, 1971	45-71	X	—	X	X	—	25	X	
<i>E. abadona</i>									
Culiacán, Sinaloa, Mexico, Sept. 26-27, 1972	300-72	X	—	X	X	—	40	X	
<i>E. tamara</i>									
Culiacán, Sinaloa, Mexico, Sept. 26-27, 1972	301-72	X	—	X	X	—	41	—	
<i>E. vitticollis</i>									
Cotaxtla Agr. Exp. Sta., Veracruz, Mexico, Sept. 30, 1972	302-72	X	—	X	X	—	42	—	

TABLE 1 — (Continued)

Species, locality, date	Note number	Usage						Rearing number	Ovariole counts
		Feeding		Sexual Behavior					
		Obs.	Tests	Obs.	Films	Tests			
<i>E. unilineata</i>									
Cotaxtla Agr. Exp. Sta., Veracruz, Mexico, Sept. 30, 1972	303-72	X	—	X	X	—	43	—	
<i>E. monachica</i>									
Amaicha del Valle, Tucumán, Argentina, Dec. 25, 1964	20-64	X	—	X	X	—	—	—	
Santiago del Estero, Santiago del Estero, Argentina, Dec. 20-28, 1972	100-72	X	—	X	X	—	32	X	
<i>E. luteolineata</i>									
Santiago del Estero, Santiago del Estero, Argentina, Dec. 23-27, 1972	103-72	X	—	X	X	—	33	—	
<i>E. leopardina</i>									
Santiago del Estero, Santiago del Estero, Argentina, Dec. 20-27, 1972	101-72	X	—	X	X	—	34	X	
Villa María, Córdoba, Argentina, Dec. 30, 1972	—	X	—	—	—	—	—	—	

<sup>a</sup>Also Exp. 27.

cept for daily exposure for a period of one hour to an individual of the opposite sex. Pairings of beetles to be exposed to each other were established as soon as possible after emergence of adults and were maintained until the death of the female of the pair.

For the daily period of exposure to each other the two adults of an established pair were placed in a clean type C cage with white blotter paper on the floor and with a small piece of food plant at the center of the cage, on the paper. Temperature was monitored during the exposure period by means of a thermistor probe placed in a dummy cage. For all species and races each pair was observed continuously for at least the first 15 minutes. During the first 15 minutes we recorded whether courtship occurred and made descriptive notes of the behavior. Occasionally certain activities were timed by means of stop watches. In addition, we recorded whether copulation was initiated dur-

ing the hour period, and in many cases we recorded the total duration of the copulatory behavior.

In addition to providing data on the ontogeny and patterning of reproductive behavior during adult life, the study of reared adults in the paired situation yielded detailed information on oviposition behavior of the females. Egg masses laid by females were collected daily and incubated. Subsequently, the number of eggs in each mass, the number developing to a recognizable embryo, and the number hatching were determined.

In the case of paired adults of *E. vittata* (typical race), *E. occidentalis*, *E. temexa*, *E. monachica*, and *E. luteolineata* detailed daily records of male courtship activity were made by using an Esterline-Angus 20-pen event recorder. For each pair of these species behavior was recorded continuously for 15 minutes, beginning with the first appearance of courtship

behavior in the daily period of exposure. However, if no courtship was expressed during the first 15 minutes of the hour, the detailed quantitative recording was omitted for that day.

Several females each of *E. vittata* (typical race), *E. occidentalis*, *E. tamara*, *E. monachica*, and *E. luteolineata* were kept in total isolation throughout their adult lives but otherwise treated precisely in the manner of females in the paired situation. We refer to these as virgin females, and frequent comparison is made between them and their counterparts in the paired situation.

It is useful to define two data sets derived from our studies of adults in the paired situation and virgin females. In the course of our study we obtained quantitative data relating to reproductive behavior for 61 pairs of adults in the paired situation and 44 virgin females. The data for these adults, taken together, constitute the *full reproductive data set*. This data set was used in the analysis of adult longevity and the relation of egg size to female body size. For the remainder of the analyses of reproductive behavior we restricted the data set to one consisting of information on 46 pairs and 15 virgin females. Criteria for inclusion in this *restricted reproductive data set* were that (1) the female lived for at least one month and died naturally; (2) she oviposited at least twice; (3) accurate counts of her egg masses were obtained; and (4), for sexual pairs, at least one of her egg masses hatched.

**MAINTENANCE OF ADULTS IN THE LABORATORY:** Adults were kept in a windowless room with a light-tight door. Two fluorescent light fixtures on the ceiling, each with two 40-watt tubes, operated automatically to provide a 12-hour daily photophase. Temperature averaged about 25°C., with maximum fluctuation daily of 3°C. Relative humidity in the room varied from 40 to 60 percent.

Two types of cages were used for field-caught adults in the mixed group situation. *Cage type A* measured internally 21 cm. in length, width, and height and was constructed largely of lucite plastic with sliding sheets of glass on the top and front. The two sides and back were provided with screened ports 10 cm. in diameter. *Cage type B*, also used for field-

caught adults, was somewhat smaller and rectangular, measuring internally 18.3 cm. in length, 13 cm. in width, and 9.5 cm. in height. This cage was entirely plastic in construction; its lid had a screened port 7 cm. in diameter. Beetles held in cages of type A and B were free to interact with one another except for occasional periods when the sexes were isolated for special purposes. *Cage type C*, used for maintenance and observation of adults in the paired situation and of virgin females, was a smaller version of cage type B, measuring internally 12 cm. in length, 8 cm. in width, and 6 cm. in height and with the screened port in the lid 3.8 cm. in diameter.

All cages had a floor covering of white blotting paper. Food provided was simply laid on the floor of the cage. Cages containing one or more females had a circular plastic dish 5.1 cm. in diameter and 3.6 cm. in depth filled with moistened silica sand as a medium for oviposition. The sand was prepared by adding de-ionized water to air-dried sand in the amount of 10 percent of its volume.

Very early in the study we found that adults were congregating on the moistened sand, when available, and this and other indications made it apparent that the humidity was below optimum for the species. We therefore adopted as standard procedure the covering of the cage ports with white blotter paper, in order to increase the humidity within the cages.

Daily care of the beetles in the laboratory involved cleaning the cages, replacement of the blotting paper on the floor, replacement of the oviposition dishes, and the addition of fresh food. Leaves of *Solanum dulcamara* and *S. tuberosum* were the principal food materials. Occasionally it was necessary to use leaves of *Amaranthus retroflexus* or *Lycopersicum esculentum* as a supplement or substitute for those of the *Solanum* species.

**RECORDING OF BEHAVIOR:** In the field, observations and filming were carried out in sunlight or light shade. Observations, recording, and filming in the laboratory were conducted in a room with physical conditions like those of the adult maintenance room except that the illumination consisted of a fluorescent light fixture suspended 32 cm. above the floor of the

cage in which the beetles were confined. For observation and recording two 40-watt tubes were used in the fixtures. Most of the motion pictures were taken with an Arriflex 16 mm. Camera outfitted with a macro lens. During filming, two additional 40-watt tubes in the light fixture were turned on, providing sufficient light for the use of an f-stop between 8 and 11 at 24 fps. with Kodak Plus-X negative film. In addition to several hundred still photographs we took 10,000 feet of motion picture film of behavior (primarily courtship).

**FEEDING CHOICE TESTS:** These tests consisted of exposing adults in individual type C cages to inch-square leaf sections of two different plants and recording, after a period of one hour, the relative amount of feeding on the sections. Adults were deprived of food for about six hours before the beginning of a test. Every experiment of this sort involved simultaneous testing with at least two species of *Epicauta*. Care was taken to balance the experiments with respect to the spatial arrangement of the leaf sections within cages. Adults were assigned to cages randomly.

**INCUBATION OF EGGS:** Eggs masses were recovered from cages daily, placed in individual autoclaved, cotton-stoppered 3-dram lip vials, and incubated in darkness at 27° C. and 100 percent RH. Humidity was maintained by keeping the vials in large desiccator jars having 500 ml. of distilled water in the bottom. Larvae not used in rearings were killed and preserved in 70 percent ethyl alcohol a few days after hatching occurred.

**REARINGS:** Most of the reared adults used in the study were obtained from a series of carefully controlled experimental rearings conducted at three temperature cycles. All rearings (and incubation) were carried out in darkness in temperature control cabinets. The means of the cycles were 22, 27 and 32° C., respectively. Each cycle was restricted to a range of 7° C., the thermostat of the incubator being set at the minimum of the cycle for 12 hours and at the maximum for 12 hours daily. Temperature settings were established by use of thermistor probes inserted in dummy rearing tubes. Relative humidity was 100 percent; it was maintained in the manner described above. Larvae were confined individually in glass tubes stop-

pered at each end with cotton and containing eggs of the acridid grasshopper *Melanoplus differentialis* laid in the laboratory by females collected locally in the field. Complete details and the analysis of the results of these rearings will be presented elsewhere.

Some additional rearings of the nature described were carried out to obtain supplemental adults of *E. vittata* (typical race), *E. occidentalis*, *E. monachica*, and *E. luteolineata*. Further rearings of samples of each taxon were conducted to obtain larval specimens in the different instars. In the case of *E. luteolineata*, limited rearings were attempted using larvae hatched from eggs produced by virgin females. A rearing of *E. occidentalis* was undertaken specifically to investigate possible inheritance of ontogenetic patterns. Finally, hybrids of the two races of *E. vittata* were reared.

**ANALYSIS OF DATA:** Most of the statistical analyses in this work are in the form of analyses of variance of multiple regression models. Readers not familiar with the procedures involved may consult the texts of Li (1964) and Searle (1971). In presenting test statistics we have used one, two, three, and four asterisks to denote significance at the 5, 1, 0.5, and 0.1 percent levels, respectively.

In the comparison of taxa, having established overall significance among taxa in a biological character, our primary interest has been in determining whether real differences exist between populations occurring together and interacting in nature. Differences of this nature have special importance in suggesting possible lines of further investigation into the general problem of how species so generally similar in behavior, ontogeny, anatomy, and, apparently, ecology as the members of the Vittata Group are able to coexist. Secondly, we have been interested in the extent to which the geographical races of *E. vittata*, recognized mainly on the basis of anatomical characters, are differentiated in behavioral characters. As a result of these considerations, we have restricted comparisons of taxa to a series of orthogonal contrasts between sympatric species or, in the case of *E. vittata*, geographical races. In particular, we repeatedly contrast *E. vittata* with *E. occidentalis*, *E. occidentalis* with *E. temexa*, *E. abadona* with *E. tamara*, *E. vitticollis* with *E. unilineata*, *E. monachica* with *E. luteolineata*,

the last two species with *E. leopardina*, and the typical race of *E. vittata* with the lemniscate race. Selection of the two contrasts involving the South American species is, admittedly, rather arbitrary. From our field experience we judged that *E. monachica* and *E. luteolineata*

were likely to resemble each other rather closely in most biological characters and that direct comparison of these two species would be of greater interest than the comparison of either one, singly, with *E. leopardina*.

## ECOLOGY AND BEHAVIOR

This section is concerned primarily with the geographical and ecological relationships of the species of the group and aspects of behavior not immediately concerned with reproduction.

The analyses of geographic and seasonal distributions incorporate data from the literature but are based very largely on information associated with preserved specimens in our own collection and those of the numerous institutions whose material has been so kindly made available to us. The treatment of nonreproductive behavior includes information from the literature and from museum specimens (feeding records, in particular) as well as extensive original data obtained in the course of this study. Analyses of the development of behavior and of longevity are based on data from systematic observation and recording of adults of the various species reared by us in the laboratory.

### GEOGRAPHIC DISTRIBUTION

#### GENERAL

The Vittata Group is confined to, and widely distributed in, the New World, where it ranges from about 45° N (in southern Quebec, near the Vermont border) to about 40° S (in the province of Neuquén, Argentina). On the basis of what appear to be major disjunctions of range, we recognize four geographic regions in which the group occurs.

**TEMPERATE EASTERN AND CENTRAL NORTH AMERICA:** The species of this region are *E. vittata*, *E. temexa*, and *E. occidentalis*.

*Epicauta vittata* (fig. 1) has the most extensive geographic distribution of any species of the group. Its range extends, more or less continuously, from extreme southern Quebec and Connecticut south to southern Florida, southwest to Louisiana and Missouri, and west to eastern Oklahoma, Kansas, and central South

Dakota. Along the coastal region of South Carolina and southern Georgia and in Florida, the species is represented by a well-differentiated population we call the lemniscate race. This and other aspects of geographic variation in *E. vittata* are discussed elsewhere (see Systematics).

To the west and southwest, over roughly one-third of its range, *E. vittata* is sympatric with *E. occidentalis*. The latter species (fig. 2) ranges from southern Indiana, Tennessee, and extreme western Georgia west to the Great Plains of Nebraska, South Dakota, and Colorado and to eastern Texas, where it extends south along the Gulf Coast at least to the Mexican border. The area of sympatry with *E. vittata* involves about half the range of *E. occidentalis*.

So far as known, only the typical race of *E. vittata* is overlapped geographically by *E. occidentalis*. However, possible sympatry of the lemniscate race and *E. occidentalis* is suggested by the close approach of the limits of range of these taxa in Georgia.

In examining records of *E. occidentalis* we noted a temporal pattern strongly suggesting that this species may be extending its geographic range east and thus encroaching more and more on that of *E. vittata*. As reference to table 2 indicates, records of *E. occidentalis* in the Great Plains states, Texas, and Louisiana extend back, in fairly good numbers, to the turn of the century, with a few as early as the 1880s. However, there is only one record of the species in Arkansas-Missouri region before 1920 and none in more eastern states before 1930. At the same time, there are abundant records of *E. vittata* in the area of sympatry going back well into the past century. Even considering regional differences in entomological interest and activity and patterns of popula-



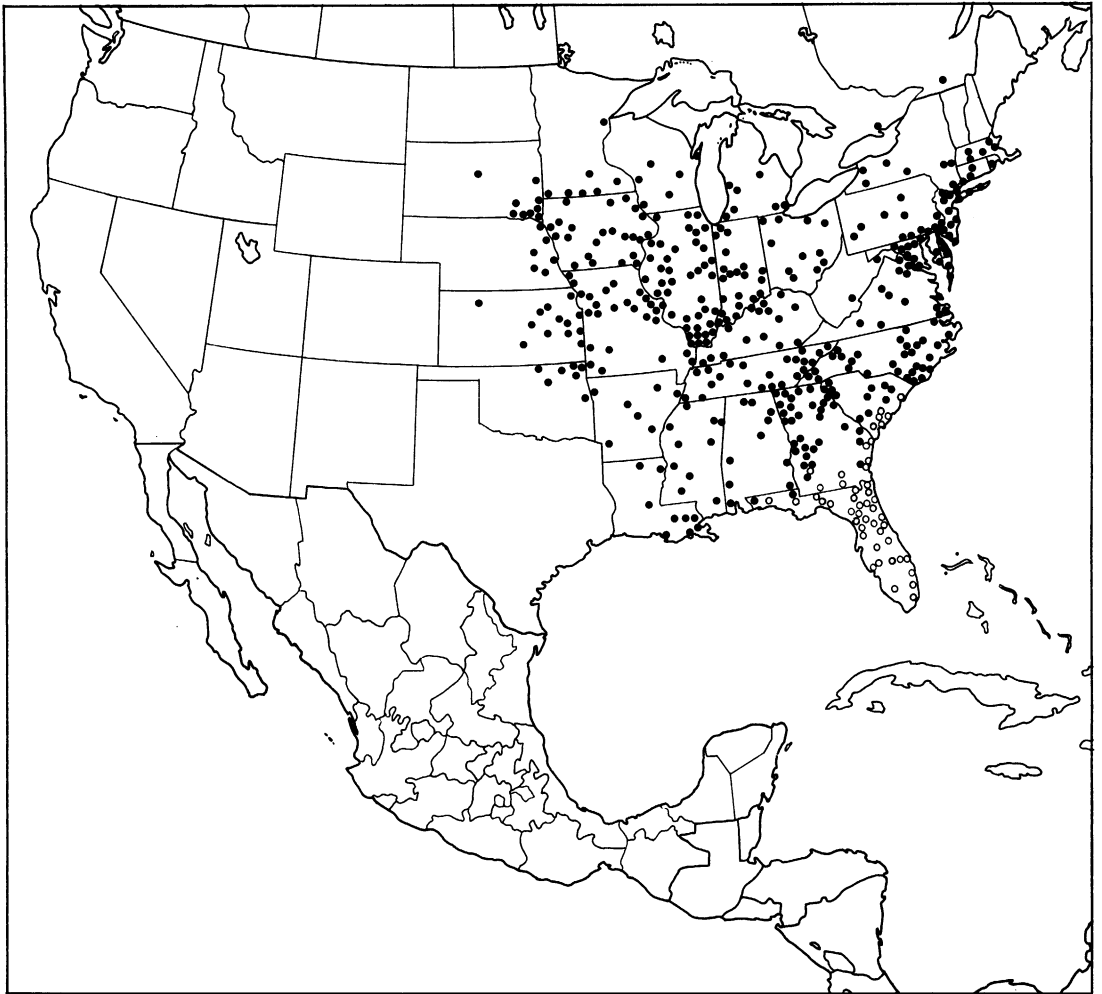


FIG. 1. Geographic distribution of *Epicauta vittata*. Typical race indicated by solid circles, lemniscate race by open circles.

tion of the general area of concern, we believe that the data reflect a major eastward extension of the range of *E. occidentalis* during this century or at least a marked increase in its population density in the eastern part of its present range. In Illinois, Tennessee, and Mississippi, at least, *E. occidentalis* seems to be presently as abundant as *E. vittata*, if not more so. Similar evidence of marked, relatively recent changes in geographic range was suggested for *E. segmenta* and *E. valida* by Selander and Mathieu (1969).

*Epicauta temexa* (fig. 3) ranges over the southern two-thirds of Texas south to San Luis Potosí and northern Veracruz in Mexico. There is apparently no overlap with *E. vittata*, although at Dallas, Texas, *E. temexa* is recorded within about 175 miles of the southwestern limit of range of that species, in southwestern Arkansas. A relatively narrow band of sympatry between *E. temexa* and *E. occidentalis* extends from Dallas south to Brownsville, Texas. Details of the distributional relationships of *E. temexa* and *E. occidentalis* are shown in

TABLE 2  
 Frequency Distribution of Records (Series) of *Epicauta occidentalis* by Decades

Region	Decades (beginning year)									
	1880	1890	1900	1910	1920	1930	1940	1950	1960	1970
Texas, Louisiana	1	1	8	14	20	19	24	19	21	5
Oklahoma, Kansas	—	—	8	19	18	42	10	42	39	1
Nebraska, South Dakota	2	—	2	12	3	7	9	4	1	—
Arkansas, Missouri	—	—	—	1	5	32	22	29	29	—
Illinois, Indiana	—	—	—	—	—	1	5	26	5	14
Tennessee, Kentucky	—	—	—	—	—	2	9	11	4	4
Mississippi, Alabama, Georgia	—	—	—	—	—	—	9	20	7	2
Colorado, New Mexico	—	—	—	—	1	1	—	—	2	1

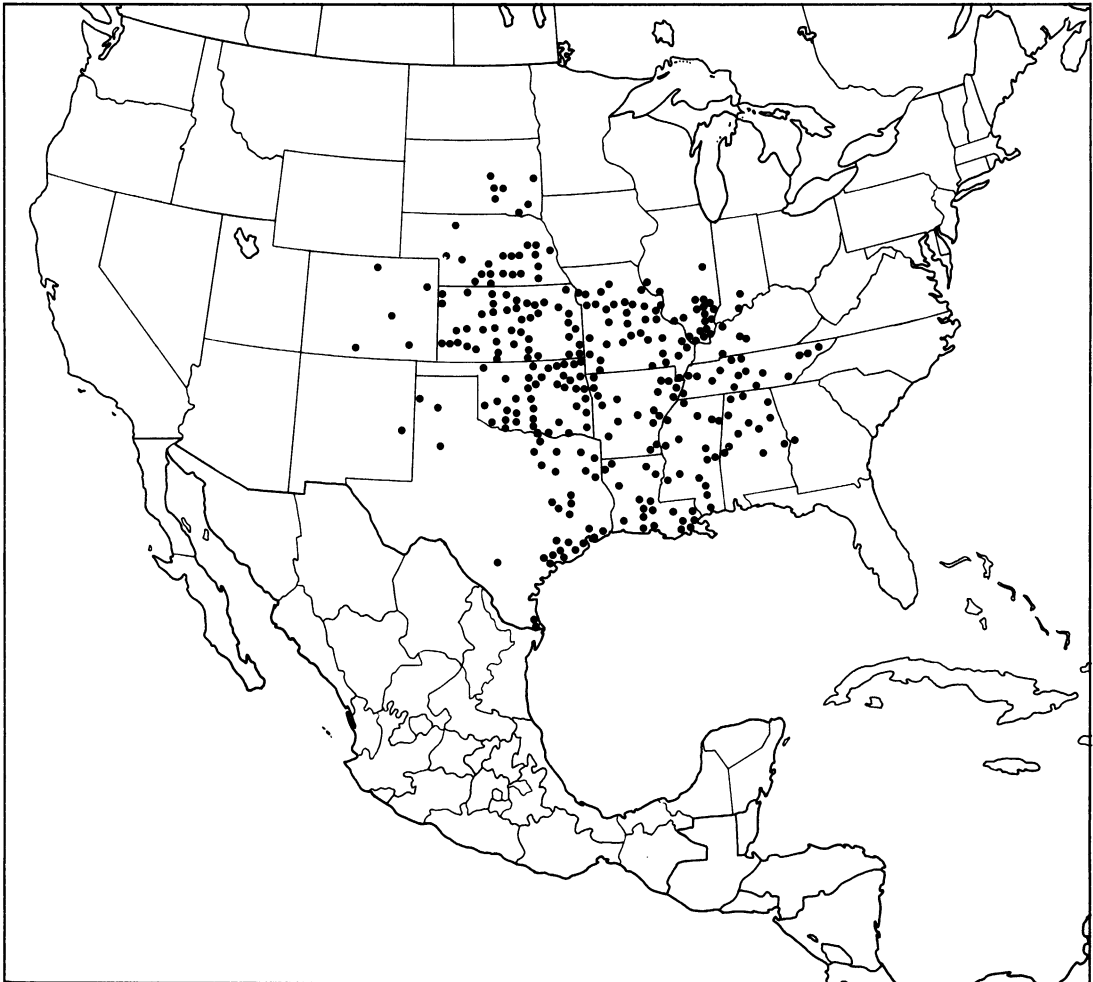


FIG. 2. Geographic distribution of *Epicauta occidentalis*.



FIG. 3. Geographic distribution of *Epicauta temexa*.

figure 4, where records of the two species in Texas are mapped by county.

**WESTERN NORTH AMERICA:** Two species, *E. abadona* and *E. tamara*, are found in the Sonoran Desert and south along the arid, subtropical coast of Mexico. To the east they are isolated from the previous region by the Sierra Madre Occidental and the Central Plateau of Mexico and to the southeast from the next region by the southern Mexican highlands.

*Epicauta abadona* (fig. 5) is the more widely distributed species, ranging from south-

ern Arizona through Sonora to the southern border of Sinaloa. *Epicauta tamara* (fig. 6) has been recorded from southern Sonora south through Sinaloa to Nayarit, which is apparently the only area in which it occurs without *E. abadona*.

**TROPICAL MEXICO, CENTRAL AMERICA, AND NORTHERN SOUTH AMERICA:** Six species occur in this region. Two are confined to the North American continent, three to South America, and one occurs on both continents.

*Epicauta vitticollis* and *E. unilineata* are

both strictly North American in distribution and are, on the basis of rather limited information, largely allopatric. *Epicauta vitticollis* (fig. 6) ranges from northern Oaxaca and southern Veracruz east into the Yucatán Peninsula, Guatemala, Honduras, and Nicaragua. The range of *E. unilineata* (fig. 5) is, for the most part, more southern; it extends from Puebla and southern Veracruz to Guatemala and El Salvador. Very likely there is sympatry between *E. unilineata* and *E. vitticollis* in central Guatemala, but at present the two species are definitely known to occur together only at Cotaxtla, Veracruz.

A new species, *E. aragua* (heretofore misidentified as *E. grammica*), that we have studied (but too late for detailed consideration in this work) ranges from El Salvador, where it occurs with *E. unilineata*, south through Honduras, where it occurs with *E. vitticollis*, to Venezuela and central Colombia (fig. 7). In Venezuela and Colombia the range of *E. aragua* partially overlaps that of another new species, *E. apure*, which extends south to Bolivia. Additional species of the Vittata Group in northern South America are *E. fuliginosa* from Colombia and *E. subvittata* from Guyana; detailed distributional information is available for neither of these species.

**SOUTHERN SOUTH AMERICA:** In the northern half of Argentina and adjacent areas in southern Bolivia, Paraguay, southern Brasil, and Uruguay there are 17 nominal species either definitely or tentatively assigned to the Vittata Group. Among these are *E. monachica* (fig. 8), ranging from Santa Cruz, Bolivia, through northwestern Argentina to the provinces of Mendoza and San Juan; *E. leopardina* (fig. 10), occupying much the same region of Argentina as *E. monachica* but extending farther south (to Neuquén Province), east (to Buenos Aires Province), and northeast (to the state of Río de Janeiro, Brasil); and *E. luteolineata* (fig. 9), presently known only from the province of Santiago del Estero, Argentina, where it occurs with both *E. monachica* and *E. leopardina*.

Additional species in this region are listed below, together with an indication of their recorded ranges. None of these species has been

studied in detail; most probably have more extensive ranges than indicated.

*Epicauta aemula*—Brasil (São Paulo)

*Epicauta borgmeieri*—Brasil (Matto Grosso)

*Epicauta bosqi*—Argentina (Buenos Aires, Chaco, Formosa, Salta, Santa Fé, Buenos)

*Epicauta clericalis*—Argentina (Misiones, San Juan, Santa Fé)

*Epicauta floydwerneri*—Argentina (Misiones) and Bolivia (Santa Cruz)

*Epicauta franciscana*—Argentina (Buenos Aires, La Rioja, Santa Fé) and Uruguay

*Epicauta grammica*—Brasil (states unknown) and Argentina (Córdoba, Formosa, Salta, Santa Fé)

*Epicauta purpureiceps*—Argentina (Córdoba)

*Epicauta missionum*—Argentina (Misiones)

*Epicauta philaemata*—Argentina (Misiones) and Brasil (Río de Janeiro, Santa Catarina, São Paulo)

*Epicauta rutilifrons*—Argentina (Jujuy)

*Epicauta xanthocephala*—Brasil (Goyaz)

*Epicauta yungana*—Bolivia

*Epicauta zebra*—Argentina (Catamarca,

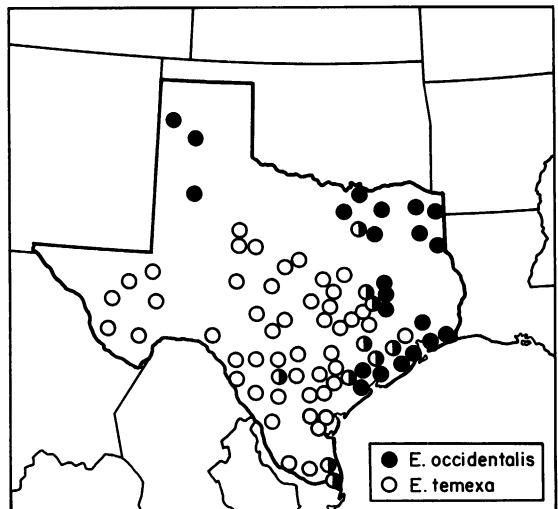


FIG. 4. Sympatry of *Epicauta occidentalis* and *E. temexa* in Texas. Each circle represents a county in which one or both species are recorded.



FIG. 5. Geographic distributions of *Epicauta abadona* (circles) and *E. unilineata* (squares).

Córdoba, La Rioja, Mendoza, Misiones, Salta, Santiago del Estero, Tucumán) and Paraguay

Finally, there are three South American species recorded from unknown localities in Brasil. These species are *E. kraussi*, *E. nattereri*, and *E. strigata*.

#### HABITATS

As indicated by the information just presented, the Vittata Group is primarily temperate and subtropical in distribution, with only poor representation in truly tropical areas. The vari-

ety of habitats occupied by the group is, of course, enormous. Particularly impressive in this regard is the North American *E. occidentalis*, which, in addition to occurring through much of the Great Plains, ranges well into the Eastern Deciduous Forest and extends south to the seasonally arid subtropics of southern Texas, and the South American *E. leopardina*, which ranges from the moist tropical, forested regions of southern Brasil through the arid subtropics of northern Argentina south to temperate Mendoza and Neuquén.

During the present study, we have had the



invaluable opportunity of observing and collecting adults of the Vittata Group in all the major geographic regions in which they occur. Whether in the eastern United States, Mexico, Venezuela, or Argentina, we have been constantly impressed with the fact that the Vittata Group coexists very successfully with man. One of the key elements in this is the ability of the species of the group to utilize as food many of the crops and garden plants cultivated by man as well as many of the weeds associated with his agriculture. It is also reasonable to assume that the species are especially success-

ful in parasitizing grasshoppers associated with agriculture. Wherever we have gone, we found the adult beetles to be decidedly most abundant in and around cultivated fields and pastures, in and around farming communities, and in the outskirts of cities. Whether in Illinois, Texas, Sinaloa, Veracruz, or Santiago del Estero, one can almost be assured of finding adults of one or more species by searching in cultivated fields, pastures, and vacant lots in the day and by looking under lights on farms, at gas stations, at store fronts, and along the roads at night.



FIG. 6. Geographic distributions of *Epicauta tamara* (circles) and *E. vitticollis* (squares).

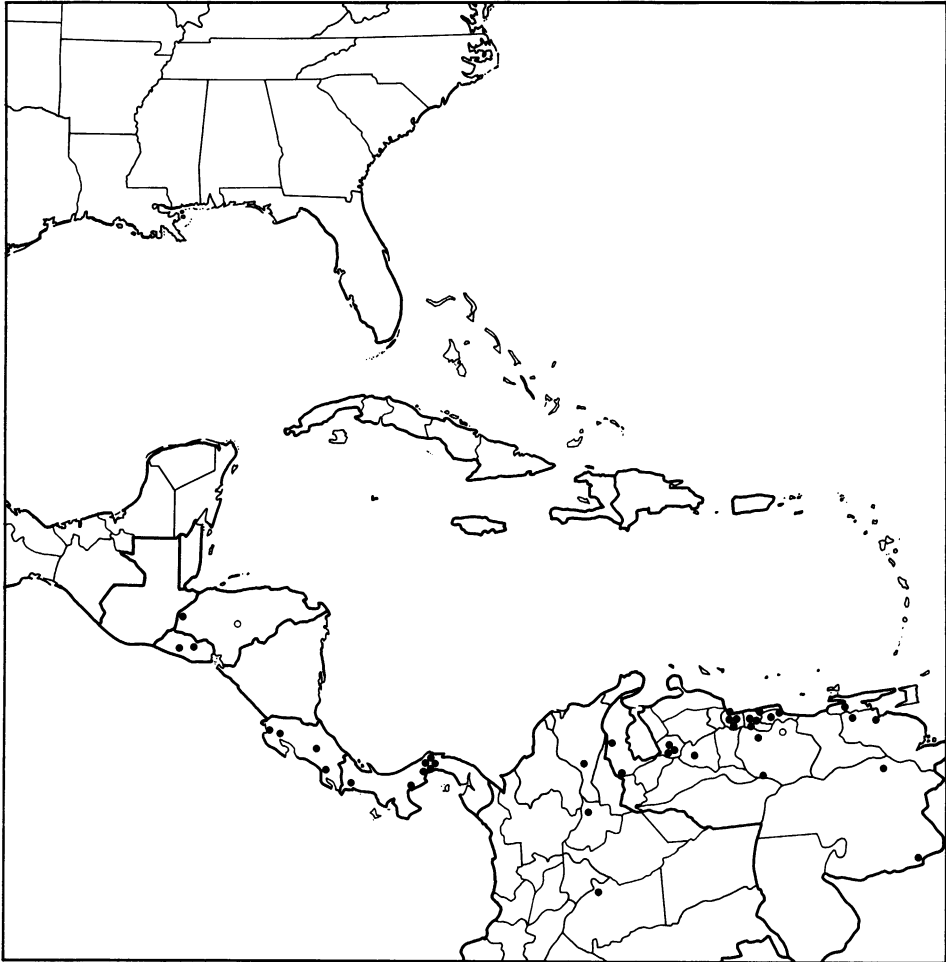


FIG. 7. Geographic distribution of *Epicauta aragua*.

We have, of course, found the species in more natural environments, such as forested regions in the eastern United States, open grazing land in the southwestern United States, and desert or near-desert areas in western Mexico and again in Argentina. However, we have had by far the greatest success in highly disturbed areas, as described above.

So far in the study, we have found no habitat differences among sympatric populations. This holds for those of *E. vittata* and *E. occidentalis* in the central and southern United States, *E. occidentalis* and *E. temexa* in southern Texas, *E. abadona* and *E. tamara* in Sinaloa, *E. vitticollis* and *E. unilineata* in

Veracruz, and *E. monachica*, *E. luteolineata*, and *E. leopardina* in northern Argentina. Further, as described in later sections, there is no evidence of significant ecological isolation of sympatric populations on the basis of seasonal activity periods, diel periodicity, or feeding behavior of adults.

## SEASONAL DISTRIBUTION

### ADULT STAGE

In North America the pattern of seasonal distribution of records of adults of the Vittata Group (table 3) is similar in most respects to that reported for the Albida Group of the genus

*Epicauta* by Selander and Mathieu (1969). In most populations adults are not found com-

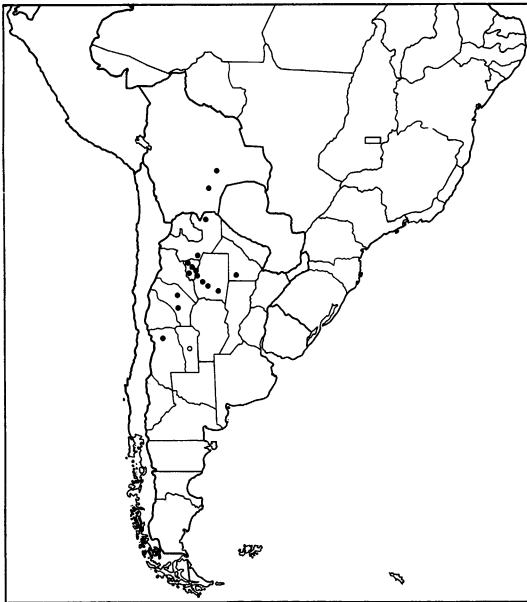


FIG. 8. Geographic distribution of *Epicauta monachica*. Open circle indicates a province record, without precise locality information.



FIG. 9. Geographic distribution of *Epicauta luteolineata*.

monly in the field before late May or early June, and there is a rather abrupt decline in numbers in late September or early October. Similarly, there is evidence in several species for progressively earlier appearance of adults with decreasing latitude. However, in the case of *E. temexa*, which ranges geographically from Texas south to northern Veracruz, Mexico, the peak of adult activity apparently occurs later in the year in the southern portion of the range than in the northern. The distribution of records of this species in table 3 is based primarily on material collected in Texas. In contrast, the frequency distribution by month of adults of *E. temexa* taken by Hernández (1960) in a light trap at the Apodaca Agricultural Experimental Farm near Monterrey, Nuevo León, Mexico, in 1959, indicates relatively light adult activity before August. Between May 25 and November 5, Hernández captured 1340 adults, with the following percentage distribution by month: May 2.1, June 3.2, July 9.2, August 16.8, September 33.5, October 29.4, November 5.7. The light trap was placed near irrigated agricultural fields, and it is possible that the distribution recorded reflects late-season move-

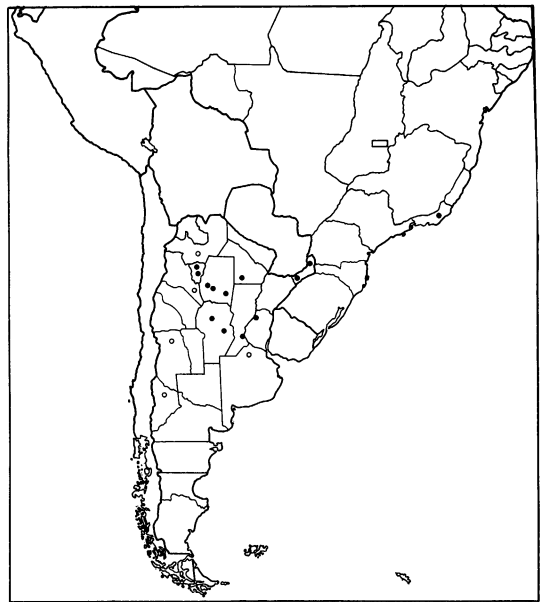


FIG. 10. Geographic distribution of *Epicauta leopardina*. Open circles indicate province records, without precise locality information.

TABLE 3  
Percentage Distribution, by Months, of Records of Adults of Species of the Vittata Group

Species	Months												N records
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
NORTH AMERICAN SPECIES													
<i>E. vittata</i>													
Northern range <sup>a</sup>	—	—	0.4	0.4	1.6	13.4	42.8	32.3	8.1	0.8	0.2	—	507
Southern range	—	—	—	2.1	12.5	25.0	22.9	18.5	14.3	4.8	—	—	336
Florida	—	—	—	24.5	24.5	18.1	11.8	8.5	8.5	4.3	—	—	94
<i>E. occidentalis</i>													
Northern range <sup>a</sup>	—	—	—	1.6	2.2	20.9	32.8	28.5	12.7	1.4	—	—	369
Southern range	—	—	—	0.3	11.6	28.8	27.1	20.2	9.2	2.7	—	—	292
<i>E. temexa</i>	—	—	0.6	2.8	16.4	24.9	15.8	17.5	14.1	6.2	1.7	—	177
<i>E. abadona</i> <sup>b</sup>	—	—	—	—	—	8.8	12.3	50.9	22.8	1.8	1.8	—	57
<i>E. tamara</i>	—	—	—	—	—	11.9	42.9	23.8	16.7	2.4	2.4	—	42
<i>E. vitticollis</i>													
Mexico	—	—	—	5.6	—	16.7	11.1	44.4	11.1	5.6	—	5.6	18
Central America	—	10.0	5.0	24.0	24.0	5.0	5.0	5.0	5.0	10.0	5.0	—	20
<i>E. unilineata</i>	—	—	—	—	6.7	20.0	20.0	40.0	6.7	—	—	6.7	16
SOUTH AMERICAN SPECIES													
<i>E. monachica</i>	16.7	33.3	11.1	—	—	—	—	—	—	5.5	11.1	22.2	18
<i>E. luteolineata</i>	—	50.0	—	—	—	—	—	—	—	—	—	50.0	2
<i>E. leopardina</i>	25.0	25.0	25.0	—	—	—	—	—	—	—	6.2	18.8	16

<sup>a</sup>Northern range includes all localities north of 37° N latitude, southern range all those south, except in *E. vittata*, where Florida records are tabulated separately.

<sup>b</sup>Includes 25 collections in Arizona reported by Werner, Enns, and Parker (1966).

ment of adult populations to such fields as the natural vegetation deteriorated.

Without exception, sympatric populations have broadly overlapping seasonal ranges in the adult stage (table 3). This relationship and some details regarding geographic variation in seasonal range are discussed in the following paragraphs.

*Epicauta vittata* and *E. occidentalis* have surprisingly similar seasonal distributions of records of adults, both in their northern and southern areas of sympatry (table 3). Relatively little geographic effect on seasonal range is evident for *E. occidentalis*, but quite a marked one is indicated for *E. vittata*. Thus, while adults are decidedly most abundant in midsummer in the northern part of the range of *E. vittata*, the season is sufficiently advanced in

the Florida population that peak adult activity occurs during the spring months. In this respect the Florida population resembles the Central American population of *E. vitticollis*.

Detailed analysis of the records of *E. vittata* in South Carolina, Georgia, and Florida fails to demonstrate significant seasonal differences between the typical and lemniscate races at or near the line of demarcation that we have drawn between these populations. The more southern lemniscate race shows sizeable adult activity earlier in the year than does the typical race. At comparable latitudes, however, the recorded seasonal distributions of the two races in the adult stage are essentially the same.

Returning to *E. temexa*, the data indicate complete seasonal overlap with sympatric *E. occidentalis* in Texas. The frequency distribu-

tion of records of *E. temexa* in Texas is more dispersed than that of *E. occidentalis* in that state, but the distributions are similar in other respects, including coincidence of their modal months.

There is apparently complete seasonal overlap between *E. abadona* and *E. tamara*, which are sympatric on the west coast of Mexico. However, the distribution of records of the latter species is strongly skewed to the right, with the result that its peak is reached one month earlier than that of *E. abadona*. Neither species presents evidence of geographic variation in seasonal range.

As shown in table 3, there is substantial indication that adults of *E. vitticollis* tend to emerge earlier in Central America than in Mexico. The few data for *E. unilineata* suggest that the seasonal range of this species is similar to that of the Mexican population of *E. vitticollis* with which it is sympatric.

The seasonal ranges of adults of the three South American species studied are similar to those of the North American representatives of the Vittata Group with respect to both the seasonal placement and length (table 3). The earliest records are in October and November and the latest in March.

*Epicauta monachica* and *E. leopardina* have an extensive area of sympatry in northern Argentina. The third species, *E. luteolineata*, is known only from the province of Santiago del Estero where it occurs with both of the other species. The rather meager amount of information on seasonal distribution of the adult stage presently available does not suggest any degree of seasonal isolation among the South American species studied.

Although some reared individuals in our laboratory lived six months or more as adults, mean longevity in the adult stage was on the order of three months. The fact that the seasonal ranges of species of the group in nature may extend for six to eight months may be accounted for by staggered emergence of adults of a single generation and the presence of additional generations.

Ingram and Douglas (1932) reported that adults of *E. occidentalis* (as *E. lemniscata*) usually emerged following a rain. Further, they

found that adults remained in glass rearing tubes for five days before burrowing out. In our experience, recounted elsewhere, adults of this and other species of the Vittata Group reared in the laboratory burrowed from their pupal cells within a few hours of reaching the adult stage. Possibly the delay in emergence mentioned by Ingram and Douglas resulted from the soil in the rearing tubes becoming dry and hardened. In any event, it is not unlikely that some differences in the time of appearance of adults in the field arises from variation in the texture and moisture content of the soil. This factor, together with geographical differences in temperature and environmentally and genetically determined differences in the length of the diapause period in over-wintering larvae, could easily account for the fact that the recorded seasonal range of the adult stage for most taxa is much longer than mean adult longevity.

The incidence of multiple generations of species of the Vittata Group in nature has not been investigated in detail. Previously published reports, referring exclusively to *E. vittata* or *E. occidentalis* or a mixture of these species, indicate that populations are generally univoltine in the northern United States, have a sizeable incomplete second generation in intermediate areas, and may have a second, and possibly third complete generation in the South (Riley, 1877; Forbes and Hart, 1900; Ingram and Douglas, 1932; Gilbertson and Horsfall, 1940; Horsfall, 1943).

Two mechanisms of producing multiple generations are known in the genus *Epicauta* (Selander and Weddle, 1969). Interestingly, both were first discovered in species of the Vittata Group. One, in which the larva skips the normally over-wintering coarctate larval instar and subsequent prepupal instar and pupates a few days after completing feeding, was first reported by Ingram and Douglas (1932) in *E. occidentalis* (as *E. lemniscata*) in Louisiana. The other, involving suppression of diapause in the coarctate larva, was first reported by Gilbertson and Horsfall (1940) in *E. "lemniscata"* (= *E. vittata* or *E. occidentalis* or both) in South Dakota. Experimental rearings in our laboratory indicate that both mechanisms are possessed by most, if not all, species of the



group and are expressed rather commonly. Further, our findings are in substantial agreement with the reports, cited above, suggesting a latitudinal gradient in the incidence of multivoltinism.

#### IMMATURE STAGES

Postembryonic ontogeny in the Vittata Group will be treated in detail in a separate work. In order to pursue the discussion of multivoltinism, however, it will be useful to outline here the life cycle, with particular attention to the seasonal distribution of the immature stages.

Eggs may be present in nature from shortly after the beginning of the adult season until shortly after its end. For example, Ingram and Douglas (1932) found eggs of *E. occidentalis* in the field from June to November in Louisiana, and Horsfall's (1943) table of the seasonal distribution of life stages in *E. "lemniscata"* in Arkansas, which we reproduce in modified form as table 4, shows the egg stage represented from June to September.

Larvae feed during the first instar of the triungulin phase and the four (exceptionally five) following instars, in which the larva is grublike in appearance (first grub phase). On completing feeding, the first grub larva prepares a cell in the soil apart from the grasshopper egg pod on which it fed and typically becomes, at ecdysis, a heavily sclerotized, immobile coarctate larva. Unless it is to take part in the production of a second generation during the same season, this larva enters diapause and passes the winter or other unfavorable period of the year in the coarctate phase. When, near the beginning of the next season of adult activity, the larva undergoes ecdysis, it again becomes grublike in form (second grub phase). This phase, which entails only one instar, is followed shortly by pupation and adult emergence.

As indicated in table 4, Horsfall found coarctate larvae from September to the following May and pupae from May to June. Although under summer regimes of temperature, larvae may complete feeding and reach the coarctate phase in a month or less, Horsfall reported that larvae completing feeding in October or later over-wintered in the first grub

TABLE 4  
Normal Seasonal History of *Epicauta*  
"lemniscata"<sup>a</sup> in Arkansas  
(Adapted from Horsfall, 1943, table 19.)

Month	Stage, Phase, and Instar <sup>b</sup>
January	FG <sub>5</sub> , C <sub>6</sub>
February	FG <sub>5</sub> , C <sub>6</sub>
March	FG <sub>5</sub> , C <sub>6</sub>
April	C <sub>6</sub> , SG <sub>7</sub>
May	C <sub>6</sub> , SG <sub>7</sub> , P
June	C <sub>6</sub> , SG <sub>7</sub> , P, A, E
July	C <sub>6</sub> , SG <sub>7</sub> , P, A, E, T <sub>1</sub> , FG <sub>2-3</sub>
August	SG <sub>7</sub> , P, A, E, T <sub>1</sub> , FG <sub>2-5</sub> , C <sub>6</sub>
September	A, E, T <sub>1</sub> , FG <sub>2-5</sub> , C <sub>6</sub>
October	A, FG <sub>3-5</sub> , C <sub>6</sub>
November	FG <sub>5</sub> , C <sub>6</sub>
December	FG <sub>5</sub> , C <sub>6</sub>

<sup>a</sup>*Epicauta vittata*, *E. occidentalis*, or both.

<sup>b</sup>Larval phases are triungulin (T), first grub (FG), coarctate (C), and second grub (SG); instars are designated by subscripts. P, A, and E designate the pupal, adult, and egg stages, respectively.

phase (table 4). The table does not indicate over-wintering in instars before the fifth, but it is known that *E. pennsylvanica* (DeGeer) can over-winter in any of the first six instars (Horsfall, 1943) and it is probable that the same is true of species of the Vittata Group.

Adopting the symbols of phases used in table 4, the extended life cycle just described for the Vittata Group may be represented as T-FG-C<sub>(diapause)</sub>-SG-P-A. The two alternate patterns of development mentioned, leading to completion of the first generation in a single season, may be represented as T-FG-P-A and T-FG-C<sub>(nondiapause)</sub>-SG-P-A, respectively.

Both Ingram and Douglas (1932) and Horsfall (1943) associated the occurrence of the pattern T-FG-P-A with midsummer conditions, and Horsfall specifically implicated high temperature. In an experimental study of *E. segmenta*, a member of the Albida Group, Selander and Weddle (1969) demonstrated that high temperature in instar FG<sub>5</sub> induces this abbreviated pattern. Subsequent studies in our laboratory indicate that thermal induction of the pattern is possible in a wide variety of species of *Epicauta*, including *E. vittata*, *E. occidentalis*, and several other members of the Vittata Group. According to Horsfall, larvae of *E.*

"*lemniscata*" following the abbreviated pattern in Arkansas appear as adults in mid- and late-August or later and give rise to an incomplete second generation which over-winters in the FG or C phase. Information given by Ingram and Douglas for *E. occidentalis* in Louisiana suggests that second generation adults may emerge as early as July and third generation adults by September.

The second alternate pattern of development, in which the coarctate larva does not diapause, was recorded by Gilbertson and Horsfall (1940) in "a few cases" in rearings of *E. "lemniscata"* in South Dakota. In these cases, ecdysis to the SG phase occurred in five to eight days and presumably was followed by pupation and adult emergence, without further delay. In our rearings, this particular pattern was recorded for all taxa of the Vittata Group with the exception of *E. abadona* and *E. leopardina*. As a general rule, however, the duration of the coarctate phase was considerably longer than that reported by Gilbertson and Horsfall. Further, in several of the taxa the pattern occurred as commonly as, or even more commonly than, the pattern T-FG-P-A.

## ECONOMIC IMPORTANCE

### DAMAGE TO CULTIVATED PLANTS

Species of the Vittata Group have a long history as pests of garden and field crops in the United States, Mexico, and Argentina. Damage to potatoes, tomatoes, and alfalfa is most commonly mentioned in the literature, but soybeans, sugar beets, cotton, and a variety of truck crops and garden vegetables are also attacked. An inventory of food plants of species of the group is given in the section on Feeding Behavior.

All three of the species occurring in the United States (*E. vittata*, *E. occidentalis*, and *E. temexa*) are of economic importance. In South America the species of primary importance as pests are *Epicauta monachica* and *E. leopardina* (Bosq, 1934, 1943; Hayward, 1942, 1960).

In what is perhaps one of the earliest papers on economic entomology in the United States, Chapman (1799) reported damage to potatoes, beets, and purslane in gardens in Pennsylvania

by adults of *E. vittata*. Two years later Fabricius (1801), who seldom included ecological information in his works, noted for *E. vittata*: "Habitat in Americae Solano tuberoso folia depascens, destruens."

According to Forbes (1905) and others, striped blister beetles were known in the United States as "old-fashioned potato bugs" or "long Johns." Referring perhaps to *E. vittata*, Sanborn (1916) said that "before the advent of the Colorado potato beetle this bug ranked first in the wholesale destruction of potato vines." Among the many other reports of damage to economic plants by *E. vittata* are those of Forbes (1886), Claypole (1880), Hamilton (1895), Forbes and Hart (1900), Blatchley (1910), Watson (1917), Davis (1926), Mutchler and Weiss (1924), Brimley (1938), Milliron (1958), and Kirk (1969, 1970). Reports of damage by *E. occidentalis* are those of Ingram and Douglas (1932), Douglas (1935), and Dillon (1952). Reports by Calvino, Ramírez, and Inda (1920) and Hernández (1960) apply to *E. temexa*. Those of Sanderson (1905), an anonymous author (1908), Swenk (1913), Bruner (1916), Baerg (1925), Gilbertson and Horsfall (1940), Fenton and Howell (1957), Smith and Franklin (1961), Maxwell, Lefever, and Jenkins (1965), and Murray, Verhalen, and Bryan (1965) refer to *E. vittata* or *E. occidentalis* or both.

A review of the economic literature gives the distinct impression that striped blister beetles are of less importance as pests than they were until perhaps the 1940s. Presumably this reflects a decline in population size from a height reached during the dust bowl days of the 1930s in the Midwest, the advent of modern insecticides, and decreased interest in gardening. It is our experience, in Illinois, that *E. pestifera* (Werner) is now a commoner and more troublesome pest of potatoes and tomatoes than is either *E. vittata* or *E. occidentalis*.

### CONTROL MEASURES

In earlier, simpler times, control of striped blister beetles involved burning them while they are on foliage with a torch or kerosene soaked rag (Ingram, 1927), knocking them into buckets containing water and kerosene, or driv-

ing them from fields or into piles of straw or trenches where they were then burned (Chittenden, 1911; Baerg, 1925; Ingram, 1927).

Among the various insecticides used or tested against striped blister beetles are several arsenic compounds (Baerg, 1925; Ingram, 1927), calcium cyanide and pyrocide (Smith and Franklin, 1961), sodium and barium fluosilicate (Baerg, 1925; Ingram, 1927; Swingle and Mayer, 1944), rotenone (Horsfall, 1942), sabadilla (Dorman, 1946), and semicarbazones (Gertler, 1946). Ingram (1927) noted that when sodium fluosilicate was dusted on plants, "the beetles die, not from eating poisoned foliage, but from getting the poison on their feet and then raking the feet through the mouth to get the irritating stuff off." A similar observation was made by Horsfall (1942).

More recently, DDT has often been used in the control of species of the Vittata Group and other blister beetles. Currently, carbaryl, marketed under the tradename Sevin, is recommended for use as a dust or spray.

Finally, it is perhaps worth noting that Brett (1946) found that an extract of indigobush (*Amorpha fruticosa*) had insecticidal properties when dusted on lettuce leaves given to striped blister beetles as food.

#### PREDATION ON GRASSHOPPER EGGS

Although no formal study of the economic importance of blister beetles as predators of grasshopper eggs has been undertaken, one would suppose that larvae of species of *Epicauta* commonly attacking grasshoppers that attack crops are perhaps, on the whole, beneficial. Several authors have noted a correlation between the sizes of populations of grasshoppers and blister beetles of the Vittata Group (Swenk, 1913; Whelen, 1939).

Riley (1877) recorded the grasshoppers *Melanoplus differentialis*, *M. femur-rubrum*, *M. atlantis*, and *Oedipoda sulphurea* as larval hosts of striped blister beetles (presumably *E. vittata*) in Missouri. Horsfall (1943) stated *Melanoplus differentialis* and *M. bivittatus* are the preferred hosts of striped blister beetles in Arkansas.

#### MEDICAL IMPORTANCE

Adults of the Vittata Group, like those of many other meloids, may be a nuisance because, when crushed or rubbed on the skin, they are capable of producing blisters. This well-known property of meloids is due to the presence of cantharidin in the hemolymph.

As early as 1799, Chapman reported on the use of dried, powdered adults of *E. vittata* in plasters for the treatment of various diseases and suggested that beetles of this species could serve as a replacement for the commercial Spanish Fly [*Lytta vesicatoria* (Linnaeus)]. Saunders (1976) found adults of *E. vittata* to be fully equal to the Spanish Fly as a vesicant.

In South America, *E. leopardina* is said to be able to kill grazing animals in pastures by producing lesions in their throats (Bosq, 1943).

#### POSSIBLE TRANSMISSION OF PLANT DISEASES

Wolf (1916) found 27 conidia of the peanut leaf spot [*Cercospora personata* (B. & C.)]. Ellis in two fecal "discharges" of adults of striped blister beetles in Alabama. In greenhouse tests in Mississippi, striped blister beetles were implicated as possible vectors of bean pod mottle virus, a disease of soybeans (Anon., 1971).

#### NONREPRODUCTIVE BEHAVIOR

##### BEHAVIOR OF NEWLY EMERGED ADULTS

In our rearings of the species of the Vittata Group, adults emerged from pupae that had formed in cells excavated by last-instar larvae in a moist mixture of sand and soil in glass tubes. Almost invariably the cells were visible through the sides of the tubes, and the emergence of the adults and their subsequent behavior were easily observed. As they reached the adult stage, individuals were transferred, still in their tubes, to a room used for the maintenance of adults, as described in the section on Materials and Methods. Here the cotton plugs were removed from the tubes and the tubes were placed in separate cages of type C with food.

The course of events from shedding of the pupal skin to the first expression of sexual be-

havior closely parallels that described for species of the Albida Group of *Epicauta* (Selander and Mathieu, 1969), but adults of the Vittata Group are more precocious. Under the same physical conditions provided adults in the present study, those of the Albida Group generally rested for three or four days following emergence. During this time they were capable of walking but were reluctant to do so and seemed ill-coordinated. Feeding began at the adult age of four to six days. Sexual behavior first appeared at a mean age of about 10 days.

In the Vittata Group there was no distinctive resting behavior except for the first few hours of adult life, during which time full coloration was attained. Even without our assistance, adults usually dug out of their cells on the day of emergence from the pupa or on the following day. Once out they were immediately capable of walking, grooming, and defensive behavior. Mean age at first feeding was three days (unweighted mean of taxa means), with an overall range of one to seven days. One male of *E. vittata* courted and copulated on the day that it attained the adult stage, and another male of that species did so at the age of only two days. Otherwise, the minimum age of males at first courtship was six days, with a mean of taxa means of about eight days. Detailed analysis of data on the ontogeny of sexual behavior, presented elsewhere, indicates that males are generally capable of copulating when courtship is first displayed.

For 230 reared adults of the Vittata Group we recorded adult age at deposition of the meconium and at first feeding. The two variables are very highly correlated. As a general rule the deposition of the meconium occurs a few hours to a day before feeding begins; exceptionally it precedes feeding by as much as two days. In no case did we record feeding before deposition of the meconium.

The data on age of adults at first feeding are summarized in table 5. These data were analyzed by fitting a multiple regression model incorporating terms for taxa, sex, and the interaction of taxa and sex (table 6). Relatively little of the variation is explained by the model (about 16%), due in part to the coarse scale of

measurement used (days). In this connection, we recognize that the total range (one to seven days) is somewhat smaller than a desirable minimum for application of statistical procedures involving the assumption of continuity.

There is no reliable indication of interaction or a main effect of sex (table 6). However, the taxa factor is highly significant. Among the standard contrasts of taxa, that between *E. vittata* (typical race) and *E. occidentalis* is highly significant ( $F_{1,208} = 15.35^{****}$ ). Reference to table 5 shows that, on the average, adults of *E. occidentalis* required about a day longer to begin feeding than did those of *E. vittata* (typical race). None of the other contrasts reaches the 5 percent level of significance.

TABLE 5  
Age (Days) of Reared Adults at which Feeding First Occurred

Species	Mean	SE	N
<i>E. vittata</i>			
Typical race	2.3	0.13	26
Lemniscate race	2.9	0.19	15
<i>E. occidentalis</i>	3.4	0.23	24
<i>E. temexa</i>	3.2	0.20	43
<i>E. abadona</i>	3.5	0.34	6
<i>E. tamara</i>	3.1	0.22	16
<i>E. vitticollis</i>	3.5	0.24	17
<i>E. unilineata</i>	3.0	0.42	8
<i>E. monachica</i>	2.7	0.15	33
<i>E. luteolineata</i>	2.4	0.14	29
<i>E. leopardina</i>	3.0	0.32	13
Mean (unweighted)	3.00	—	—

TABLE 6  
Analysis of Variance of Multiple Regression Model for Age (Days) of Reared Adults at which Feeding First Occurred  
(Data summarized in table 5.)

Source	df	MS
Taxa	10	3.62****
Sex	1	2.17
Interaction	10	0.66
Residual	208	0.99
$R^2 = 0.156$	—	—

### DIEL PATTERNING OF ACTIVITY

In the laboratory, under relatively constant conditions of temperature and humidity, we found no evidence of diel periodicity in adult behavior in any of the species of the group studied with the exception of *E. apure*, adults of which shunned bright lights, such as those used in taking motion pictures of behavior, and were definitely more active in semidarkness and darkness than in daylight or under "normal" levels of room illumination.

In nature a rather marked diel periodicity of adult activity is commonly observed, presumably in response largely to varying conditions of heat and humidity.

In hot, arid areas, such as southern Texas, western Mexico, and northern Argentina, we found that adults tend to remain on or near the ground, under dense foliage for the greater part of the day. Similar observations, apparently of mixed populations of *E. vittata* and *E. occidentalis*, were reported by Swenk (1913). Gilbertson and Horsfall (1940), and Horsfall (1942), who stated that adults "huddled" in the shade in alfalfa fields during the "heat of the day," in very dense aggregations. In cooler, less arid areas, such as the eastern United States, adults appear to be equally active day and night, but even in these areas they tend to occur most commonly on plants that are at least partially shaded.

In southern Texas, in particular, we had difficulty collecting adults of *E. temexa* and *E. occidentalis* in the day, even at localities where they swarmed at lights in large numbers at night. Some of the most effective collecting was done by locating patches of *Amaranthus* or *Solanum* under street or farm lights during the day and returning at night, at which time the beetles crawl to the top of the vegetation to feed and carry on other activities. It was possible, of course, to find adults in these patches during the day, but only with difficulty, since they remained near the ground and were relatively inactive.

In Santiago del Estero, over a period of about three weeks, we seldom found an adult of any species of the group feeding in an exposed situation in the daytime. Rather, we learned to look for them in masses of dense,

recumbent foliage, especially in low areas where local seepage or drainage kept the soil moist. On one occasion, near Las Termas, our attention was attracted to extensive defoliation of *Amaranthus* plants along a roadside gully. Recognizing the damage as being caused by meloids, we examined the plants carefully but could find no beetles. Subsequently we began turning over mats of *Portulaca* growing under and alongside the *Amaranthus* and found literally hundreds of adults of *E. monachica*. Since there was little evidence of feeding on the *Portulaca*, we surmised that the beetles were using this plant for shelter from the sun.

It is perhaps worth mentioning that, in general, the behavior of adults of the Vittata Group that are "attracted" to light at night differs strikingly from that of typical nocturnal meloids. The latter are often initially hyperactive and apparently disoriented, as though "dazzled" by the light; subsequently they become still and, as though mesmerized, may remain motionless for hours at a time. In contrast, adults of the Vittata Group usually behave quite normally in such situations. Feeding behavior, grooming, and flight are not inhibited or disrupted and, in fact, courtship and copulation may occur.

### GROOMING BEHAVIOR

We have verified that adults of all species studied clean the antennae with the forelegs, in the manner described as typical for the genus *Epicauta* by Selander and Mathieu (1969).

### GREGARIOUSNESS

In a family of Coleoptera noted for gregarious behavior, the Vittata Group is noteworthy with respect both to the sheer number of beetles that may assemble and the great density in which they commonly occur. In regions where two or more species are found, swarms are usually heterospecific. For example, in southern Illinois on July 8, 1972, we sampled large aggregations of adults on *Amaranthus* in soybean fields at Goreville and a few miles away at Golconda. Both swarms contained *E. vittata* and *E. occidentalis*. At the Goreville site we collected 217 beetles, 29 percent of



which were *E. vittata*; at Golconda we took 92 beetles, 88 percent of which were *E. vittata*.

Associated with, and presumably facilitating, their highly developed gregarious behavior, adults of the group are remarkably tolerant of each other in individual encounters. This tolerance seemingly extends to individuals of related species as well as to conspecifics. Threats or actual attacks were seldom observed, even under severely crowded conditions, except in *E. leopardina*. But even this species is less antagonistic than the majority of species of *Epicauta* that we have studied.

Part of the notoriety that various of the species of the group have attained as pests of crops and garden plants stems from the fact that, by gathering in large swarms, the beetles rapidly produce severe damage in local areas. Swenk (1913), referring probably to mixed populations of *E. vittata* and *E. occidentalis*, reported that one of his correspondents, near Dakota City [Nebraska], had found "five rows of his field [of potatoes] . . . completely stripped for a distance of 100 feet and each hill had 50-300 beetles working on it." Swenk also reported extensive damage to alfalfa in several Nebraskan counties in July 1911 by swarms containing many thousands of beetles. These swarms, which individually covered an area from a square foot to "dozens" of square feet, each "moved slowly along in a solid body, attacking first the alfalfa blossoms and later often stripping the plants of their leaves and leaving only the bare stems. . . . After the alfalfa was cut the beetles would collect for a time in piles on the ground in some places a couple of inches deep, and later would disperse by flying or crawling to new feeding grounds." Horsfall (1942), in Arkansas, found alfalfa fields to be assembly centers for large adult swarms. His report presumably applies to *E. vittata*, *E. occidentalis*, or both.

Blatchley (1910) gave an entertaining account of an experience of his father, H.S. Blatchley, with a large swarm of *E. vittata* in a potato garden in Indiana:

On one occasion, after sprinkling with London purple and trampling and mashing five bushels, more or less, of the beetles into the ground, he wrote of his experience as follows: 'On the next day, for every

one that had been killed a dozen had come to their funerals. A dashing rain having washed the poison from the vines, the bugs went for them again and not until after they had devoured the last leaf and sucked the juice from the stalks did they leave for greener pastures. I have heard some people hint, in a sly kind of way, as though they were fearful of offending some august personage, that these blister beetles were the devil's own.'

#### FEEDING BEHAVIOR

Adults of the species of the Vittata Group are primarily leaf feeders. They generally begin chewing on the edges of leaves and tend to feed systematically and persistently, leaving only the larger leaf veins.

As indicated elsewhere, mean age of adults at first feeding was three days among reared adults in the laboratory. Once feeding behavior had developed, adults fed every day of their adult lives. This pattern differs from that of the Albida Group, where females generally did not feed for one or two days before ovipositing (Selander and Mathieu, 1969).

Because of their highly developed gregarious behavior, it is not uncommon to find swarms of beetles attacking and defoliating one or a few plants while nearby plants of the same species remain untouched. If no other food is available, the beetles will chew on succulent stems. In addition, they attack the flowers and fruits of several plants.

The literature contains relatively few references to feeding on flowers or floral parts. Reports of one or more species feeding on corn silk (Forbes, 1905; Milliron, 1958), rice pollen (Ingram, 1927), cotton flowers (Sanderson, 1905), and alfalfa flowers (Swenk, 1913; Smith and Franklin, 1961) have already been mentioned. Damage to flowers of Compositae in gardens was reported by Blatchley (1910), referring to *E. vittata*, and by Gilbertson and Horsfall (1940), referring to *E. vittata* or *E. occidentalis* or both. According to the latter work, plants of the genus *Calendula* are especially favored.

In our experience, adults of the group are not particularly attracted to flowers. However, both Swenk and Smith and Franklin indicated that the flowers of alfalfa are preferred over the

leaves. In addition, in the case of the milkweed *Asclepias incarnata* (= *pulchra*), it appears that the flowers, but not the leaves, are acceptable to adults of *E. vittata*. Feeding on flowers of this plant was first recorded by Weiss and Dickerson (1921) and subsequently verified by Robertson (1929), who reportedly observed the behavior frequently. Yet in feeding-choice tests in our laboratory, adults of both *E. vittata* and *E. occidentalis* consistently ignored *A. incarnata* leaf samples offered along with those of *Amaranthus retroflexus* (see below). Moreover, in a further test in which groups of about 50 adults of each of these blister beetles were given only leaves of the *Asclepias* for a period of 24 hours, there was no feeding. Unfortunately, we were unable to run tests with flowers of the *Asclepias*. As an interesting sidelight, we note that adults of both *E. vittata* and *E. occidentalis* readily accepted leaves of another species of Asclepiadaceae, *Ampelamus albidus*, offered them in the laboratory.

Newly formed fruits of Leguminosae (*Medicago sativa*) and ripe fruits of Solanaceae are also eaten by adults of the Vittata Group. We have seen photographs of adults of *E. vittata* eating tomato fruits in a garden, and adults of all the species studied commonly ate the mature fruits of *Solanum dulcamara* in the laboratory. On one occasion we supplemented the daily feeding of several species of the group with thin slices of potato tuber and found that they were generally acceptable. We mention this as a possible means of maintaining adults temporarily when other food is not available.

**INVENTORY OF RECORDED FOOD PLANTS:** On the basis of records from the literature, labels on specimens in museums, and our own field and laboratory work, we have compiled a list of nearly 70 species of angiosperm plants on which adults of species of the Vittata Group are known or reported to feed (table 7). According to the classification of Benson (1959), these represent some 55 genera, 23 families, and 16 orders. All but four of the families (Alismaceae, Liliaceae, Cyperaceae, and Gramineae) are dicotyledonous. Three of the species included in the list have not been recorded as food plants in nature but were readily accepted by adults of at least one of the species of the group in the laboratory and are included for

this reason. These are *Froehlichia campestris* and *Stellaria* sp., eaten by adults of *E. vittata*, and *Ampelamus albidus*, eaten by adults of both *E. vittata* and *E. occidentalis*.

As the information presented in table 7 attests, the species of the Vittata Group are quite opportunistic with respect to selection of food plants, each having a broad range of acceptable food items. Marked differences in the number and variety of recorded food plants among species of the group are evident but are very likely attributable to differences in the intensity of sampling in various parts of the New World.

In terms of number of records, the most important families of plants are Amaranthaceae, Solanaceae, and Leguminosae. The most commonly recorded genera are *Amaranthus*, *Solanum*, and *Medicago*. All three genera occur over the entire range of the Vittata Group and are typically well represented in the cultivated field edges and other weedy places where the beetles tend to congregate. In our experience, *Amaranthus* is utilized as a food source much more frequently than either *Solanum* or *Medicago* by adults of *Epicauta vittata* (both races), *E. occidentalis*, and *E. temexa*. In the state of Veracruz, Mexico, we found *E. vitticollis* and *E. unilineata* only on *Amaranthus*. In Santiago del Estero, Argentina, *E. monachica*, *E. luteolineata*, and *E. leopardina* adults in confinement ate leaves of *Amaranthus*, *Solanum*, and *Portulaca* readily, with a definite preference for the first two genera. In the field, *E. monachica* was recorded several times on *Amaranthus* and *Portulaca* but never on *Solanum*. *Epicauta leopardina* was recorded on all three genera as well as on *Chenopodium*. *Epicauta luteolineata* was found at only one locality (La Banda), where a few individuals were feeding on *Solanum* at night. Although we did not record any of the South American species from *Medicago*, there are literature records of both *E. monachica* and *E. luteolineata* damaging *M. sativa*.

**FOOD PLANT PREFERENCES:** It is difficult, of course, to detect real food plant preferences from casual field observations such as those just described or from information associated with material in the museum. In particular, differences in abundance, conspicuousness, and seasonality may confuse the picture, not to





TABLE 7 — (Continued)

Plants	<i>Epicauta</i> Taxa <sup>a</sup>										
	<i>vittata</i> (typical race)	<i>vittata</i> (lemniscate race)	<i>occidentalis</i>	<i>temexa</i>	<i>abadona</i>	<i>tamaru</i>	<i>vitticollis</i>	<i>unilineata</i>	<i>monachica</i>	<i>luteolineata</i>	<i>leopardina</i>
Compositae <sup>c</sup>											
<i>Cichorium endivia</i>	—	—	—	—	—	—	—	—	—	F	F
<i>Solidago</i> sp.	F	—	—	—	—	—	—	—	—	—	—
Salicaceae											
<i>Salix</i> sp.	F	—	—	—	—	—	—	—	—	—	—
Alismaceae											
<i>Sagittaria</i> sp.	F	—	—	—	—	—	—	—	—	—	—
Liliaceae											
<i>Asparagus officinalis</i>	—	F	—	—	—	—	—	—	—	—	—
Cyperaceae											
"Small, fine sedge" <sup>d</sup>	—	—	F	—	—	—	—	—	—	—	—
Gramineae											
<i>Oryza sativa</i>	—	—	F	—	—	—	—	—	—	—	—
<i>Zea mays</i>	F	—	F	—	—	—	—	—	—	—	—
<i>Undet.</i> sp.	F	—	—	—	—	—	—	—	—	—	—

<sup>a</sup>F indicates feeding recorded in the field, L feeding recorded in the laboratory, and an asterisk (\*), a negative feeding response in a laboratory test.

<sup>b</sup>Negative response in a choice test.

<sup>c</sup>*Calendula* sp. (flowers) recorded for "*E. lemniscata*" (= *E. vittata* or *E. occidentalis* or, possibly, both) by Gilbertson and Horsfall (1940).

<sup>d</sup>Ingram (1927).

mention the bias introduced by the entomologist's special interest in plants of economic importance. Fortunately, several authors have made systematic observations of feeding behavior in the field or have carried out experiments relating to food plant selection by members of the Vittata Group.

INFORMATION IN THE LITERATURE: In recording the lemniscate race of *E. vittata* (as *E. lemniscata*) from several garden crops at Miami, Florida, Chittenden (1903) noted that "beet tops were the favorite food, preferred to all others." Preferential feeding on beets was mentioned earlier by Chapman (1799), referring to the typical race of *E. vittata*. Another observation by Chittenden (1911) indicates a decided

fondness for *Amaranthus* by adults of typical *E. vittata*. He found them almost completely defoliating *Amaranthus retroflexus* but "scarcely touching other plants occurring in their line of march."

A particularly striking example of preferential feeding by *E. occidentalis* (reported as *E. lemniscata*) was described by Douglas (1935). In 1933, at the Rice Experimental Station at Crowley, Louisiana, beetles defoliated an experimental row of *Crotalaria intermedia* and then moved to a nearby planting of soybeans, completely ignoring an adjacent row of *C. spectabilis* plants.

Three studies indicate that certain cultivated varieties of plants are more attractive to adults

of *Epicauta vittata* than are others of the wild "variety." Murray, Verhalen, and Bryan (1965) reported that *E. vittata*, which "does not normally attack cotton," appeared in heavy infestation on a glandless variety of cotton in Oklahoma in 1964. The beetles defoliated the glandless variety across three replications of field plots in which that variety and a "related glanded check variety" were planted side by side, without harming the glanded variety. Strong preference for the glandless variety was verified in tests in which beetles were introduced into cages over three-foot sections of rows of glandless and glanded cotton plants. That the glanded variety either had little or no attraction for the beetles or was actually repulsive was shown by the fact that when beetles were given only the glanded variety, there was "no appreciable feeding" on it even after 72 hours.

Preference for glandless varieties of cotton was also reported by Maxwell, Lefever, and Jenkins (1965) for "*Epicauta vittata*" in Mississippi. Unfortunately, none of the beetles was preserved, and it is impossible to say whether the observations refer to *E. vittata* (typical race) or *E. occidentalis* or both. Thousands of adult beetles migrated into cotton from nearby fence- and turn-rows and stripped the lower leaves of glandless cotton varieties Acala 4-42-77 and Rex Smooth Leaf. Subsequently the beetles moved through plantings of glanded varieties of Acala 4-42-77, Rex Smooth, and Deltapine Smooth Leaf without damaging them. The authors noted that the beetles attack cotton only when deprived of suitable food around cotton fields. In a later study, Clark et al. (1972) found a few differences among commercial "cultivars" of cotton with respect to the amount of damage produced by field-caught beetles confined with test plots for several days. Again, the specific identity of the beetles is questionable.

The chemical basis of selection of commercial varieties of sweet clover (*Melilotus*) by adults of the typical race of *Epicauta vittata* was investigated in an interesting study by Gorz, Haskins, and Manglitz (1972). These authors recorded *E. vittata* as one of four species of the genus *Epicauta* feeding preferen-

tially in Nebraska on plants of the genus *Melilotus* containing relatively low concentrations of coumarin and related compounds. Laboratory feeding experiments with adults of *E. vittata* utilized four genotypes of *Melilotus alba* differing in content of *o*-hydroxycinnamic acid (*o*-HCA) and  $\beta$ -glucosidase, which is necessary for the conversion of *cis*-*o*-HCA to coumarin. Test beetles were obtained from low-coumarin plants in the field. Plants with low *o*-HCA concentration suffered complete defoliation in the experiments, while those with high concentration were largely or completely ignored. The presence of  $\beta$ -glucosidase resulted in slightly improved protection (0% versus 3% defoliation) in the presence of high levels of *o*-HCA, indicating that coumarin itself has a deterrent effect on feeding. Similar results were obtained in experiments with other species of *Epicauta*. Additionally, it was determined that for at least *Epicauta pestifera*, it is only the *cis* form that is responsible for the deterrent effect of *o*-HCA.

**LABORATORY TESTS DURING THIS STUDY:** In the course of this study we carried out a series of formal food-choice tests, utilizing field-caught adults of several species, as described in the section on Materials and Methods. These tests were undertaken primarily to detect possible differences in feeding behavior between *Epicauta vittata* and *E. occidentalis*. In three of them we were able to incorporate adults of *E. temexa* as well; in addition, we tested all three of the South American species simultaneously for preference between *Solanum tuberosum* and *Lycopersicum esculentum*.

The results of the tests, insofar as *E. vittata* and *E. occidentalis* are concerned, are given in table 8. In the first series of tests, there are two cases (i.e., *Amaranthus* versus *Passiflora* and *Amaranthus* versus *Solanum tuberosum*) in which a preference for one of the choices is statistically significant for *E. vittata* but not for *E. occidentalis*. However, in no case in this or any of the other test series were the responses of the two species different enough that a test of independence of meloid and plant species yields significance at the 5 percent level or less.

Taken together, the data for the first test

series suggest that *Solanum*, *Lycopersicum*, *Passiflora*, and perhaps *Medicago* are preferred to *Amaranthus* and that the latter is preferred to *Glycine*, *Chenopodium*, and *Asclepias*. *Ampelamus* and *Datura* appear to be about as attractive as *Amaranthus*.

In the second series, comparing *Lycopersicum* with two species of *Solanum* and with *Glycine*, the only statistically significant finding is the decided preference for *Lycopersicum* over *Glycine* by adults of both *E. vittata* and *E. occidentalis*.

With respect to the attractiveness of *Glycine* as a food source for adults of these species, the results of the feeding-choice tests just described are supported by the fact that we have found

adults of both species feeding on *Amaranthus*, *Passiflora*, and *Solanum* in and around soybean fields on many occasions but have seldom seen the beetles attacking soybeans themselves. As already noted, however, there is no doubt but adults of both species sometimes feed on soybeans in large numbers and may become serious localized pests of that crop.

In feeding-choice tests of *Solanum dulcamara* versus *Portulaca*, *Petunia*, and *Digitaria*, *Portulaca* was nearly or entirely ignored by both *E. vittata* and *E. occidentalis* and crabgrass (*Digitaria*) completely so. *Petunia* was preferred to the *Solanum* by both species of meloids but not to a significant extent.

In the final test series summarized in table

TABLE 8  
Results of Feeding-choice Tests with Adults of *Epicauta vittata* and *Epicauta picauta occidentalis*

Alternate plant	<i>E. vittata</i>		<i>E. occidentalis</i>	
	N feeding	% preferring test plant <sup>a</sup>	N feeding	% preferring test plant <sup>a</sup>
Test plant: <i>Amaranthus retroflexus</i>				
<i>Passiflora incarnata</i>	23	<u>17</u>	27	37
<i>Chenopodium</i> sp.	48	<u>67</u>	41	<u>80</u>
<i>Ampelamus albidus</i>	18	44	18	39
<i>Asclepias incarnata</i>	17	<u>100</u>	16	<u>100</u>
<i>Datura stramonium</i>	28	61	22	45
<i>Lycopersicum esculentum</i>	59	<u>34</u>	53	<u>28</u>
<i>Solanum tuberosum</i>	48	<u>33</u>	45	38
<i>Glycine max</i>	26	<u>88</u>	19	<u>84</u>
<i>Medicago sativa</i>	16	38	21	43
Test plant: <i>Lycopersicum esculentum</i>				
<i>Solanum dulcamara</i>	29	48	19	63
<i>Solanum tuberosum</i>	56	54	54	63
<i>Glycine max</i>	23	<u>74</u>	57	<u>91</u>
Test plant: <i>Solanum dulcamara</i>				
<i>Portulaca oleracea</i>	28	<u>96</u>	19	<u>100</u>
<i>Petunia</i> sp.	24	29	24	29
<i>Digitaria sanguinalis</i>	29	<u>100</u>	20	<u>100</u>
Test plant: <i>Passiflora incarnata</i>				
<i>Asclepias incarnata</i>	22	<u>100</u>	19	<u>100</u>
<i>Solanum tuberosum</i>	22	68	17	65

<sup>a</sup>Underlining indicates that the probability of outcomes (two-tailed) at least as deviant from a 1:1 ratio as that recorded is less than 5%. For N < 25 exact binomial probabilities were computed; otherwise a goodness-of-fit analysis was made using Pearson's Chi-square as the test statistic.

8, *Asclepias incarnata* leaves were completely ignored (as in the first series of tests), and no clear-cut preference between *Passiflora* and *Solanum tuberosum* was shown.

Besides refusing to eat leaves of *Asclepias* and *Digitaria* in the tests just described, adults of both *E. vittata* and *E. occidentalis* ignored offerings of leaves of *Phaseolus vulgaris*, *Abutilon theophrasti* (Malvaceae), *Plantago rugelii* (Plantaginaceae), and the composites *Ambrosia trifida* and *Cichorium intybus*. The negative results with the *Phaseolus* are of more than passing interest because both *E. vittata* and *E. occidentalis* are recorded as pests of *Phaseolus lunatus*.

The only concrete indication of a difference in food-plant preference between *Epicauta vittata* and *E. occidentalis* obtained in our work resulted from a test in which 10 adults of each of these species were provided with leaves of *Froehlichia campestris*, without other food. At the end of one day we recorded that moderate feeding by *E. vittata* had occurred but none by *E. occidentalis*.

In the three tests involving *Epicauta temexa*, *Amaranthus retroflexus* was tested against *Lycopersicum esculentum*, *Chenopodium* sp., and *Datura stramonium*, respectively. The percentages of beetles preferring *Amaranthus* were 22.2, 57.1, and 100, respectively, with Ns of 9, 7, and 8, respectively. The preference for *Amaranthus* over *Datura* is significant ( $P = 0.016$ ). Comparing the responses of *E. temexa* and *E. occidentalis* (table 7) in these tests, the only significant difference is found in the failure of the former species to eat *Datura* and the lack of preference for *Amaranthus* over *Datura* by *E. occidentalis* ( $X^2_{(1)} = 4.308^*$ ).

In a test of preference for *Solanum tuberosum* or *Lycopersicum esculentum* in which four adults of *E. monachica*, 24 of *E. luteolineata* and 12 of *E. leopardina* fed, the percentages of beetles preferring *Amaranthus* were 50.0, 41.7, and 54.2, respectively. None of these departs significantly from expectation under the hypothesis of no preference.

#### DEFENSIVE BEHAVIOR AND ENEMIES

**DEFENSE:** Adults of the species of the Vittata Group are noticeably less wary than those

of the Albida Group (Selander and Mathieu, 1969) and therefore lend themselves more readily to behavior studies. In our experience, the first response to disturbance is to become immobile. If the disturbance is intensified, they characteristically drop to the ground and run rapidly for several inches to several feet, searching for hiding places, such as clods of earth or leaves in contact with the ground. Several authors, including Claypole (1880), Gilbertson and Horsfall (1940), and Horsfall (1942), have previously called attention to this behavior. If pursued the adults continue to run, and there are accounts of attempts to save gardens from destruction by driving or herding swarms of beetles from them (e.g., Baerg, 1925). In comparison with species of the Albida Group, those of the Vittata Group recover rapidly from disturbance.

We seldom observed "death feigning" by adults even when they were shaken or pinched roughly in a deliberate effort to induce this behavior. Similarly, reflexive bleeding, with or without death feigning, is not a common response to handling. The only literature report of bleeding is that of Dohrn (1876), in reference to *E. zebra*.

All species of the group are capable of flight. We seldom observed flight in the laboratory, presumably because of the relatively low temperature at which the beetles were maintained (25° C.).

**ENEMIES:** There are surprisingly few records of other organisms as enemies of members of the Vittata Group.

Eggs of *E. occidentalis* are attacked by a fungus of the *Aspergillus ochraeus* group and larvae and adults by a fungus tentatively identified as *Borrrytis delacroisii* (Ingram and Douglas, 1932; as *E. lemniscata*).

Four species of araneid spiders are predators of *E. vittata* adults in Ohio (Bilsing, 1920). Beetles were found in 2 percent of 1250 webs of *Argiope aurantia* Lucas (as *A. riparia* Hentz) and in an unspecified number of webs of *Argiope trifasciata* (Forskål), *Araneus trifolium* (Hentz), and *Araneus bicentenarius* (McCook) (as *Epeira gigas* Leach). All four species of spiders also prey on adults of *Epicauta pennsylvanica* (DeGeer), and the species



of *Argiope* capture and eat adults of *E. pestifera* Werner (= *E. marginata*) as well.

Flint (1914) placed an unspecified number of adults of *E. vittata* near a nest of the ant *Lasius niger* and found that the beetles were killed after a "hard struggle."

Forbes (1880) found an unspecified number of adults of *E. vittata* in the stomachs of one or two mocking birds (*Mimus polyglottus*) and one adult in the stomach of a catbird (*M. carolinensis*). Adults of an unidentified species of the Vittata Group (reported as *E. lemniscata*) were found in two of 129 stomachs of the flycatcher *Muscivora forficata* (from unknown localities in the United States and Canada) analyzed by Beal (1912).

Finally, Wilson (1917) reported a large, unidentified asilid fly capturing adults of *E. vittata* in Florida, and Ingram (1927) found the asilid *Dizonias tristis* Walker preying on *E. occidentalis* (as *E. lemniscata*) in Louisiana.

A rare opportunity to observe asilid predation on an adult of *E. leopardina* presented itself in the course of our work in Argentina in 1971. The resulting information is sufficiently interesting and unique to be related in detail.

At 2:30 PM on the afternoon of December 31, at the experimental station of INTA at La Banda, Santiago del Estero, observation cages of *E. leopardina* and another (presently unidentified) species of *Epicauta* were set outside in the shade on a table for observation and filming of sexual behavior. Air temperature was 37½° C.

About 4:35 PM, an asilid male flew up to one of the cages (type B) containing adults of the second species of *Epicauta* and attempted to enter it. The fly then walked about the outside of the cage and several times lunged at adults within it. At 4:40 PM, we removed an adult of *E. leopardina* from its cage and placed it on the table. The fly immediately pounced on the beetle and inserted the beak through the left elytron at its basal third. The fly was then caught, with its prey, and put in a type A cage, where it sat for nearly 15 minutes with its beak inserted in the beetle in the original position.

Early in this period we noted a droplet of liquid issuing from the femoro-tibial joint on two of the beetle's legs, presumably as the

result of reflex bleeding. As time progressed the beetle gradually lowered its antennae. At 4:55 PM the fly moved around a bit. It then grasped the beetle with the forelegs, rapidly rotated the beetle on its long axis 180 degrees, withdrew the beak, and, after turning the beetle end-for-end and rotating 90 degrees to an upside-down position, inserted the beak in the end of the abdomen. In response the beetle moved the antennae and legs rather feebly. After feeding from the end of the abdomen for two minutes, the fly at 4:57 PM grasped the beetle with all six legs, falling on its side as it did so. It then turned the beetle end-for-end again and inserted the beak between the prothorax and mesothorax on one side. At this time the right front leg of the beetle flicked weakly, tapping on the fly's right antenna. The contact did not seem to disturb the fly in the least. This was the last movement that the beetle made; thereafter its antennae were directed loosely backward and its legs hung limply.

Two minutes later at 4:59 PM, the fly began to manipulate the beetle again, this time rolling on its side and grasping the beetle with the fore and middle legs. From this position, and now holding the beetle with its head again posterior and the dorsum facing the fly's venter, the fly inserted the beak between the fourth and fifth abdominal terga; in so doing it pushed the beetle's abdomen sharply downward, away from the elytra. At 5:05 PM the fly assumed a nearly upright posture. A minute later the beetle was turned upside-down and rotated slightly to one side and the beak was inserted in the neck.

At 5:10 PM, 30 minutes after first attacking the beetle, the fly suddenly dropped it and began to clean itself. It first cleaned the forelegs with the mouthparts and then both antennae simultaneously with the forelegs. Next it rubbed the tarsi and tibiae of the forelegs together and then cleaned the front of the head and the beak with the forelegs. The beetle lay on its side, motionless and very limp.

A minute after releasing its prey the fly began to buzz. An adult of the second species of *Epicauta* was then introduced into the cage, but for the first time since its appearance at the table the fly now seemed to be disturbed by our

presence. During the next 15 minutes it periodically cleaned its abdomen and wings, totally ignoring the second beetle, which crawled about the cage.

The fly and the second beetle remained together in the cage overnight. Both were still alive and active at noon the next day, at which time we noted that there was no capture response even when the beetle touched the fly. On the contrary, the fly was quite agitated and repeatedly tried to escape from the cage.

Subsequently we obtained a record of an adult of the same species (as yet unidentified) of asilid capturing an adult of *E. leopardina* in the field in Santiago del Estero.

In the course of these observations we noted with particular interest the fact that the beetle, which seemed to be nearly paralyzed from the outset of the attack, had no time or opportunity to struggle or defend itself, and the fact that the fly seemed completely oblivious of its surroundings before and during the attack. Most impressive of all, however, were the great speed and dexterity with which the fly manipulated its prey and the variety of positions in which the beak was inserted into it. Speaking anthropomorphically, it was obvious that the fly knew the anatomy of blister beetles very well indeed, and we should not be surprised to find that this species of asilid specializes in capturing meloid beetles.

#### ADULT LONGEVITY

Data on the longevity of 90 adult females reared in the laboratory and maintained in the paired situation or under comparable environmental conditions are summarized in table 9. For mated females the unweighted mean of taxa means is 94.1 days. Analysis of variance (table 10) indicates that, on the average, female adult life was significantly shorter in *E. abadona* (70.0 days) than in *E. tamara* (129.0 days) and significantly longer in *E. monachica* (122.4 days) than in *E. luteolineata* (84.6 days). In three species of the Albida Group studied by Selander and Mathieu (1969), no significant interspecific or sexual differences in adult longevity were detected. In 90 individuals of that group, the mean length of adult life was

TABLE 9  
Adult Longevity (Days) of Reared Females of the Vittata Group

Taxa	Mean	SE	Range	N
MATED FEMALES				
<i>E. vittata</i> (typical race)	47.5	9.10	28-72	4
Lemniscate race	74.4	13.42	31-112	5
<i>E. occidentalis</i>	97.0	13.60	60-123	4
<i>E. temexa</i>	90.0	14.29	40-158	7
<i>E. abadona</i>	70.0	10.60	57-91	3
<i>E. tamara</i>	129.0	31.83	14-196	5
<i>E. vitticollis</i>	102.6	22.25	36-154	5
<i>E. unilineata</i>	122.0	10.01	101-147	4
<i>E. monachica</i>	122.4	11.25	37-151	10
<i>E. luteolineata</i>	84.6	12.97	33-133	8
<i>E. leopardina</i>	95.4	9.57	66-116	5
VIRGIN FEMALES				
<i>E. vittata</i> (typical race)	64.0	9.83	38-91	5
<i>E. occidentalis</i>	50.2	6.58	24-79	8
<i>E. temexa</i>	79.4	5.44	55-94	7
<i>E. tamara</i>	112.4	9.20	79-135	5
<i>E. luteolineata</i>	121.2	7.47	97-139	5

TABLE 10  
Analysis of Variance of Adult Longevity of Reared, Mated Females of the Vittata Group (Data summarized in table 9.)

Source	df	MS
Among taxa	10	3031.67*
Typical <i>E. vittata</i> vs lemniscate race	1	1608.02
<i>E. vittata</i> (typical race) vs		
<i>E. occidentalis</i>	1	4900.50
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	124.73
<i>E. abadona</i> vs <i>E. tamara</i>	1	6526.88*
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	836.36
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	6350.40*
<i>E. monachica</i> and <i>E. luteolineata</i>		
vs <i>E. leopardina</i>	1	407.11
Within taxa	49	1430.34

81.0 days (range of 8-181) under conditions similar to those of the paired situation of the present study.

Analysis of longevity in mated and virgin females for the five taxa of the Vittata Group represented by both types of females is given in table 11. Mated females lived longer than vir-

TABLE 11  
**Analysis of Variance of Multiple Regression  
 Model for Adult Longevity for Taxa  
 Represented by both Mated and Virgin Females**  
 (Data summarized in table 9.)

Source	df	MS
Taxa	4	6465.250****
Mating status	1	208.498
Interaction	4	2855.201*
<i>E. vittata</i>	1	605.000
<i>E. occidentalis</i>	1	5828.164*
<i>E. temexa</i>	1	391.039
<i>E. tamara</i>	1	688.904
<i>E. luteolineata</i>	1	4117.195
Residual	48	1039.002

R<sup>2</sup> = 0.435

gins in *E. occidentalis*, *E. temexa*, and *E. tamara*, but virgins lived longer in *E. vittata* (typical race) and *E. luteolineata*. The only significant difference occurs in *E. occidentalis*, where mated females lived nearly twice as long, on the average, as virgin females.

All females in the paired situation and all virgin females in the present study were allowed to live out their adult lives. But it was sometimes convenient or necessary (when food supplies were limited) to kill males after the death of their female partners. As a result, our data for male longevity are truncated. We can, however, compare sexual differences in longevity in some 38 pairs of beetles in which neither sex was killed after the death of its partner.

Sexual differences in these pairs are summarized in table 12. As adults, females lived longer in 25 cases and males longer in only 12 ( $X^2_3 = 3.982^*$ ); in one pair of *E. vittata* (typical race) longevity of the partners were identical. Except in the typical race of *E. vittata*, mean longevity was greater for females than for males in all taxa. Moreover, except in *E. vittata* (typical race) and *E. abadona*, female longevity was greater in at least a majority of pairs representing a taxon. On this basis it would appear that females tend to live longer than males. However, the analysis of variance presented in table 13 fails to support this contention. The model adopted for the analysis

included nine terms for taxa, 28 pairs in taxa, one for sex, and nine for the interaction of taxa and sex. This is a factorial mixed model, with taxa and sex representing fixed, crossed factors and pairs a random factor nested in species. There are no significant effects for taxa, sex, or their interaction. Pairs in taxa is just significant at the 5 percent level. For the present, then, it is questionable whether there are real sexual differences in adult longevity in the Vittata Group.

The only previous estimate of adult longevity in the Vittata Group is Ingram and Douglas's (1932) statement that adults of *E. occidentalis* (as *E. lemniscata*) in Louisiana live 35-50 days in the summer.

TABLE 12  
**Difference (Female Minus Male) in Adult  
 Longevity (Days) of Reared Beetles Paired  
 Sexually**

Taxa	Mean	SE	Range	N
<i>E. vittata</i>				
Typical race	-46.2	25.33	-108-0	4
Lemniscate race	32.3	14.62	13-61	3
<i>E. occidentalis</i>	9.2	16.31	-39-31	4
<i>E. temexa</i>	57.5	20.50	37-78	2
<i>E. abadona</i>	2.0	3.00	-1-5	2
<i>E. tamara</i>	44.2	28.42	7-127	4
<i>E. unilineata</i>	35.0	17.92	-10-69	4
<i>E. monachica</i>	7.7	18.49	-90-61	7
<i>E. luteolineata</i>	16.0	24.80	-43-74	5
<i>E. leopardina</i>	10.0	20.60	-31-34	3

TABLE 13  
**Analysis of Variance of Multiple Regression  
 Model for Adult Longevity of Reared Beetles  
 Paired Sexually**  
 (Data summarized in table 12.)

Source	df	MS
Regression	47	2443.4**
Species	9	3482.3
Pairs in species	28	2386.0*
Sex	1	3965.8
Species × sex	9	1414.0
Residual	28	996.0

R<sup>2</sup> = 0.805

## REPRODUCTIVE BIOLOGY

We consider here sexual behavior (courtship and copulation), oviposition, and the development and hatching of eggs. As mentioned earlier, larval development and other aspects of postembryonic ontogeny will be treated in a separate work, based on extensive experimental rearings of all taxa of the Vittata Group considered in this work.

### COURTSHIP

Sexual behavior in the Vittata Group is readily divided into *courtship*, or the sexually oriented activities of both sexes occurring before the genitalia are coupled, and *copulation*, or behavior during the period of genital coupling. With respect to the organization of sexual behavior, the Vittata Group is typical of Meloinae (Selander, 1964). Males assume the active role in courtship and spend a good proportion of their time in that behavior, which involves repetitive performance of specific, highly stereotyped acts of display. As described in detail later, females become sexually responsive only periodically, with the result that most courtship behavior, both in nature and in the laboratory, does not culminate in copulation. Male courtship display involves touching or stroking of the female with the antennae, mouthparts, and abdomen (including the sclerotized portion of the genitalia) as well as, in some species, the legs. Visual stimulation of the female by the male apparently plays little or no part in the behavioral interaction. Whether the physical contact of the sexes during courtship involves more than tactile stimulation is unknown.

In nature, courtship occurs during both the day and night. In this regard, we note again the unusual fact that, even after having been attracted to lights at night, males of the Vittata Group may perform courtship behavior. Although we did not make a formal study of ecological conditions affecting sexual behavior, we did observe frequently that presence of food is not necessary for its performance and that

neither high intensity or absence of light inhibit courtship or copulatory behavior. Whether there is an element of diel periodicity in this and other behavior, however, remains to be determined.

### DESCRIPTION OF THE BEHAVIOR

In the present section we describe the form of the courtship behavior, with particular attention to differences among taxa. As outlined in the Materials and Methods section, our descriptions are based on extensive observation and filming of both field-caught and reared beetles. As far as we have been able to determine, there is no difference in the behavior of adults from these two sources. In subsequent sections we treat the patterning of courtship behavior during adult life, largely from a quantitative viewpoint, and present the results of observations and tests of heterospecific sexual behavior.

### MALE COURTSHIP BEHAVIOR

If one releases females of a species of the Vittata Group in a cage containing conspecific males, there is an almost immediate increase in the incidence of male antennal waving, head turning, and walking, even though the females may not be visible to the males. Similar behavior has been noted in other Meloidae (Selander, 1964; Selander and Mathieu, 1969; Pinto and Selander, 1970). In several species of other groups of *Epicauta* it has been demonstrated that males introduced into cages previously containing females or containing air drawn from female cages may be stimulated not only to search for females but also to perform at least part of the male courtship display (Selander, ms). It is therefore likely that olfaction is involved in sexual recognition and stimulation in the Vittata Group. There is, however, no evidence that males are able to locate females by olfactory clues, at least under laboratory conditions. Rather, they appear to depend on random searching. Once within an inch or

two of females they orient on them and approach directly.

**PHASES OF COURTSHIP:** It is convenient to recognize three phases of courtship in the Vittata Group. We will call these the preliminary phase, Phase A, and Phase B. These are comparable to the preliminary, dorsal, and genital phases of courtship in the genus *Meloe*, as defined by Pinto and Selander (1970).

The first or *preliminary phase* of courtship includes orientation on the female and initial positioning of the male with respect to the female. Initial contact with a female may be made from any direction, but almost invariably the male rapidly moves behind her before display begins. In approaching and contacting a female, the male shows little, if any, hesitancy and performs no specific acts suggesting either visual stimulation or, in particular, testing of her responsiveness. Lack of prolonged investigation of the female before display begins is consistent with the general lack of antagonism among conspecific adults of the Vittata Group in nonsexual interactions.

In the course of courtship beyond the preliminary phase, males of all species of the group *extrude* the sclerotized portion of their genitalia and *touch* or push it against the end of the abdomen of the female, at or near her genital opening. This behavior, or *genital presentation*, occurs only periodically in all but one species, periods of presentation alternating with periods in which the genitalia are withdrawn into the abdomen. For periods of courtship in which genital presentation is not performed we will use the term *Phase A* and for those in which it is performed *Phase B*. The distinction is generally useful since alternation of phases is usually associated with marked changes in the form of the male's display or his position with respect to the female or both. Males of *E. tamara* are exceptional in that they attempt to present the genitalia to the female continuously; under the present scheme their display consists entirely of Phase B behavior.

**CHARACTERISTIC POSITIONS AND ACTS:** Description and comparison of male courtship behavior in the taxa of the group require frequent reference to the position of the male with re-

spect to the female and to the form of specific movements or acts of display that occur repetitively. These are defined as follows:

A male is *fully mounted* on a female when positioned above her and contacting (holding) her with all of his legs or (*E. tamara*) bringing, at most, one of the hind legs to the substrate to the side of, or behind, her. He is *partially mounted* when positioned somewhat farther posteriad, and holding her with only the forelegs or the fore and middle legs. Finally, he is *unmounted* when standing behind a female and not contacting her with any of his legs.

In several species whose males present the genitalia while partially mounted, as well as in *E. abadona*, which does so while fully mounted, the head is lowered and pulled in against the prothorax, with the mouthparts directed nearly posteriad. This behavior, or *head tucking*, is associated with, and evidently facilitates, *antennation* (see below). *Head nodding* is rapid, rhythmical forward-and-backward movement of the head. *Palpation* or palpating is the act of repeatedly touching or dabbing the maxillary palpi on the body of the female.

Fully mounted males commonly direct the antennae laterad during Phase A of courtship. In several of the taxa they curve gradually ventrad from near the base and are said to be *drooped*. In the typical race of *E. vittata* they are held in a nearly *horizontal* position, with appreciable curvature only in the distal third or less.

One of the most characteristic features of male courtship behavior in the group is *antennal curling* or marked curvature of the distal third or so of the antennae. Degree of curvature varies with taxa and, evidently, with intensity of stimulation of the male. Males of all species are capable of curling the antennae into at least a semicircle; in some species a full or nearly double circle may be, and commonly is, formed.

We have used *antennation* for any contact, other than accidental touching, of the male's antennae on the female. *Antennal rubbing* is a rapid, not precisely controlled, lashing or stroking of the distal two-thirds of the antennae on the female's head, pronotum, or elytra from a fully mounted position. *Antennal brushing* is a

precisely controlled, side-to-side movement of the antennae on the female, contact being made generally with the entire flagellum. It is performed from a partially mounted position and in Phase B only. The exact form of brushing and its rate vary among taxa; in addition, it may occur either as a prolonged, continuous act or in short, discrete, rapidly repeated bouts. *Antennal tapping* is a controlled, delicate, repetitive touching of the distal third or so of the antennae on the female's elytra or abdomen or both from the unmounted position. A bout of tapping consists of many separate touches, each of momentary duration. The rate at which taps occur is relatively slow in Phase A when the female is not responding negatively; a noticeable increase in rate occurs after movement by a female and at genital presentation. Insofar as possible, males that perform antennal tapping attempt to do so throughout courtship.

There is a high degree of fixity within taxa in the manner in which the forelegs of the male are used to hold the female. In the commonest pattern of behavior, which we will call, simply, *grasping*, the end of the tibia or the first tarsal segment or both are placed on or near the lateral edge of the female's elytron. Generally the remaining tarsal segments do not touch the female, but in some cases the tarsi may be curved around the abdomen. *Foreleg locking* and *clasping* are special forms of holding in *E. vittata* and *E. abadona*, respectively, as described later.

The use of the middle legs in holding the female is generally somewhat less stereotyped than that of the forelegs. In all cases the use of the middle legs fits the pattern described as *grasping* above. The positioning of the hind legs is generally even more variable, depending a great deal on the relative size of the sexes and the nature of the display behavior being performed by the male.

*Hind leg rubbing* is a precisely controlled, forward and backward movement of the male's hind legs on the female's elytra from the fully mounted position. The legs move simultaneously but generally in alternate directions; most or all of the movement results from flexure of the femur. The movement results in scraping of the distal end of the tibia and the

tarsus on the female, except in *E. abadona*, where contact is made with the hind tibial spurs. A single rub is defined as a movement forward and backward of a leg.

*Stretching* is a behavior peculiar to *E. vittata*. While in the fully mounted position the male lifts the head and pushes his body upward, as though tightening his hold (lock) on her with the forelegs. The behavior occurs at irregular intervals and is of short duration.

In order to make genital presentation, as described above, it is necessary for the male to curve the abdomen at least slightly. *Abdominal curvature* is necessarily minimal when performed from the fully mounted position and maximal from the unmounted position. It is important to note that curvature is not synonymous with genital presentation, since partial or complete curvature may occur without genital extrusion, and extrusion may occur during curvature without touching of the genitalia on the female.

*Genital tapping*, as opposed to touching, is an elaborate, vigorous tapping of the genital over the end of the female's abdomen by the male of *E. abadona* in Phase A of courtship (see below).

**BEHAVIORAL PATTERNS:** In contrast to the marked structural homogeneity of the Vittata Group, there are striking interspecific differences in patterns of male courtship behavior. In some groups of Meloidae it is feasible to present a general description of behavior, applicable to the group as a whole, and then to contrast specific patterns rather concisely (e.g., Selander and Mathieu, 1969). In the Vittata Group, however, the fact that males of different species court from different positions makes a general descriptive account of the behavior extremely difficult and unwieldy.

A useful, and perhaps basic, distinction may be made between species of the group in which the male is fully mounted on the female (and does leg rubbing) for at least part of the time in courtship and those in which he either remains unmounted or at most partially mounts her. The first category includes *E. vittata*, *E. abadona*, and *E. tamara*, in which the male is fully mounted in both phases A and B, and *E. temexa*, in which he is fully mounted in Phase A

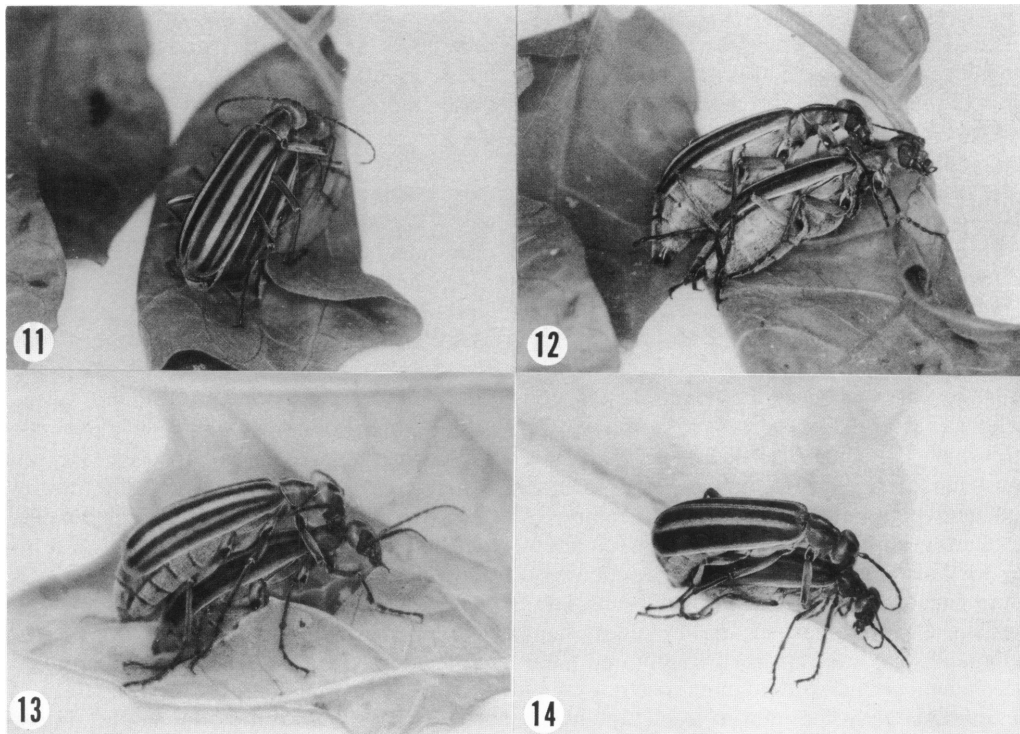
but moves backward to a partially mounted position in Phase B, grasping the female with only the fore and middle legs.

In the species of the second category the male courts in Phase A while standing behind the female in the unmounted position. In *E. leopardina* he moves forward to a partially mounted position in Phase B, grasping the female with the fore and middle legs and thus adopting essentially the same position as in *E. temexa* in that phase. The male of *E. unilineata* also takes a partially mounted position in Phase B but grasps the female with only the forelegs. Finally, in *E. occidentalis*, *E. vitticollis*, *E. monachica*, and *E. luteolineata* the male remains unmounted in Phase B, never grasping the female with any of the legs.

*Epicauta vittata*, Typical Race. Having oriented on a female, the male rapidly takes a position behind her. Usually there is no contact

between the sexes before the male mounts, although occasionally he touches her elytra lightly with his antennae as he approaches her. Once behind the female, the male raises and spreads the forelegs and then rushes forward abruptly (often seeming to leap forward) and takes a fully mounted position on her dorsum. In the mounted position (figs. 11-14), the male holds the female very tightly with the forelegs, which are placed behind her fore coxae in such a way that the distal ends of the male's tibiae are near her ventral midline. Here principal contact is made with the end of the tibia and the first tarsal segment. The tarsi are held straight, not wrapped around her body. This form of holding the female, which we have called foreleg locking, is unique to *E. vittata*.

The positioning of the male's middle and hind legs is somewhat variable. Generally the distal ends of the tibiae touch on the sides of



FIGS. 11-14. Courtship in *Epicauta vittata* (typical race). 11-12. Male fully mounted, with forelegs locked behind fore coxae of female, palpi on her pronotum, and antennae horizontal in position and curved only at tips. 13. Same but male antennae swept backward. 14. Genital presentation and antennal rubbing by male.

the elytra or abdomen of the female and the tarsi are curved to conform to her body. In any case, the fore and middle coxae rest on the female and the abdomen is held nearly straight, not contacting her. Through most of courtship the maxillary palpi and mandibles are pressed on the female's pronotum and the antennae are directed laterad, in the horizontal position already described (fig. 11).

Phase A behavior occupies most of the male's time in courtship. Phase B behavior occurs at irregular intervals and is generally of short duration. Frequently in Phase A the male's antennae are twitched or vibrated and occasionally the position of the middle or hind legs is adjusted in response to movements by the female. In a few instances we noted that males riding on rapidly walking females brought the antennae nearly straight back, paralleling the sides of the head (fig. 13). This behavior evidently helps to protect the antennae; it is, however, seldom performed in this species.

Hind leg rubbing is performed at irregular intervals during Phase A. In cases of especially intense rubbing the middle legs may mimic the rubbing movements of the hind legs. Rubbing with the hind legs occurs in short, rapid bursts and is typically forceful enough to cause the male to shake from side-to-side. It is very likely to occur just after a previously still female moves or, again, just after a female that has been walking comes to a stop. However, the behavior was very commonly observed in situations not associated with evident change in the behavior of the female.

The act of stretching also occurs at irregular intervals in Phase A; commonly it is interspersed with bouts of hind leg rubbing.

In entering Phase B, the male loosens the foreleg lock and moves backward far enough to bring the end of his abdomen even with that of the female. As he does so, he extrudes the genitalia and may touch them lightly on the female. When genital presentation occurs, antennal rubbing may be performed (fig. 14). However, in this taxon it is rarely observed in courtship except in males that have been deprived of females for a few days. That it is, indeed, associated with high level motivation or

intense stimulation of the male is confirmed by the fact that it is frequently performed at the beginning of copulation. In this act the male brings the antennae forward and downward and lashes them along the sides of the female's head. Principal contact is made by the mesal surface of the curved distal third of each antenna.

The duration of Phase B varies from a few seconds to a half-minute or so, apparently as a result of variation in the female's response. Any movement by the female, however subtle, terminates the phase. There is then an immediate, often abrupt, return to Phase A.

*Epicauta vittata*, Lemniscate Race. Courtship in this race is very similar to that of the typical race, but not identical. On the basis of observations and films of what is, admittedly, a rather limited sample of adults, the lemniscate race differs as follows:

Stretching behavior is absent. In the laterad position the antennae are drooped. Hind leg rubbing is less vigorous and occurs in longer bouts. Bouts of antennal rubbing in Phase B occur more frequently and with greater regularity.

*Epicauta abadona*. This species has the most elaborate courtship of any of those studied. This applies to the behavior of both the male and female.

In initiating courtship the male moves behind the female while waving the antennae, which are curled at the ends to form a semicircle. While standing behind her, he rubs the distal ends of his antennae on the sides and dorsum of her abdomen and lightly palpates her abdomen. This behavior may occur for several minutes. In response, the female lifts her elytra partially, opens the end of her abdomen, extends the abdomen greatly, and directs it downward, toward the male's head, and steps backward. The male then usually walks rapidly onto the female; however, he may raise the forelegs and leap on her, as in *E. vittata*.

The fully mounted position taken by the male in Phase A differs in several important respects from that in *E. vittata*. The forelegs are not extended as far forward as in that species. Main contact is made by the single, curved spur of each tibia, which is pressed



against the side of the metathorax. The middle legs are directed back obliquely, so that the distal end of the tibia is near the junction of the second and third visible abdominal sterna. The hind legs show greater fixity of positioning than in other species of the group; they are directed back obliquely, with the end of the tibia touching the female on the lateral edge of the elytron. The tarsi of all legs are held straight and do not contact the female. As in *E. vittata*, the fore and middle coxae rest on the dorsum of the female.

The head is closely appressed to the female and is tucked. The palpi rest on either the pronotum or elytra. The antennae are directed laterad or slightly back (at an angle of at most 20 degrees) and are drooped. Vibration of the antennae is commonly observed, as in *E. vittata*.

Hind leg rubbing is performed more slowly than in *E. vittata* and the rubbing occurs farther forward on the female's elytra. In performing the rubbing the legs are held close against the male's body and the femora are much elevated. Contact with the female's elytra is made by the enlarged, flattened hind tibial spurs of the male.

Bouts of leg rubbing are accompanied by genital tapping. In genital tapping, which is a behavior unique to this species, the genitalia are strongly extended and vibrated in such a way that the tip is tapped rapidly on the abdomen of the female. As tapping occurs the male swings the abdomen from side-to-side, moving the genitalia from the anterior margin of the fifth visible abdominal sternum of the female, over her pygidium, to the other side and then returning.

Genital tapping may lead to genital presentation (see below) or an elaborate, second type of Phase A display. The latter behavior involves marked head nodding by the male, agitated palpation, rapid antennal rubbing on the sides of the thorax and elytra of the female, and continued hind leg rubbing. After a few seconds of this behavior the female raises her head, carefully lays one and then the other of her antennae back, in a parallel position, on her dorsum, and opens her mandibles. The male then lifts the hind legs off the female and di-

rects them upward, balancing on the female with minimal contact and with the antennae and abdomen still. After settling back on the dorsum of the female, the male usually begins hind leg rubbing and genital tapping again.

When Phase B is entered and genital presentation made, the hind leg rubbing continues but is performed at a slower rate than in Phase A. If the male is unsuccessful in establishing genital contact within a few seconds, he resumes hind leg rubbing and genital tapping, in Phase A.

The sequence of activities in the courtship of *E. abadona* is summarized in figure 15.

*Epicauta tamara*. The male usually mounts immediately after positioning himself behind the female, but he may first stand for a second or two with the antennae in a lyre-shaped position and touching the female's abdomen and elytra. In any case, the mount is made much more deliberately than in either *E. vittata* or *E. abadona*.

As the male mounts he performs vigorous head nodding and palpation (fig. 24). In the fully mounted position his head and forelegs are at the level of the basal two-fifths of the female's elytra. The ends of the fore tibiae are placed in a precise grasp on the lateral edges of the female's elytra, with the first tarsal segment on the abdomen just ventrad. The position of the middle and hind legs is variable; the tarsi may or may not conform to the curvature of the female's body.

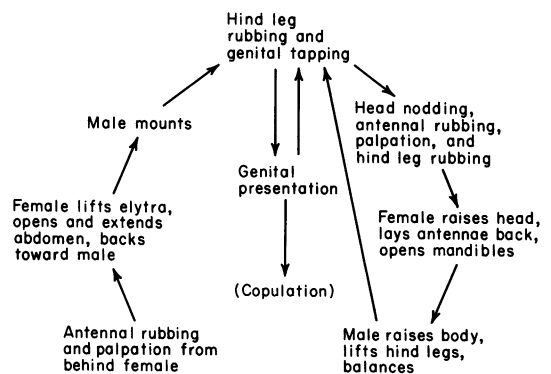


FIG. 15. Sequence of courtship activities in *Epicauta abadona*.

Once mounted, the male does hind leg rubbing, antennal brushing, and genital presentation simultaneously and, unless he is disturbed, continuously. Except for brief interruptions of display in response to movement by the female, all courtship behavior by the male is in Phase B.

Hind leg rubbing involves slower, more deliberate strokes than in the other species that court from the fully mounted position. The grasp is held principally by the end of the tibia and first tarsal segment, but the tarsi are curved under the abdomen and directed forward, where they make extensive contact with the female. As previously mentioned, the male at times may brace himself against the substrate with one of the hind legs; in this case the other leg continues to rub on the female. More commonly, both hind legs remain on the female and are rubbed simultaneously.

Throughout the courtship display, the male's head is tucked (fig. 25), with the maxillary palpi resting on the female. The antennae are directed straight backward, between his forelegs, where they rest on the female's elytra and are weakly curled in the distal third. Antennal brushing from this position is precisely controlled, deliberate, and of moderate speed. Contact is made by the distal third to half of the flagellum. Movement of the first antennal segment produces passive movement of the flagellum, from side-to-side over the elytra and sides of the abdomen of the female.

In dismounting from the female the male performs head nodding and palpation on her elytra, just as he did on mounting.

*Epicauta temexa*. The male mounts somewhat less abruptly than in *E. vittata*; before mounting he may touch the female with his antennae. On mounting, he assumes a fully mounted position, which is maintained throughout Phase A. Regardless of the relative size of the sexes, the male positions his head at the base of the elytra of the female and presses his mouthparts on it (fig. 17). The positioning of the legs in Phase A is very similar to that of *E. tamara*. The foreleg grasp constitutes the main hold; principal contact is made by the first tarsal segment, which is noticeably enlarged. The tarsi are held straight, not touching the

female. The position of the middle and hind legs is quite variable. The tarsi of these legs are curved around the abdomen.

The antennae extend laterad, in the drooped position (fig. 16). As in *E. vittata*, the male may put his antennae back, parallel to his head, when the female is walking rapidly. Here again, this probably serves to protect the antennae from injury.

Phase A is characterized by frequent bouts of hind leg rubbing. The legs are moved much as in *E. vittata* but less forcefully and more slowly. Contact is made by the hind tibial spurs and tarsal segments, the latter usually rubbing over the last two or three visible abdominal sterna of the female.

As a general rule, there is a fairly regular alternation of phases A and B. In entering Phase B, the male moves backward, bringing his head to the level of the middle or distal third of her elytra (figs. 18, 19). The fore and middle legs are allowed to slip backward but retain their grasp. The hind legs, however, are brought completely off the female and to the substrate. As he moves back, the male tucks the head and palpates the female's elytra. At the same time, the antennae are lowered from the drooped position, directed backward between the male's legs, and laid on the female's elytra. As the antennae are lowered, they are curled progressively tighter, reaching maximum curvature just as they are brought under the male, at which time they attain nearly a double circle. They are then carefully straightened before brushing occurs. Several bouts of antennal brushing are performed during genital presentation. The brushing action is a rapid side-to-side movement. Nearly the entire flagellum contacts the female.

If, as is generally true, genital presentation does not lead to copulation, the male withdraws the genitalia and moves forward with great deliberateness and once again takes the fully mounted position, at the same time bringing the antennae from beneath him and extending them in the laterad, drooped position.

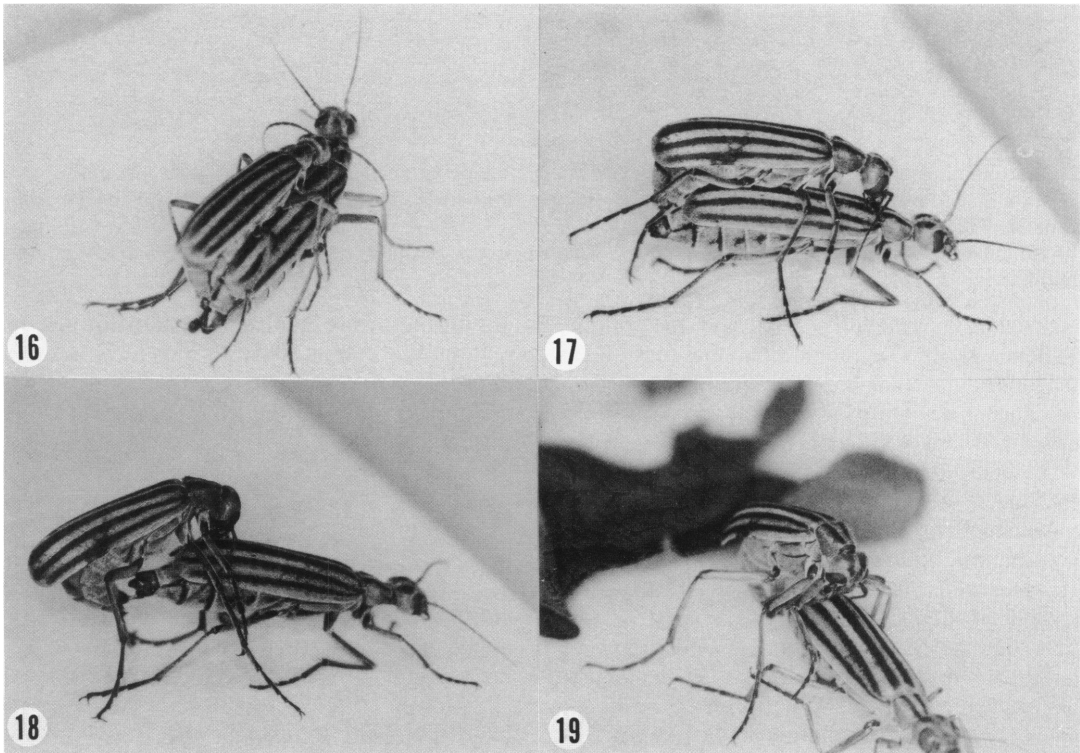
When copulation is imminent, the male often interrupts genital presentation to move forward almost to the fully mounted position and then performs antennal rubbing on the

sides of the female's head and pronotum. Under other circumstances this behavior is only rarely and sporadically performed.

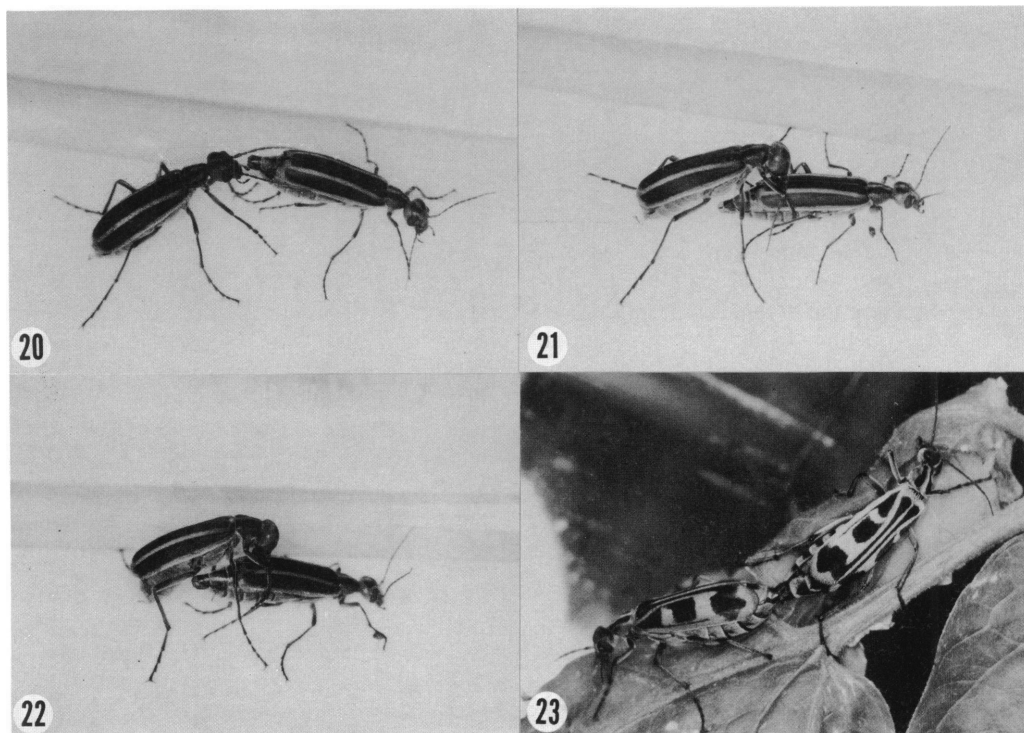
*Epicauta leopardina*. The male of this species is unmounted in Phase A and partially mounted in Phase B. During Phase A the male attempts to stand as near the female as possible, with his head nearly touching the end of her abdomen. The antennae may be curled in a half to full circle. Antennal tapping is performed by directing the antennae sharply downward, contact being made by the curled portion. When abdominal curvature occurs, the genitalia are invariably extruded and genital presentation is performed or attempted. As the abdomen is curving, the male walks forward, grasping the female with both the fore and middle legs; palpation frequently occurs at this time. Because of the movement of the male,

the antennae are now directed beneath him and between his legs. During presentation of the genitalia, light antennal brushing on the elytra is performed. Following presentation the male backs off the female, at the same time bringing the antennae from beneath his body and directing them forward. He may then either abandon the female or resume antennal tapping in Phase A.

*Epicauta unilineata*. Antennal curling in this species is of moderate degree; a full circle is never attained. The behavior in Phase A is similar to that of *E. leopardina* (fig. 20). As in that species, abdominal curvature is not performed unless genital presentation is to be made. Except for the fact that the male grasps the female with only the forelegs (figs. 21, 22), the behavior in Phase B is also like that of *E. leopardina*.



FIGS. 16-19. Courtship in *Epicauta temexa*. 16-17. Male fully mounted, with forelegs grasping female at lateral edges of elytra, palpi on base of her elytra, and antennae drooping in a gradual curve. 18-19. Genital presentation by male while partially mounted.



FIGS. 20-22. Courtship in *Epicauta unilineata*. 20. Male tapping antennae on female before mounting. Note elevation of end of female's abdomen. 21. Male moving into partially mounted position. 22. Antennal brushing by male while partially mounted.

FIG. 23. Copulation pair of *Epicauta leopardina* in linear position characteristic of *Epicauta* and other Meloinae.

*Epicauta occidentalis*. This and the following three species agree in that the male does not mount the female, even partially, at any time during courtship, and the abdomen may be curved forward without genital extrusion or, if the genitalia are extruded, without genital presentation.

Antennal tapping, accompanied frequently by palpation, constitutes the display behavior of *E. occidentalis* in Phase A. The antennae are capable of being curled into at least a full circle. Exceptionally tight antennal curling and an increase in the rate of tapping are associated with movement of the female during Phase A and with genital presentation in Phase B.

Males in Phase A frequently tilt the body up and down rapidly. We have not observed this behavior in the other species.

*Epicauta monachica* (figs. 28-31). Except for the absence of body tilting in Phase A, we

are unable to distinguish the courtship behavior pattern of this species from that of *E. occidentalis*.

*Epicauta vitticollis*. The behavior of the male of this species is similar to that of *E. occidentalis* and *E. monachica* with respect to the form of antennal tapping and the occurrence of palpation. As abdominal curvature occurs, however, the male's body is elevated, lifting palpi off the female. Abdominal curvature occurs more frequently in this species than in either of the other two species and generally is not maintained for as long.

*Epicauta luteolineata* (figs. 26, 27). We have found no significant differences between the pattern of courtship behavior of this species and that of *E. vitticollis*.

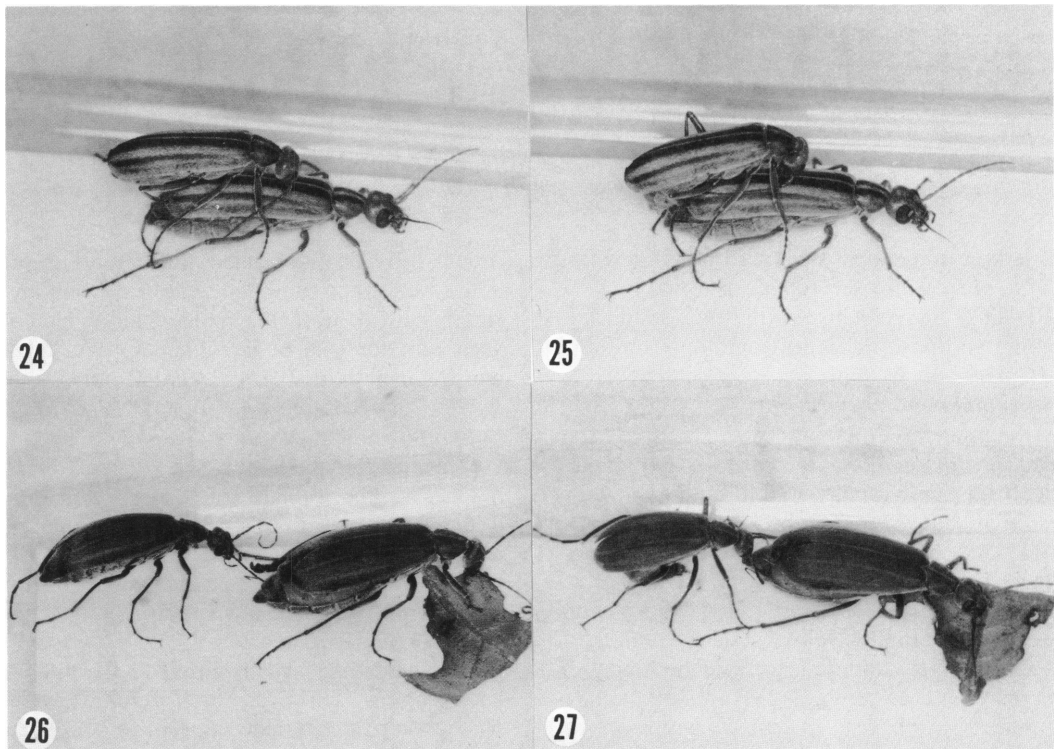
#### FEMALE RESPONSE TO MALE COURTSHIP

Females are often completely passive during

courtship. At other times, except in *E. abadona* and *E. temexa*, they perform one or more acts that interfere with the male's courtship or discourage him from initiating or continuing it. Whether the elaborate behavior of females of *E. abadona*, already described, is of this nature is discussed at the end of this section.

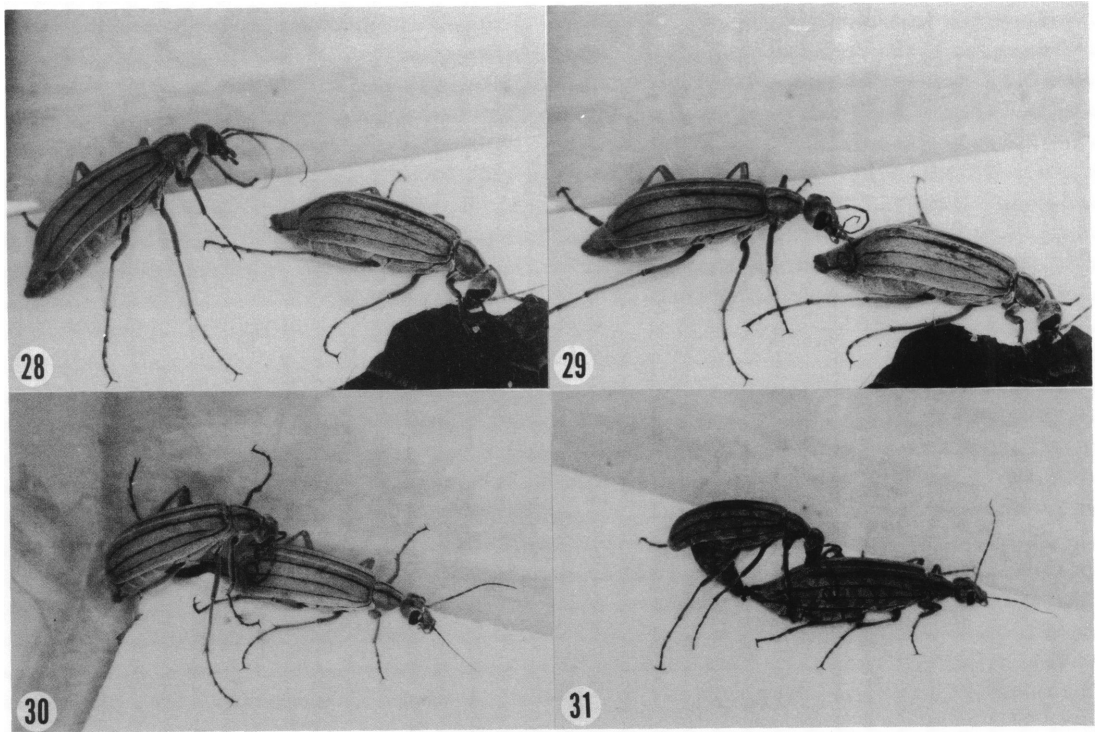
Females of *E. temexa* are remarkably tolerant. Although we observed courtship in this species perhaps more than in any of the others of the group, we never observed an overt negative response on the part of a female. At the other end of the spectrum, we frequently observed female attacks on males in *E. leopardina*. In this species the female commonly turns to face a courting male, which is often enough to discourage him. If not, she may lunge toward him with the mandibles open and may bite him.

In the Albida Group of *Epicauta*, raising or tilting the posterior end of the body upward is a positive female response to courtship performed commonly as an invitation for the male to mount and initiate copulation (Selander and Mathieu, 1969). Similar tilting behavior occurs in the Vittata Group but is performed only by unreceptive females and appears to have an inhibitory effect on male courtship behavior. Tilting was recorded in *E. vittata*, *E. tamara*, *E. unilineata*, *E. occidentalis*, and *E. vitticollis*; in the first three species, it occurs during the preliminary phase. In *E. vittata* and *E. unilineata* the female frequently sways the body from side-to-side while in the tilted position. In *E. tamara*, *E. leopardina*, *E. monachica*, *E. vitticollis*, and *E. luteolineata* she frequently jerks the end of the abdomen rapidly up and down in front of a male standing behind her.



FIGS. 24-25. Courtship in *Epicauta tamara*. 24. Male just mounting. 25. Genital presentation and antennal brushing by male.

FIGS. 26-27. Courtship in *Epicauta luteolineata*. 26. Male approaching female from behind. 27. Antennal tapping and abdominal curvature by male.



FIGS. 28-31. Courtship in *Epicauta monachica*. 28. Male approaching female with antennae weakly curled. 29-30. Antennal tapping by male with antennae tightly curled. 31. Genital presentation by male.

The jerking movement occurs in *E. tamara* and *E. vitticollis* while the female is tilted.

Fending movements with the hind legs (kicking and pushing) were commonly observed in females of *E. vittata*, *E. leopardina*, *E. occidentalis*, and *E. vitticollis*.

An unreceptive female of *E. vittata* often makes energetic attempts to brush a mounted male from her with the middle and hind legs. A similar but less vigorous brushing of the middle and hind legs over the elytra is performed by females of *E. occidentalis* in response to male antennal tapping and genital presentation. Finally, females of *E. unilineata* and *E. vitticollis* sometimes brush the hind legs over the elytra. In all cases the brushing behavior appears to be derived from cleaning movements. Another presumed extension of cleaning movements is seen in *E. unilineata*, in which the female sometimes rubs the hind legs together under the end of her abdomen.

In those species in which the male does not

mount fully on the female, the female is often able to interrupt courtship simply by walking or running away from the male. This response is seen commonly in *E. luteolineata*, with moderate frequency in *E. occidentalis* and *E. vitticollis*, and relatively rarely in *E. leopardina*, *E. unilineata*, and *E. monachica*.

The functional significance of courtship behavior of the female of *Epicauta abadona* deserves investigation. From its very elaborateness and high degree of stereotypy, as well as the contexts in which it occurs, we are inclined to regard it as more than a highly developed series of negative responses. In particular, by greatly extending and lowering of the abdomen and stepping backward in the preliminary phase of courtship, the female appears to solicit male courtship rather than discourage it. Similarly, while opening of the mandibles by the female in Phase A of courtship may be interpreted as threat behavior, the female does not attempt to kick or push the male from her at this or other

times. Moreover, the careful, precisely controlled laying of the female's antennae back along her dorsum at this time does not seem to interfere with the male's behavior at all.

#### MALE COURTSHIP BEHAVIOR IN THE FEMALE

One possible and one definite case of performance of male courtship behavior by females were observed in *E. abadona*. In the first case a female approached a female that was being courted by a mounted male and placed the mouthparts against her body, with the front of the head touching a middle leg of the male.

Prolonged courting of a female by another mounted female was observed in the second case. Just after mounting, the courting female twitched her antennae repeatedly while holding the hind legs off her partner. She then performed several bouts of rather feeble hind leg rubbing and head nodding, without the flurries of antennal rubbing and palpation characteristic of the full male display. Subsequently, she opened the end of the abdomen and moved it erratically near the tip of her partner's abdomen, in a manner strongly suggesting the genital tapping behavior of the male. Better developed and more controlled hind leg rubbing occurred later. The courted female remained passive throughout the bout of courtship.

Male courtship behavior in the female has been reported previously in Meloidae in two species of *Meloe* (Pinto and Selander, 1970). Its function, if any, and its cause remain unknown.

#### TAXONOMIC SUMMARY OF COURTSHIP BEHAVIOR

**DIAGNOSIS OF THE GROUP:** On the basis of qualitative characters of courtship behavior, the Vittata Group may be characterized as follows:

The preliminary phase of courtship, or period from initial orientation of the male on the female to initiation of full male display, is short and simple. During this phase the male positions himself, if possible, directly behind the female, without prolonged investigation of her and with little or no hesitancy. The courtship display of the male appears to be entirely tactile (or possibly chemotactile), without ele-

ments of visual stimulation of the female. The male antennae are curled distally to some extent, commonly in the form of a semicircle or complete circle. Antennation of the female, which occurs in one form or another in all species, is invariably directed to the body of the female, with no attempt to stroke or grasp the antennae of the female. In Phase A of courtship the male is either fully mounted or unmounted; partial mounting occurs only in Phase B. Males that fully mount never completely dismount and those that take an unmounted position never fully mount during courtship. When mounted, males never perform the balancing behavior (laterad extension of the middle legs) typical of species of the subgenus *Macrobasis*. Hind leg rubbing of the elytra or abdomen or both of the female is characteristic of males that fully mount the female. Genital presentation is made only periodically, at irregular intervals, except in *E. tamara*, where the male attempts to present the genitalia continuously. The irregularity of occurrence of genital presentation appears to reflect sensitivity of the male to the way in which the female is behaving. A similar irregularity, presumably stemming from the same cause, is seen in the periodicity of occurrence of many of the individual acts of male display.

Females are, in general, quite tolerant of male courtship and, except in *E. leopardina* do not attack males. Unreceptive females of most species tilt the posterior end of the body upward or jerk the body up and down rapidly or both in an apparent attempt to discourage males.

**INTERTAXA DIFFERENCES:** A summary of the principal intertaxa differences in courtship is presented in table 14. In general, differences involving the form of a specific act of display, especially those of a subtle nature, are not reflected in this tabulation.

#### PATTERNING OF COURTSHIP DURING ADULT LIFE

##### THE ONTOGENY OF COURTSHIP

**AGE OF MALES AT FIRST COURTSHIP:** The onset of courtship behavior was investigated in 59 pairs of reared, virgin beetles representing the 10 species considered in this work as well

as both races of *E. vittata*. Examination of the data showed that males eight or more days old at first exposure to females almost invariably courted on the first day of exposure. For the analysis of effects of age and taxa, we therefore excluded the data for males more than a

week old at first sexual exposure. This reduced the number of pairs to 44, distributed among species and races as shown in table 15.

Statistical analysis of the data involved fitting a regression model incorporating main effects and interactions of taxa, female age at

TABLE 14

**Principal Intertaxa Differences in Courtship Behavior in the Vittata Group**

A plus sign (+) means that an Act occurs; a negative sign (-) indicates that a Position or Act is physically possible but does not occur; a dash (---) means that the comparison being made is inappropriate for a particular taxon.

Behavior	<i>E. vittata</i> , typical race	<i>E. vittata</i> , lemniscate race	<i>E. abadona</i>	<i>E. tamara</i>	<i>E. temexa</i>	<i>E. leopardina</i>	<i>E. unilineata</i>	<i>E. occidentalis</i>	<i>E. monachica</i>	<i>E. vitticollis</i>	<i>E. luteolineata</i>
<b>MALE BEHAVIOR</b>											
Male fully (F) or partially (P) mounted or unmounted (U) in:											
Phase A	F	F	F	---	F	U	U	U	U	U	U
Phase B	F	F	F	F	P <sup>a</sup>	P <sup>a</sup>	P <sup>b</sup>	U	U	U	U
Forelegs hold female in a clasp (C), grasp (G) or lock (L)	L	L	C	G	G	G	G	---	---	---	---
Laterad position of antennae in Phase A horizontal (H) or drooped (D)	H	D	D	---	D	---	---	---	---	---	---
Antennae brushed (B), rubbed (R), or tapped (T) on female in:											
Phase A	R <sup>c</sup>	R	R	---	R	T	T	T	T	T	T
Phase B	R <sup>c</sup>	R	-	B	B	B	B	T	T	T	T
Antennae rubbed on elytra (E), head (H), and/or pronotum (P)	H	H	P,E	---	H,P	---	---	---	---	---	---
Antennal brushing continuous (C), or in bouts (B)	---	---	---	C	B <sup>d</sup>	B <sup>e</sup>	B <sup>e</sup>	---	---	---	---
Head tucking in Phase A or B or absent (-)	-	-	A	B	B	B	-	-	-	-	-
Head nodding	-	-	+	+ <sup>f</sup>	-	-	-	-	-	-	-
Hind leg rubbing of moderate rate (M), rapid (R), slow (S) or absent (-) in:											
Phase A	R <sup>g</sup>	M	M	---	M	---	---	---	---	---	---
Phase B	-	-	-	M	-	---	---	---	---	---	---
Palpation in Phase B	-	-	-	-	-	+	+	+	+	-	-
Genital tapping	-	-	+	-	-	-	-	-	-	-	-
Stretching	+	-	-	-	-	---	---	---	---	---	---



TABLE 14 — (Continued)

Behavior	<i>E. vittata</i> , typical race	<i>E. vittata</i> , lemniscate race	<i>E. abadona</i>	<i>E. tamara</i>	<i>E. temexa</i>	<i>E. leopardina</i>	<i>E. unilineata</i>	<i>E. occidentalis</i>	<i>E. monachica</i>	<i>E. vitticollis</i>	<i>E. luteolineata</i>
Abdominal curvature without genital presentation	-	-	-	-	-	-	-	+	+	+	+
FEMALE BEHAVIOR <sup>h</sup>											
Tilting of body	+ <sup>i</sup>	+ <sup>i</sup>	-	+	-	-	+ <sup>i</sup>	+	-	+	-
Jerking	-	-	-	+	-	+	-	-	+	+	+
Brushing with legs	+	+	-	-	-	-	+	+	+	+	+
Attack	-	-	-	-	-	+	-	-	-	-	-

<sup>a</sup>Fore and middle legs grasp female.

<sup>b</sup>Only forelegs grasp female.

<sup>c</sup>Rarely performed unless copulation is imminent.

<sup>d</sup>In several bouts.

<sup>e</sup>In 1-2 bouts.

<sup>f</sup>When mounting or dismounting only.

<sup>g</sup>Unusually forceful.

<sup>h</sup>Unique acts of *E. abadona* females not included.

<sup>i</sup>With side-to-side swaying.

TABLE 15  
Age (Days) of Males at First Courtship, Adjusted (Except as Noted) for Ages of Males and Females at First Exposure to Each Other (Data restricted to males exposed to females at age of one week or less.)

Taxa	Mean	SE	Range	N
<i>E. vittata</i>				
Typical race	3.9	3.14	2-8	4
Lemniscate race	4.8	0.60	0-6	4
<i>E. occidentalis</i>	7.0 <sup>a</sup>	1.00	6-8	2
<i>E. temexa</i>	10.6	1.84	8-12	6
<i>E. abadona</i>	9.0 <sup>a</sup>	—	—	1
<i>E. tamara</i>	10.9	1.20	8-13	3
<i>E. vitticollis</i>	9.2	0.52	8-10	4
<i>E. unilineata</i>	10.0 <sup>a</sup>	—	—	1
<i>E. monachica</i>	7.3	0.50	6-7	8
<i>E. luteolineata</i>	7.8	0.65	6-9	8
<i>E. leopardina</i>	9.1	1.08	6-10	3
Mean (unweighted)	8.15			

<sup>a</sup>Mean not adjusted.

exposure, and male age at exposure. Because female age was constant in one species (*E. occidentalis*) and data were available for only one pair of adults each in two species (*E. abadona* and *E. tamara*), some two-way inter-

actions had to be omitted. In addition, it was not possible to obtain a nonsingular matrix when three-way interaction terms were included.

The results (table 16) establish that the length of the latency period for expression of courtship behavior in young males varies with taxa and is further affected by the ages of both males and females at first exposure to each other. Mean age at exposure was 3.0 (SE = 0.25) days for males and 5.6 (SE = 0.66) days for females. Mean values at first courtship in table 2 have been adjusted for interspecific differences in age of exposure, the adjustment points being the means for the sexes just given.

Mean age at first courtship ranged from 3.9 days in males of the typical race of *E. vittata* to 10.9 days in males of *E. tamara*. The overall, unweighted mean for the group is slightly over eight days. Except for a male of the typical race of *E. vittata* that courted at the age of two days and one of the lemniscate race that courted on the day that it reached the adult stage (age 0 days), the minimum age at first courtship was six days, as indicated in table 15. Rather limited data obtained for the Albida Group of *Epicauta* by Selander and Mathieu

TABLE 16  
**Age (Days) of Males at First Courtship. Analysis  
of Variance of Multiple Regression Model**  
(Data summarized in table 15.)

Source	df	MS
Regression	27	
Taxa	10	13.04****
Female age at exposure	1	22.76****
Male age at exposure	1	11.29****
Taxa x female age	7	2.85*
Taxa x male age	7	3.44*
Female age x male age	1	4.66*
Residual	16	1.06

$R^2 = 0.926$

(1969) indicate a somewhat longer latency to first courtship. The unweighted mean for three species in that group was 10.7 days, with a minimum age of eight days.

Returning to table 16, we find the situation complicated in the Vittata Group by the presence of main effects of the age factors. The overall effect of increasing female age at first exposure was to shorten the latency period for courtship by males. That is, males tended to court older females earlier than younger ones. It has been established in some groups of *Epicauta* and other genera of meloids that females produce a pheromone stimulating courtship behavior in males, and it may be in the present case that increased pheromone production with increasing age of females accounts for the relationship just described. An even more interesting relationship is that increasing male age at exposure tended to lengthen the latency period for the appearance of courtship behavior, indicating that daily exposure to females somehow hastened the development of ability to court in males. Here again, it is possible that a female sexual pheromone is involved having a stimulatory effect on males even before they are capable of expressing sexual behavior. Furthermore, as discussed below, there was a marked pattern of inhibition of courtship for one or more days following copulation. Otherwise, little or no systematic variation in time was evident in the courtship behavior of any of the males studied. In this respect the patterning of courtship in adult life is similar to that re-

ported for the Albida Group of *Epicauta* (Selander and Mathieu, 1969).

In the present section we summarize the data for the Vittata Group in terms of (1) the percentage of days of exposure on which courtship occurred; (2) the length of intervals without courtship; and (3) for selected species, rates, and durations of bouts of courtship and component activities.

**PERCENTAGE OF DAYS ON WHICH COURTSHIP OCCURRED:** There is no evidence in any of the taxa that the probability of courting on a given day is affected by the age of the male or the performance of oviposition by the female. Furthermore, there is nothing to indicate that males are either more less likely to court on the day before a copulation occurs than on any other day, excluding days immediately following copulation. Because the males differed in the frequency with which they copulated, we have attempted to enhance the validity of interspecific comparisons of persistence of courtship behavior by excluding consecutive days of no courtship from the data in calculating the percentage of days of exposure on which courtship occurred. To the best of our ability, then, the information presented in table 17 represents

TABLE 17  
**Percentage of Days of Sexual Exposure in the  
Paired Situation on which Male Courtship  
Occurred, Beginning with First Day of  
Courtship in Adult Life and Omitting  
Consecutive Days of No Courtship Immediately  
Following Copulation**

Taxa	Mean	SE	N pairs
<i>E. vittata</i>			
Typical race	75.7	4.4	3
Lemniscate race	85.5	2.1	5
<i>E. occidentalis</i>	87.1	5.2	3
<i>E. temexa</i>	89.5	4.7	7
<i>E. abadona</i>	62.9	14.8	3
<i>E. tamara</i>	83.6	3.2	5
<i>E. vitticollis</i>	89.9	2.3	5
<i>E. unilineata</i>	75.5	5.9	4
<i>E. monachica</i>	85.9	8.7	10
<i>E. luteolineata</i>	96.2	1.0	9
<i>E. leopardina</i>	76.6	7.2	5
Mean (unweighted)	82.58		

persistence of courtship in adult life, with the effects of copulation removed.

The mean percentage of days on which courtship occurred ranged from about 76 in *E. vittata* (typical race), *E. unilineata*, and *E. leopardina* to 96 in *E. luteolineata*, with the remainder of the taxa averaging between about 85 and 90 percent (table 17). The unweighted mean of the taxa is 83 percent. Intertaxa variation is significant at the 5 percent level, although none of the comparisons of interest reaches that level (table 18).

Data obtained for the Albida Group by Selander and Mathieu (1969) are, for the most part, comparable to those for the Vittata Group, with values of about 74 percent for *E. texana* and *E. sublineata*, 90 percent for *E. valida*, and 99 percent for *E. immaculata*. However, nothing comparable to the low of 24 percent for *E. atrivittata* in the Albida Group was recorded in the Vittata Group.

**LENGTH OF INTERVALS WITHOUT COURTSHIP:** Frequency distributions of lengths of intervals with no courtship are presented for the various taxa in table 19. Intervals beginning on the day following copulation are segregated from those occurring at other times.

From the unweighted means shown at the

bottom of the table it is evident that the vast majority of intervals not preceded immediately by copulation were of short duration, 75 percent being one day in length and 90 percent no more than two days in length. The maximum length was 11 days, recorded once each in *E. abadona* and *E. leopardina*. The most consistent courtship pattern was shown by *E. luteolineata*, the least consistent by *E. abadona*, followed closely by *E. leopardina*.

TABLE 18  
**Analysis of Variance of Percentage of Days of Sexual Exposure in the Paired Situation on which Courtship Occurred**  
 (Data summarized in table 17.)

Source	df	MS
Among taxa	10	834.0*
Typical <i>E. vittata</i> vs lemniscate race	1	178.9
<i>E. vittata</i> vs <i>E. occidentalis</i>	1	194.5
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	11.7
<i>E. abadona</i> vs <i>E. tamara</i>	1	805.2
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	459.0
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	501.8
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	1	797.4
Within taxa	48	389.0

TABLE 19  
**Percentage Distribution of Length of Intervals of One or More Days with No Courtship Immediately Following Copulation and at other Times**

Taxa	Following Copulation						Other Times					
	Length of interval (days)						Length of interval (days)					
	1	2	3	4	5-11	N	1	2	3	4	5-11	N
<i>E. vittata</i>												
Typical race	33.3	33.3	33.3			3	66.7		33.3			6
Lemniscate race	57.1	42.9				14	73.7	5.3	10.5	5.3	5.3	19
<i>E. occidentalis</i>	33.3	33.3	11.1	11.1	11.1	9	70.6	17.6	11.8			17
<i>E. temexa</i>	20.0	33.3	36.7	3.3	6.7	30	83.3	12.5			4.2	24
<i>E. abadona</i>	42.9	28.6				7	54.5	27.3	9.1		9.1	22
<i>E. tamara</i>	21.7	52.2	17.4	4.3	4.3	23	68.9	28.9	2.2			45
<i>E. vitticollis</i>	31.2	18.8	25.0	12.5	12.5	16	74.2	12.9	9.7	3.2		31
<i>E. unilineata</i>	12.5	62.5			25.0	8	73.0	16.2	8.1	2.7		37
<i>E. monachica</i>	57.1	35.7			3.6	28	87.8	2.4	7.3		2.4	41
<i>E. luteolineata</i>	82.9	11.4	2.9	2.9		35	100.0					18
<i>E. leopardina</i>	30.8	30.8	15.4	7.7	15.4	13	69.0	17.2	3.4	6.9	3.4	29
Mean (unweighted)	43.5	32.3	12.9	5.4	5.9	186	75.1	14.5	6.6	1.7	2.1	289

With rare exceptions there was complete suppression of male courtship behavior on the day immediately following copulation. In particular, in only 4 of 190 instances of copulation did the male court on that day. These exceptions occurred in *E. temexa*, *E. vitticollis*, *E. monachica*, and *E. luteolineata*. The probability of courting on the day after copulation, 0.02, contrasts sharply with the probability of courting on a day not in the immediately postcopulatory period, 0.83, estimated from the mean of species means of proportion of days courting (see above). The inhibiting effect of copulation extended to at least the second day following copulation. Thus among males that had skipped one day of courtship the probability of not courting the second day was 0.56 in the postcopulatory period and 0.25 at other times ( $X^2_{(1)} = 48.150^{****}$ ). Beyond this point, probabilities of further extension of consecutive days without courtship were slightly, but not significantly, higher for postcopulatory males (e.g., 0.63 vs 0.53 for extension to three days ( $X^2_{(1)} = 0.385$ )). These findings parallel those reported but not quantified precisely for the Albida Group by Selander and Mathieu (1969).

Taxa means for the length of intervals without courtship ranged from 1.3 to 4.3 in the postcopulatory period and from 1.0 to 2.0 at other times. Means in the two situations were positively correlated ( $r = 0.599$ ) but not significantly so ( $df = 9$ ,  $P > .05$ ).

Standard intertaxa comparisons were made, by means of contingency table analysis, in the few instances where samples sizes permitted. The only significant differences detected are for the comparison of *E. leopardina* with *E. monachica* and *E. luteolineata*. Both in the postcopulatory situation and at other times *E. leopardina* showed a greater tendency for extended intervals of no courtship ( $X^2_{(1)} = 5.910^*$  for postcopulatory situation and  $6.785^{**}$  at other times). *Epicauta luteolineata* is noteworthy for its rapid recovery from postcopulatory effects: only 17 percent of its periods without courtship following copulation lasted more than a single day. The record of this species is consistent with its exhibiting the highest mean proportion of days of courtship and the fact that it was never observed to skip more than a day of courtship except following copulation.

#### QUANTITATIVE RECORDS OF COURTSHIP ACTIVITY

For five species of the Vittata Group, daily quantitative records of certain aspects of male courtship behavior in the paired situation were obtained by means of a 20-pen Esterline-Angus event recorder operated by an observer using a push-button keyboard. These data permit us to examine patterning of behavior in considerably more detail than in the other species; in addition, the data are of value in assessing interspecific differences.

In their study of species of the Albida Group of *Epicauta*, Selander and Mathieu (1969) recorded courtship behavior for the initial 15 to 30 min. of exposure of adults in the paired situation. This procedure has the undesirable characteristic that the daily period of recording varies inversely with the latency to first courtship of the day. This results in great inefficiency since there is often in Meloidae a considerable latency to courtship following disturbance to adults as they are transferred to the observational cages. With this difficulty in mind, we adopted for the present study a fixed period of 15 min. of daily recording per pair, beginning with the first act of courtship to occur within the first 15 min. of exposure of pair members. If courtship did not occur within the first 15 min. of exposure, recording for the day was omitted, although pair members were allowed to interact for the remainder of the standard period of one hour. It was our experience that males that did not initiate courtship in the first 15 min. of exposure usually did not court during the remainder of the period.

It should be noted that there are significant interactions between taxa and the age factors and between the age factors themselves. In the case of the taxa by male age factor interaction, the level of significance is less than 2.5 percent; the other interactions are barely significant at the 5 percent level. Further investigation of what appears to be a very complex interplay of factors is certainly indicated. Unfortunately, the subject is a difficult one experimentally because it depends on obtaining adults, by rearing, on specific dates.

**AGE OF FEMALES AT FIRST COURTSHIP:** There appears to be no minimum age for females

before which they do not stimulate mature males to court. In 12 of 13 pairs in which males were more than a week old and females a week or less old at first exposure to each other, courtship occurred on first exposure of the sexes. The mean age of the 12 females at this time was 2.3 days, with a range of zero (three females) to seven days (one female). The single female not courted on the first day of exposure was one day old at the time; she subsequently received her first courtship at the age of seven days by a male partner then aged 15 days. No other male in the study required such a lengthy period for the development of courtship.

#### SUBSEQUENT PATTERNING OF COURTSHIP

Once males become sexually active, they court with great persistency and consistency for the remainder of their lives. Considerable day-to-day variation in levels of activity was observed and recorded for all species, as exemplified in the graphs of daily activity in representative pairs of *E. temexa* (figs. 32-34) and of *E. monachica* (figs. 35-37).

Besides days on which recording was omitted for the reason just explained, records are lacking for occasional days on which other demands on our time or malfunction of the event recorder prevented recording. However, pair members were consistently exposed to each other on every day of their adult lives, regardless of whether records were taken.

In summarizing the data for each measure, we initially obtained for each pair of adults a

daily rate or mean duration, which we then averaged over days of recording to obtain a single datum. These data were then averaged over pairs in taxa to yield species means. The number of pairs recorded per taxon ranged from three in *E. vittata* and *E. occidentalis* to seven in *E. temexa*, as indicated in the tables summarizing the data. The number of recording days for pairs of adults of each species is indicated in table 20.

**REPRESENTATIVE RECORDS:** Complete data for single pairs each of *Epicauta temexa* (figs. 32-34) and of *E. monachica* (figs. 35-37) are presented. The two species represent contrasting types of courtship. *Epicauta temexa* males court from a fully mounted position; those of *E. monachica* court from behind the female. The particular cases shown were selected because, with 139 and 150 days of exposure of the sexes, they are the most extensive sets of data obtained.

The record for *E. temexa* (figs. 32-34) is fairly typical. There is considerable day-to-day variation in almost every measure. At irregular intervals there is a short period of unusually high activity and at others a brief absence of courtship behavior. But apart from the marked inhibition of courtship immediately following copulation, there is no appreciable systematic variation in courtship with age and no detectable effect of oviposition by the female. Total time in courtship and number of courtship periods per day is less variable in *E. temexa* than in *E. monachica*. This difference reflects a gen-

TABLE 20  
Total Duration of Daily Courtship, Number of Periods of Daily Courtship, and Duration of Periods of Courtship in the Paired Situation

Taxa	Duration of Courtship (sec./day)		Number of periods/day		Duration of Periods (sec.)		N pairs	Number of days pairs recorded	
	Mean <sup>a</sup>	SE	Mean <sup>a</sup>	SE	Mean <sup>a</sup>	SE		Mean <sup>a</sup>	Range
<i>E. vittata</i>	155.2	90.78	3.0	0.09	49.6	27.79	3	18.7	11-22
<i>E. occidentalis</i>	599.0	19.90	4.2	0.64	148.3	24.03	3	52.0	48-50
<i>E. temexa</i>	745.3	32.55	2.2	0.16	349.1	29.82	7	76.1	27-142
<i>E. monachica</i>	402.9	40.33	4.2	0.35	101.7	15.84	5	82.8	31-122
<i>E. luteolineata</i>	556.3	46.69	10.3	1.01	55.0	6.11	4	55.5	30-69

<sup>a</sup>Mean of daily means for individual pairs of a species. Days on which no courtship occurred or on which copulation occurred are omitted.

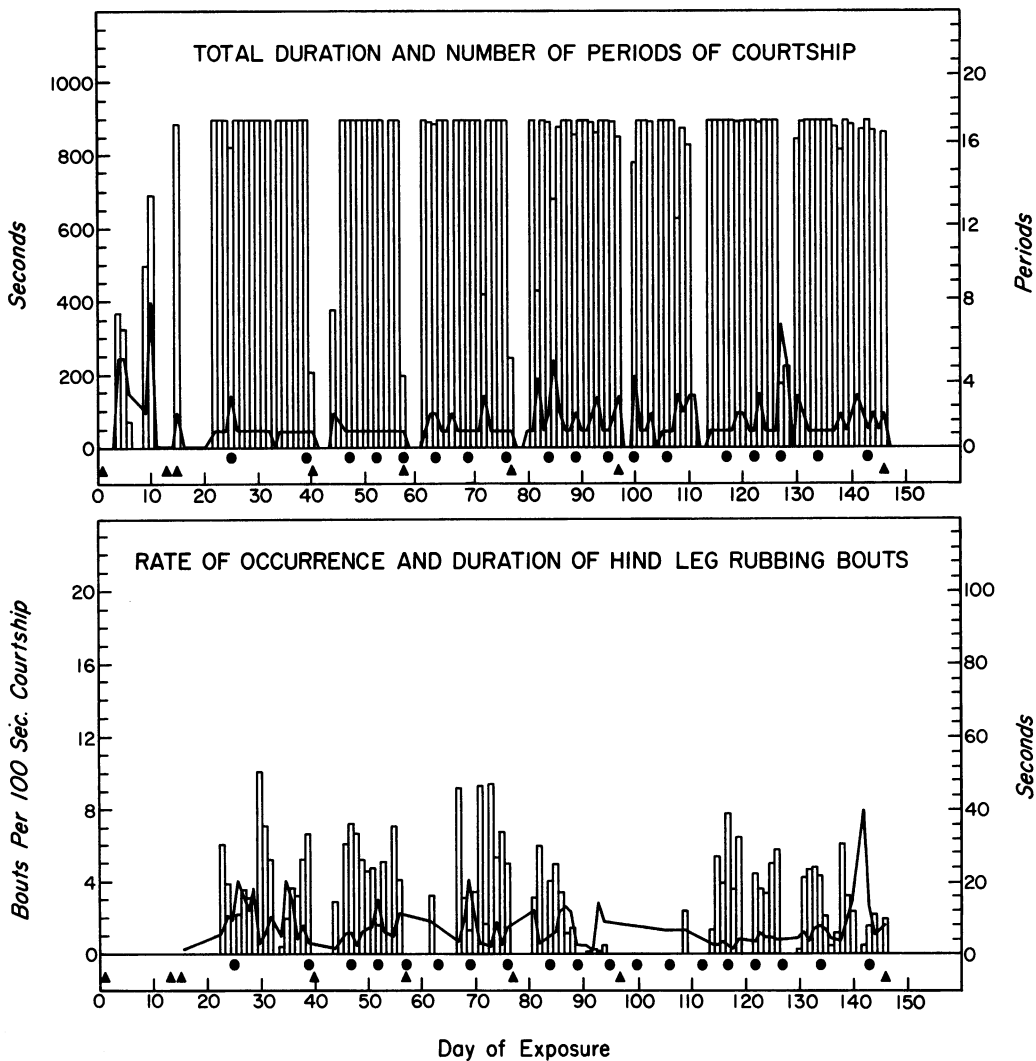


FIG. 32. *Epicauta temexa*. Daily records of periods of courtship and hind leg rubbing bouts in one pair of adults, in the paired situation. Days on which copulation and oviposition occurred are marked with a triangle and a circle, respectively. Recording was terminated by death of the female. Records of other courtship behavior for this pair are shown in figures 33 and 34.

eral pattern. Species whose males court from a mounted position tend to have one or two long bouts of courtship per day, with relatively little variation daily in total time in courtship. On the other hand, courtship in species such as *E. monachica*, where the male courts from behind the female without maintaining constant physical contact with her, tends to be divided into a larger number of relatively short periods, and

total amount of courtship per day is more variable.

The pair of *E. monachica* (figs. 35-37) is somewhat atypical. In the first place, the male was relatively inactive sexually early in adult life, with four periods of three or more successive days without courtship. Second, beyond about 100 days of exposure, there was an increase in time in courtship per day. Associated

with this there was an increase in rate of occurrence of antennal tapping and palpating. In addition, increased intensity of courtship is reflected somewhat in rates of abdominal curvature, genital extrusion, and genital touching. This is the only pair in which marked systematic variation in behavior was associated with age of the adults. We are unable to explain the change in patterning of behavior with increasing age of the beetles. It is perhaps noteworthy, however, that between days 86 of exposure and

death on day 140, the female oviposited only once. The single egg mass produced in this period (on day 116) was fertile, which eliminates our initial hypothesis that the female had depleted her sperm supply and was receptive for copulation but was somehow unable to perform the necessary behavior for it to occur. Nevertheless, we suspect that the unusual behavior of the male was somehow connected with the abnormal decrease in rate of egg production in the female late in life.

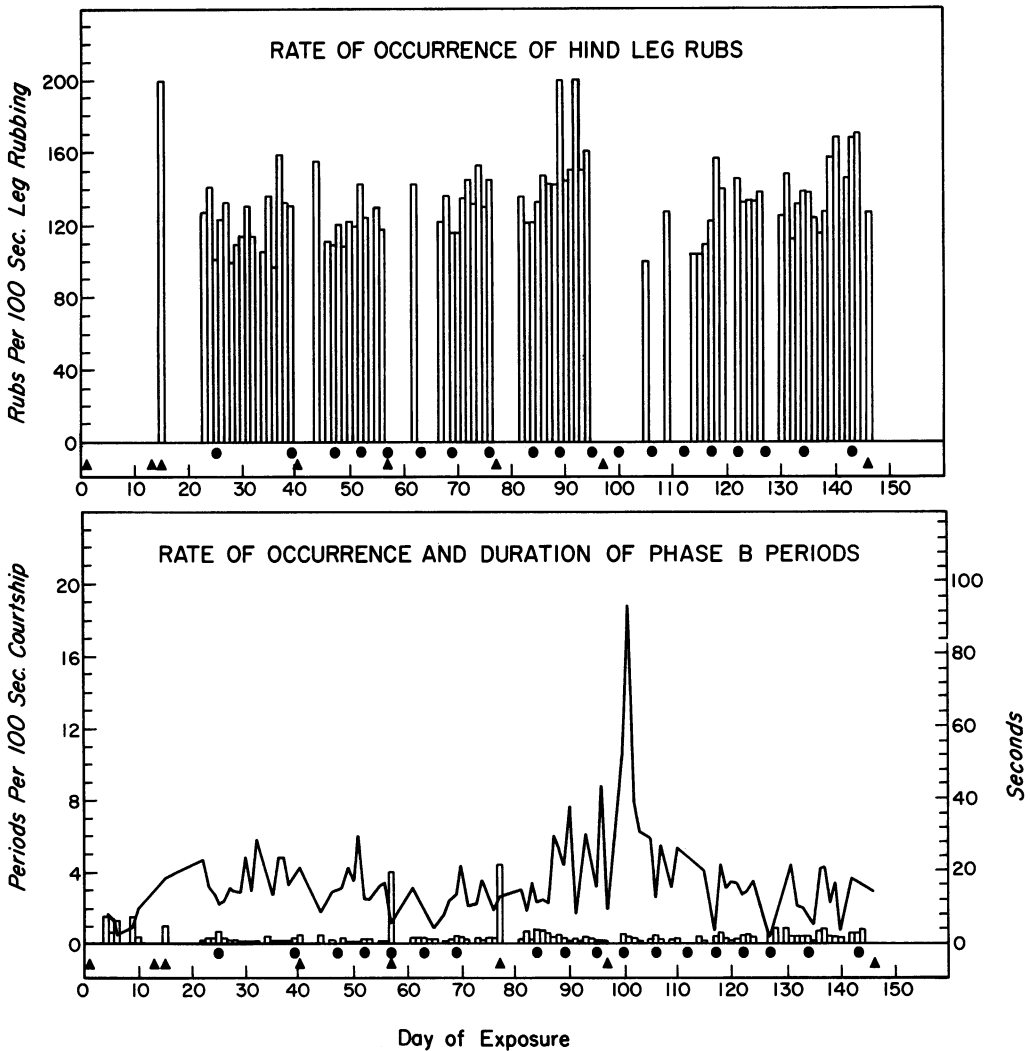


FIG. 33. *Epicauta temexa*. Daily records of hind leg rubs and phase B periods in one pair of adults, in the paired situation. See caption for figure 32.

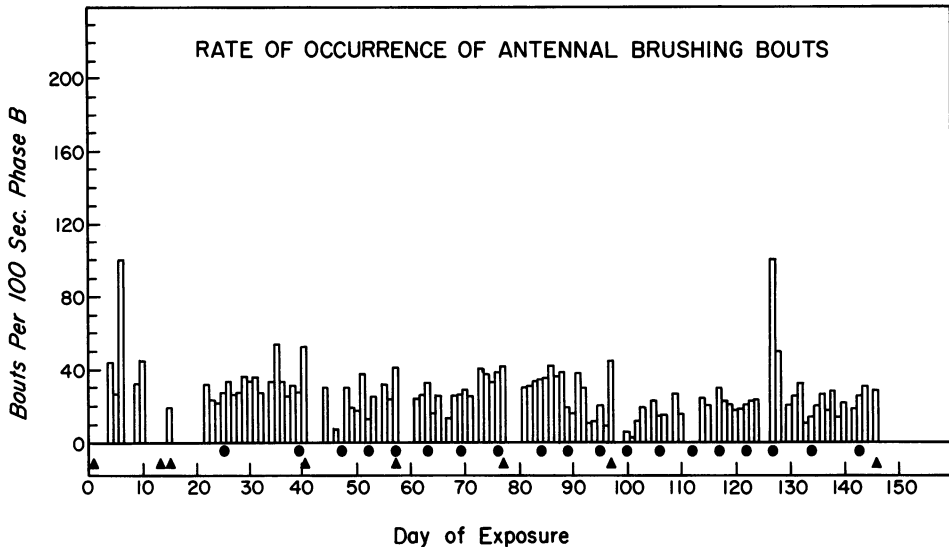


FIG. 34. *Epicauta temexa*. Daily records of antennal brushing bouts in one pair of adults, in the paired situation. See caption for figure 32.

**PATTERNING OF DAILY COURTSHIP:** Duration of courtship, number of periods of courtship per day, and duration of these periods for the five species studied quantitatively are summarized in table 20. Days on which no courtship occurred and those on which copulation occurred are omitted from these data.

Despite the obvious heteroscedasticity of the data on duration of courtship, an analysis of variance was undertaken. This analysis indicates that the interspecific variation in means is significant. Following this up with standard comparisons of sympatric populations, we find the mean duration of courtship is shorter in *E. vittata* than in *E. occidentalis* ( $F = 32.40^{***}$ ), shorter in *E. occidentalis* than in *E. temexa* ( $F = 4.931^*$ ), and shorter in *E. monachica* than in *E. luteolineata* ( $F = 5.74^*$ ) (for all comparisons,  $df's = 1, 17$ ,  $MS$  (within) = 9117.794). Males of *E. vittata* spent the least time in courtship; on the average, courtship activity in this species accounting for only 17 percent of the daily recording period. In contrast, in *E. temexa*, the most active species in this regard, males spent an average of 85 percent of the recording period in courtship. The low score of *E. vittata* is associated with, and

at least partially accounted for, the marked negative female behavior, which seems to discourage males of only moderate sexual motivation. Females of *E. temexa*, on the other hand, are highly tolerant of courting males.

Mean number of courtship periods per day ranged from a minimum of 3.0 in *E. vittata* to a maximum of 10.3 in *E. luteolineata*. Interspecific variation in means is significant. *Epicauta vittata* and *E. occidentalis* do not differ significantly, but the differences between *E. occidentalis* and *E. temexa* and between *E. monachica* and *E. luteolineata* are significant ( $F = 8.10^*$  and  $F = 78.22^{***}$ , respectively, with  $df's = 1, 17$ ,  $MS$  (within) = 1.71).

*Epicauta vittata* and *E. temexa* males had few periods of courtship per day, which reflects the fact that the females of species whose males court while mounted have difficulty in escaping from males. On the other hand, when the male courts from behind the female, without grasping her solidly, bouts are frequently interrupted simply by the female walking away from him. This was especially marked in *E. luteolineata*, females of which are unusually active. Courtship periods, on the average, lasted less than a minute in *E. luteolineata*,



about twice as long in *E. occidentalis* and *E. monachica*, and nearly six times as long in *E. temexa*. *Epicauta vittata* scored lowest in this respect, but in this case (in contrast to that of *E. luteolineata*), the short duration of courtship periods is attributable to the males' spending relatively little time in courtship activity. Again, the interspecific variation is significant.

The difference between *E. vittata* and *E. occidentalis* is significant at the 5 percent level ( $F = 4.88^*$ ) and that between *E. occidentalis* and *E. temexa* is significant at less than the 0.1 percent level ( $F = 28.27^{***}$ ) ( $df's = 1,17$  MS (within) = 2995.227 for both comparisons).

*Epicauta vittata* and *E. temexa*: Rates of occurrence and duration of several courtship

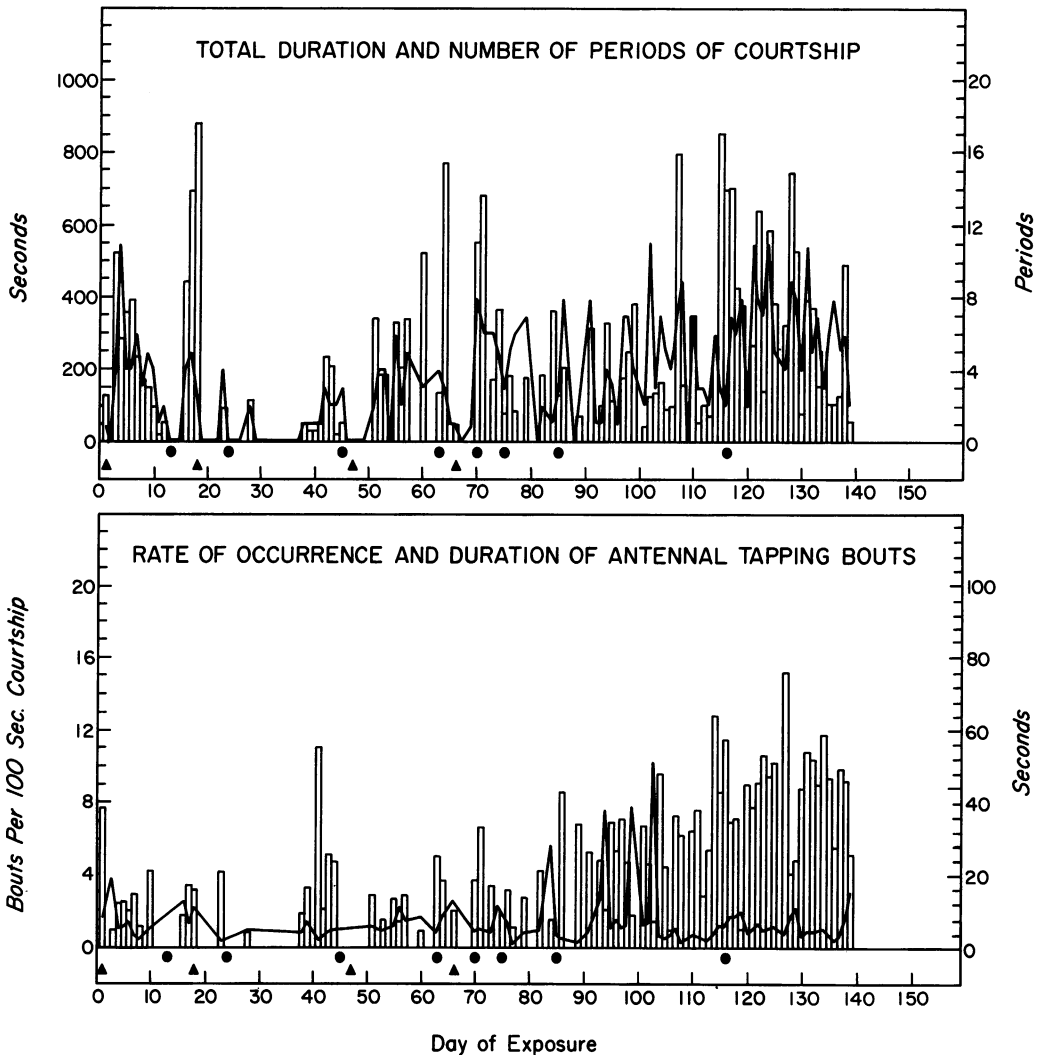


FIG. 35. *Epicauta monachica*. Daily records of periods of courtship and antennal tapping bouts in one pair of adults, in the paired situation. Days on which copulation and oviposition occurred are marked with the symbols M and O, respectively. Recording was terminated by death of the female. Records of other courtship behavior for this pair are shown in figures 36 and 37.

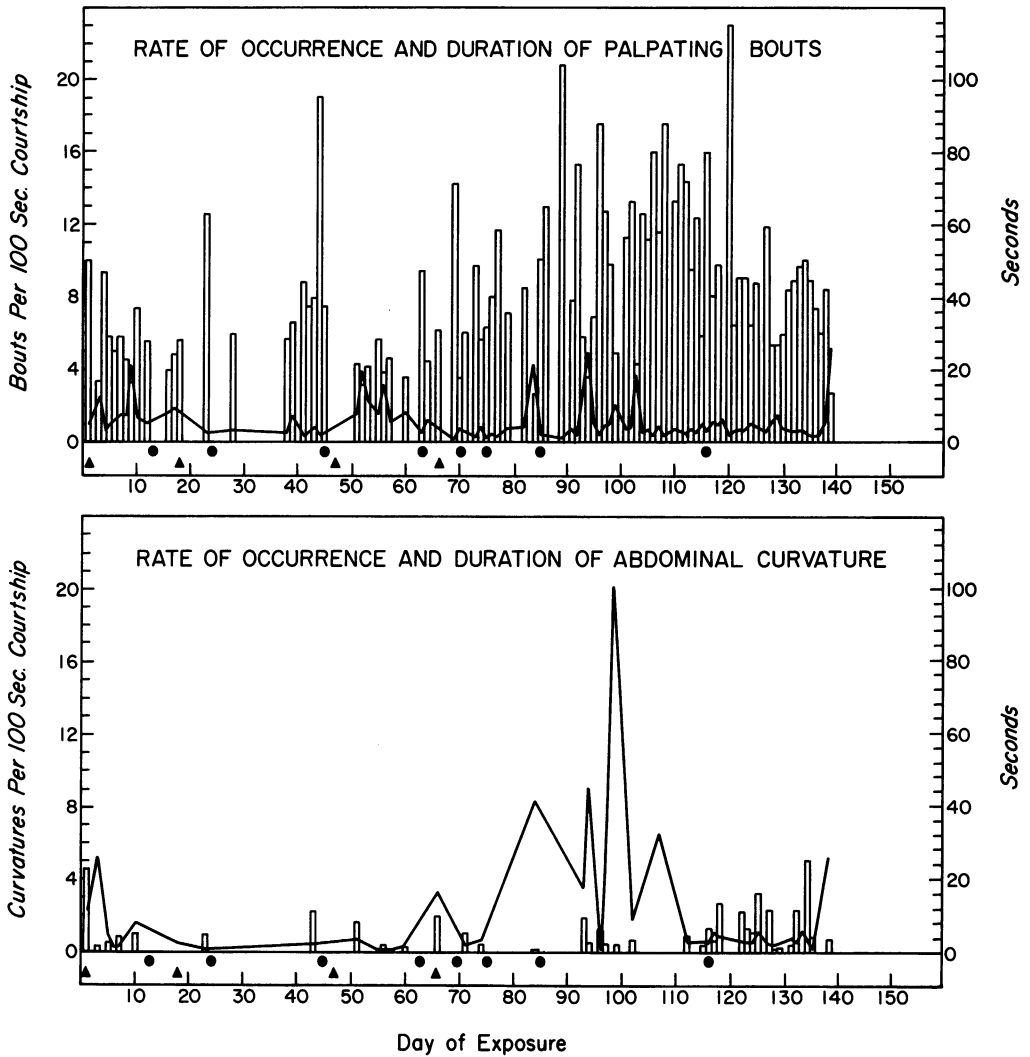


FIG. 36. *Epicauta monachica*. Daily records of palpatory bouts and abdominal curvature in one pair of adults, in the paired situation. See caption for figure 35.

activities are summarized for these species in table 21. It is interesting that in the only homologous activity recorded for the two species, hind leg rubbing, mean bout rates were identical. In *E. vittata*, similarity in rates of occurrence of bouts of hind leg rubbing and stretching reflect the tendency of these activities to accompany each other, a bout of hind leg rubbing usually being followed by a bout of

stretching. Genital touching, as indicated, is a rare activity.

In *E. temexa*, antennal rubbing, which occurs commonly at the initiation of copulation, is seen to be extremely uncommon in courtship periods not leading to copulation. In the qualitative description of courtship, we indicated that males of *E. temexa* enter the genital presentation phase relatively infrequently. This

is shown clearly in table 21. On the average, males initiated this phase of courtship only once every 200 seconds of courtship.

*Epicauta occidentalis*, *E. monachica*, and *E. luteolineata*: Rates of occurrence and duration of five homologous courtship activities in these species were recorded. The data are summarized in table 22 and analyzed in table 23. Major interest is focused on the comparison of

the sympatric species *E. monachica* and *E. luteolineata*, whose courtship behavior is nearly identical qualitatively. Quantitatively, *E. luteolineata* differs from *E. monachica* (and from *E. occidentalis*) in dividing its activity into relatively frequent bouts of short duration. Differences between *E. luteolineata* and *E. monachica* in rates of bouts of palpating do not reach an acceptable level of significance (table

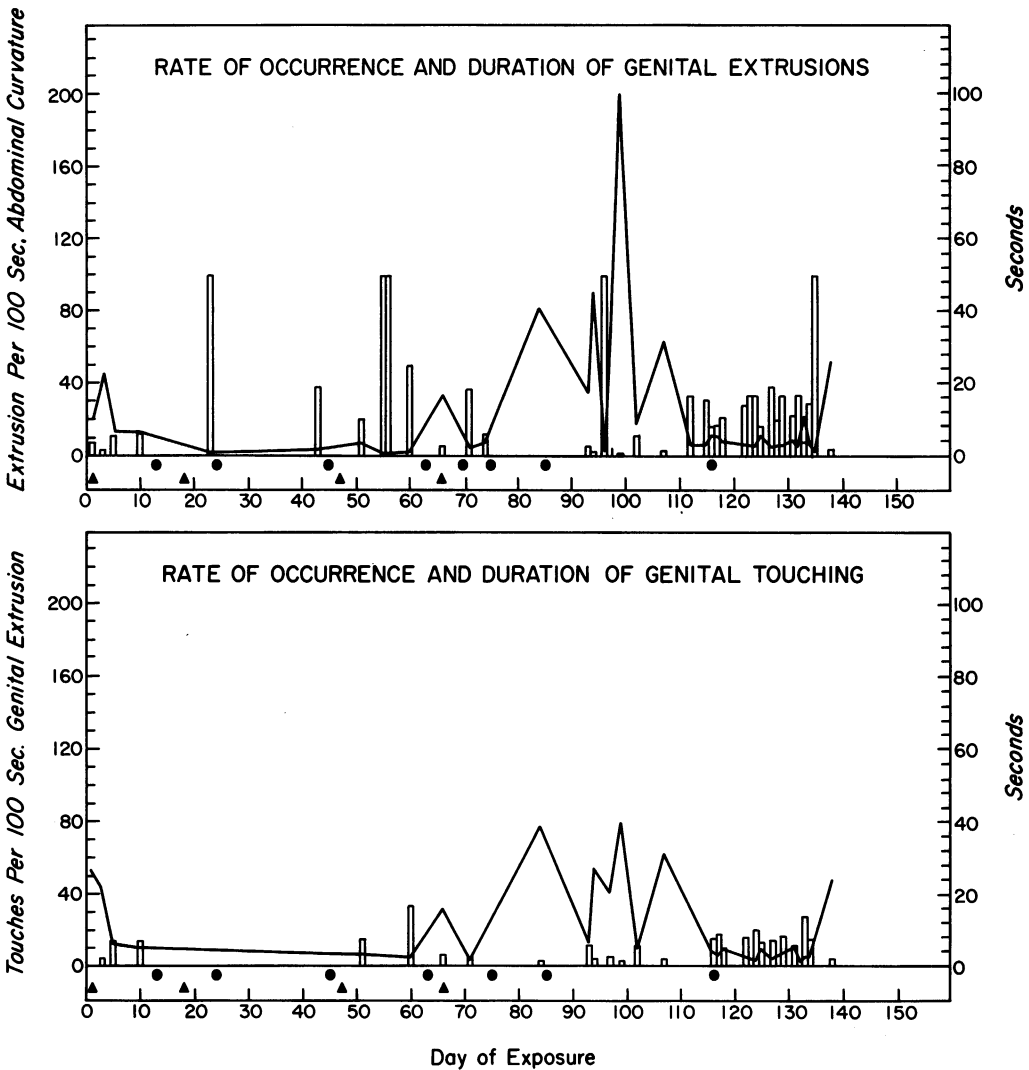


FIG. 37. *Epicauta monachica*. Daily records of genital extrusions and genital touching in one pair of adults, in the paired situation. See caption for figure 35.

TABLE 21  
**Rate of Occurrence and Duration of Some Male Courtship Activities in *Epicauta vittata* and *Epicauta temexa* in the Paired Situation**

Activity	Rate			Duration		
	Mean <sup>a</sup>	SE	N pairs	Mean <sup>a</sup>	SE	N pairs
<i>Epicauta vittata</i>						
Hind leg rubbing (bouts)	1.4 <sup>b</sup>	0.72	3	1.2	0.15	2
Stretching (bouts)	1.3 <sup>b</sup>	0.57	3	1.8	0.42	3
Genital touching	0.07 <sup>b</sup>	0.03	3	5.6	0.00	1
<i>Epicauta temexa</i>						
Hind leg rubbing (bouts)	1.4 <sup>b</sup>	0.33	7	10.5	1.93	7
Hind leg rubs	136.7 <sup>c</sup>	2.03	7	—	—	—
Antennal rubbing (bouts)	0.003 <sup>b</sup>	0.001	7	±1	—	7
Phase B (genital phase)	0.5 <sup>b</sup>	0.06	7	16.0	1.65	7
Antennal brushing (bouts)	27.7 <sup>d</sup>	3.10	7	±1	—	7

<sup>a</sup>Mean of daily means for individual pairs of a species.

<sup>b</sup>Per 100 sec. of courtship.

<sup>c</sup>Per 100 sec. of hind leg rubbing.

<sup>d</sup>Per 100 sec. of Phase B.

TABLE 22  
**Rate of Occurrence and Duration of Some Male Courtship Activities in *Epicauta occidentalis*, *Epicauta monachica*, and *Epicauta luteolineata* in the Paired Situation**

Activity	<i>E. occidentalis</i>			<i>E. monachica</i>			<i>E. luteolineata</i>		
	Mean <sup>a</sup>	SE	N pairs	Mean <sup>a</sup>	SE	N pairs	Mean <sup>a</sup>	SE	N pairs
Rate (units as indicated in footnotes)									
Antennal tapping (bouts) <sup>b</sup>	2.3	0.17	3	3.9	0.48	5	11.1	0.72	4
Palpating (bouts) <sup>b</sup>	3.3	1.02	3	6.6	0.73	5	8.2	0.93	4
Abdominal curvature <sup>b</sup>	0.4	0.35	3	0.6	0.04	5	6.0	0.42	4
Genital extrusion <sup>c</sup>	4.4	1.10	2	18.2	3.27	5	27.4	2.42	4
Genital touching <sup>d</sup>	2.4	0.95	2	6.9	1.30	5	17.7	1.65	4
Duration (sec.)									
Antennal tapping (bouts)	8.4	2.37	3	9.9	0.81	5	2.8	0.30	4
Palpating (bouts)	10.8	1.17	3	7.7	0.78	5	3.1	0.63	4
Abdominal curvature	23.2	3.85	2	14.0	1.23	5	3.8	0.55	4
Genital extrusion	17.0	2.25	2	13.9	1.07	5	3.8	0.53	4
Genital touching	14.2	6.70	2	16.2	2.99	5	3.7	0.53	4

<sup>a</sup>Mean of daily means for individual pairs of a species.

<sup>b</sup>Per 100 sec. of courtship.

<sup>c</sup>Per 100 sec. of abdominal curvature.

<sup>d</sup>Per 100 sec. of genital extrusion.

23), but it is our distinct impression from extensive observation that rate is, indeed, higher

in *E. luteolineata*. Perhaps the most striking interspecific difference found involves the un-

usually high rate of occurrence of abdominal curvature in *E. luteolineata*, which is at least 10 times higher than that in other species.

#### HETEROSPECIFIC SEXUAL BEHAVIOR

As in the case of the Albida Group of *Epicauta*, lack of rigorous ecological isolation among adult populations of sympatric species of the Vittata Group suggests that there is ample opportunity for sexual interaction of species, and the fact that interspecific differences in courtship behavior tend to be accentuated in species occurring sympatrically suggests that these differences play a significant role in reducing interspecific interactions. By this we mean not that interspecific differentiation in courtship patterns is a reproductive isolating mechanism between species, for it has not been shown that any sympatric pairs or trios of species are capable of hybridization even when heterospecific copulation occurs. Rather, we suggest that the interspecific differences in courtship may reduce the duration and intensity of heterospecific interactions and in particular the likelihood of heterospecific copulation.

In the course of this study heterospecific

courtship was observed and occasionally filmed in adult samples collected in the field or reared in the laboratory. In addition, formal investigation of heterospecific interactions was carried out in the case of the sympatric species *Epicauta vittata* (typical race) and *E. occidentalis*. Interactions between the races of *E. vittata* are discussed elsewhere.

**CASUAL OBSERVATIONS:** A male of *E. occidentalis* collected with a group of males and females of *E. temexa* at light in Pearsall, Texas, was observed in extended courtship with a female of *E. temexa* shortly after capture. The pattern of the male's behavior appeared to be normal.

On October 18, 1971, three males of *E. vittata* reared from a stock collected in southern Illinois were exposed individually to a female of *E. temexa* collected at Pearsall, Texas. All beetles had had previous sexual experience and all had been isolated individually for several days before the observations were made. The conditions of the observations were those of the paired situation. One male did not court the heterospecific female in the 15 min. period allotted him. The other two males initiated courtship within 2 and 3½ min., respectively,

TABLE 23  
Analyses of Variance of Data on Male Courtship Activities in *Epicauta occidentalis*, *Epicauta monachica*, and *Epicauta luteolineata*  
(Summarized in table 22.)

Activity	<i>E. monachica</i> vs <i>E. luteolineata</i>	<i>E. occidentalis</i> vs <i>E. monachica</i> and <i>E. luteolineata</i>	Residual MS	df
	MS	MS		
	Rate			
Antennal tapping	115.20****	51.84****	1.21	9
Palpating	5.48	35.01**	3.03	9
Abdominal curvature	64.20****	15.08***	0.73	9
Genital extrusion	186.86	521.71**	35.80	8
Genital touching	262.33****	142.72***	8.53	8
	Duration			
Antennal tapping	109.82***	1.10	5.32	9
Palpating	46.11***	59.55***	2.79	9
Abdominal curvature	228.04****	305.88****	7.93	8
Genital extrusion	225.34****	94.66***	4.57	8
Genital touching	344.73*	20.69	34.03	8

of exposure to the female and courted in single bouts for 11 and 13 min., respectively. Courtship was terminated artificially by removal of the males. Their behavior was judged to be typical in pattern and intensity on the basis of direct observation and later examination of motion pictures.

The observations just described have little bearing on the role of courtship differences in interspecific isolation apart from demonstration that heterospecific courtship is possible. A somewhat more enlightening study of this subject is described in the following section.

**HETEROSPECIFIC COURTSHIP IN *EPICAUTA VITTATA* AND *EPICAUTA OCCIDENTALIS*:** Interspecific sexual behavior was investigated in large samples of adults of both *E. vittata* and *E. occidentalis* collected in Johnson and Pope counties, Illinois, July 8-9, 1972, on *Amaranthus retroflexus*. The beetles were isolated specifically immediately after collection and on July 12, in Urbana, were also isolated sexually. Thereafter, each isolate was held at 25° C. under a 12-hour photophase in type B cages provided with cuttings of *Amaranthus retroflexus* as food and plastic dishes of moist silica sand for oviposition. Food and sand were changed daily.

Trials were initiated July 19 and continued until August 1. The physical conditions of the tests were those described for the paired situation observations and recordings. On each day of testing 12 males of *E. vittata* and 12 of *E. occidentalis* were taken from the holding cages and exposed individually in type C cages to either a homospecific or heterospecific female for a period of 20 min., the assignment of females to males being random, with the constraint that each day half the males received homospecific and half heterospecific exposure.

For each trial a preliminary period of 5 min. was followed by 15 min. of recording, at minute intervals, whether the male was engaged in courtship behavior and, if so, the level of the activity. For *E. vittata* males, level 1 was scored if a male was mounted on a female and level 2 if, in addition, he was performing hind leg rubbing, stretching, or genital presentation from the mounted position. For *E. occidentalis* level 1 was scored if a male was oriented behind a female (with or without antennal tap-

ping) and level 2 if the courting male was involved in the act of abdominal curvature or genital presentation from this position. At completion of a day's trials adults were returned to their respective holding cages. The experimental design involves, then, repeated measures without explicit recording of the identity of each individual. This is an undesirable feature but one dictated by limitations of time and facilities. The samples were large enough, however, that few if any of the adults were tested more than twice.

The results of the experiment are summarized in table 24. Based on the percentage of trials in which courtship was recorded, males of both species showed a strong and statistically significant preference for homospecific females ( $X^2_{(1)} = 16.687^{****}$  for *E. vittata* males and  $8.902^{****}$  for *E. occidentalis* males). Because courtship in *E. vittata* involves constant, extensive physical contact with the female, it was anticipated that males of this species would show a stronger preference for homospecific courtship than would those of *E. occidentalis*. The data suggest that this is the case, but the difference in strength of preference is not significant ( $X^2_{(1)} = 1.660$ ).

Turning to mean time in courtship per trial, we find the homospecific and heterospecific values identical in the case of *E. vittata* males. *Epicauta occidentalis* males courted longer with homospecifics, but not significantly so ( $F_{1,39} = 1.498$ , MS (within) = 0.267).

Percentage of courtship time spent at level 2 was computed for the purpose of measuring, roughly to be sure, whether males courted homospecific and heterospecific females with equal intensity. Analysis was done by weighted linear regression, the weights being times in courtship. The dependent variable was transformed as the arcsin of the square root of the proportion of courtship time at level 2. Data for each species were analyzed separately.

On the average, *E. occidentalis* males spent roughly a fourth of their courtship time at level 2 with homospecific females and only half that amount with heterospecifics. Again, however, the difference is not significant ( $F_{1,39} = 0.799$ , MS (residual) = 1.172). *Epicauta vittata* males showed quite the contrary behavior, spending

about four-fifths of their courtship time at level 2 with heterospecifics and roughly half that amount with homospecifics. In this case the difference is significant ( $F_{1,21} = 6.779^*$ , MS (residual) = 0.910).

The apparently more intense courtship of heterospecific females by males of *E. vittata* is perhaps the result of inappropriate response on the part of the females. In homospecific interactions leg rubbing and stretching by *E. vittata* males tend to increase in frequency when females walk or struggle, one of the principal functions of these acts apparently being to calm the female. If heterospecific females were behaving more negatively than homospecifics (unfortunately, female behavior was not recorded in the experiment), males would be expected to spend a greater proportion of their time in level 2 activities. A somewhat parallel situation has been observed in the courtship of *Meloe dianella* females by *M. angusticollis* males (Pinto and Selander, 1970).

In the course of the present experiment six *E. vittata* males and three *E. occidentalis* males copulated with homospecific females. There were no heterospecific copulations.

## COPULATION

### DESCRIPTION OF THE BEHAVIOR

At rather infrequent intervals in their adult lives, females of the Vittata Group become sex-

ually receptive. The genital presentation phase of male courtship then may culminate in insertion of his genitalia into those of the female, and an extended period of copulation may be initiated. As will be shown, it is by no means necessary for a female to copulate in order to oviposit; indeed, the common pattern is for a female to oviposit several times between copulations.

While there was no noticeable effect of impending sexual receptiveness of the female on male courtship behavior on the day before copulation occurred in the paired situation, courtship was generally intensified on the day of copulation. Most copulations in the paired situation were initiated within 15 minutes' exposure of the sexes.

**MALE BEHAVIOR AT BEGINNING OF COPULATION:** Within a few seconds of coupling of the genitalia, the male assumes a linear position with respect to the female, facing in the opposite direction (fig. 23). This position, maintained until copulation is completed, is characteristic of all species of the Vittata Group studied, as indeed of all Meloinae that have been observed. In assuming this position, the male usually walks sideways, pivoting on the genital coupling with the female. Occasionally, however, he falls over backward and then rights himself. Both methods of "turning off" the female have been observed also in other Meloinae, representing several genera.

TABLE 24  
Homospecific and Heterospecific Courtship in *Epicauta vittata* and *Epicauta occidentalis* in Experimental Trials. A Trial Was a 15 Minute Period of Exposure of a Male to a Female, During which Behavior Was Recorded at Intervals of 1 Minute

Male species	Percentage of trials with courtship <sup>a</sup>	N trials with courtship	Time in courtship <sup>b</sup>		Percentage of time at level 2	
			Mean	SE	Mean	SE
<i>E. vittata</i>						
Homospecific	29.8	19	9.0	1.33	40.9	12.95
Heterospecific	4.7	4	9.0	2.94	80.6	44.51
<i>E. occidentalis</i>						
Homospecific	36.9	28	7.4	1.07	25.5	10.53
Heterospecific	15.5	13	5.3	1.04	13.0	5.81

<sup>a</sup>N = 84 for each of the four combinations.

<sup>b</sup>In units of 1 minute.

Males of *Epicauta vittata* and *E. abadona*, which in courtship present the genitalia from a fully mounted position, with the palpi resting on the dorsum of the female, exhibit no special behavior after insertion of the genitalia. The males simply release their foreleg locks or holds of the female and turn off. In *E. vittata*, antennal rubbing by the male, initiated before copulation begins, may continue until turnoff. In the other species of the group males either commonly or invariably move forward onto the female at the beginning of copulation and bring the palpi onto her dorsum.

*Epicauta tamara* and *E. temexa* males perform most of their courtship from a fully mounted position. During genital presentation, however, the male of *E. tamara* sometimes brings one hind leg, and the male of *E. temexa* always brings both hind legs, to the substrate behind the female. Males of both species usually return to the fully mounted position briefly at the beginning of copulation. In so doing the male of *E. tamara* places the palpi on the female's pronotum. In *E. temexa*, the male commonly continues antennal rubbing as it moves forward, bringing the palpi onto the base of the female's elytra.

Males of two other species of the group make more extensive leg contact with the body of the female at the beginning of copulation than at any other time during sexual behavior. The male of *E. unilineata*, which brings only the forelegs onto the female in courtship, and then only at genital presentation, now brings the middle legs on as well; palpation is on the female's elytra. Similarly, the male of *E. leopardina*, which touches the female with fore and middle legs during genital presentation, now mounts fully, bringing the hind legs on her as well. In doing so, the male moves far enough forward to reach the female's pronotum with his palpi.

*Epicauta vitticollis*, *E. occidentalis*, *E. monachica*, and *E. luteolineata* differ from other species of the group in that males do not normally contact the female with the legs during courtship. Yet even in these species, there is partial or complete mounting at the beginning of copulation. In *E. vitticollis*, the male brings

only the forelegs on the female, with the palpi resting on her elytra. In the other three species, all recorded in the paired situation, males mounted fully and from this position palpated the female's pronotum. This behavior occurred in all five recorded copulations in *E. occidentalis*, in all 11 copulations in *E. luteolineata*, and in four of nine copulations in *E. monachica*.

Once in the linear copulatory position, both male and female beetles frequently begin cleaning their antennae and mouthparts. The partners then usually remain still for a half hour or so, after which either one or both of them commonly feed. In one exceptional observation of *E. vitticollis*, pumping movements of the male abdomen were noted within minutes of turnoff of the male. These movements are quite characteristic and conspicuous in some genera of Meloidae, such as *Lytta* and *Pyrota*, but not in *Epicauta*.

#### DURATION OF COPULATION

Duration was measured in 107 of 202 copulations obtained between partners in the paired situation. For many of these, the unit of measure was 15 min., and for purposes of summary and analyses, we have adopted this unit for all data. At the outset of our study of the data, we analyzed a multiple regression model incorporating 10 terms for taxa, 40 terms for females in taxa, and individual linear terms for temperature during each copulation and the ordinal number of the copulation in the life of each female. This analysis showed significant effects for both taxa and ordinal number of copulation. Temperature, which ranged from 24 to 28° C. (mean 25° C.), was not significant at the 5 percent level ( $F = 0.65$ ,  $df's = 1,54$ ), nor was the factor of females in species ( $F = 0.94$ ,  $df's = 40,54$ ) ( $MS$  (residual) = 4.42,  $df = 54$ ). Subsequent examination of the data indicated clearly that the effect of ordinal number of copulation resulted largely if not entirely from the fact that the first copulation of a female's life is usually shorter than subsequent ones. Our procedure then was to analyze the first and subsequent copulations separately, as two



groups. In addition, we dropped temperature as a covariate.

For the first copulation of adult life, we analyzed the actual duration recorded for each female. For subsequent copulations, we took a mean for each female. In either case, we tested for intertaxa differences by means of the analysis of variance.

Data on the duration of copulation are summarized in table 25. For convenience, the means are converted to minutes in table 26. The shortest and longest copulations recorded were on the order of two and six hours, respectively. For first copulation, taxa means range from 150 to 232 min., with an unweighted mean across taxa of 186.5 min. (3.1 hrs.). For subsequent copulations, taxa means range from 169 to 285 min., with an unweighted mean of 225.5 min. (3.7 hrs.).

An analysis of variance (table 27) showed significant intertaxa differences in the case of both first and subsequent copulations, accounting for 50.4 and 64.2 percent of the variation, respectively. *Epicauta luteolineata* had the shortest mean duration in both categories. Moreover, its values are significantly less than those of *E. monachica*. In the subsequent copulation category, the mean for *E. leopardina* is

significantly greater than the average of *E. monachica* and *E. luteolineata* means. The only other standard comparison yielding significance is that of *E. occidentalis* with *E. temexa* in the category of subsequent copulations, where the level just barely reaches 5 percent. Considering that the data are quite heteroscedastic and that the two species in question had identical means in the first category, the significance of the difference in the second category is best regarded as questionable.

In general, duration of copulation appears to be slightly longer in the Vittata Group than in the Albida Group, judging from data presented by Selander and Mathieu (1969). The present study is the first to demonstrate systematic variation in the length of copulatory periods during the life of the female.

#### PATTERNING OF COPULATION DURING ADULT LIFE

##### ONTOGENY OF COPULATORY BEHAVIOR

Age at first copulation was determined for each pair of beetles studied in the paired situation. Our treatment of this parameter parallels that accorded age at first appearance of courtship with respect both to restriction of the data

TABLE 25  
Duration (in Units of 15 Minutes) of Copulation in Reared Adults of the Vittata Group

Species	First Copulation by Female			Subsequent Copulations (mean/female)		
	Mean	SE	N Copulations	Mean <sup>a</sup>	SE	N Females
<i>E. vittata</i>						
Typical race	10.3	0.88	3	—	—	—
Lemniscate race	12.0	0.00	1	12.5	0.87	4
<i>E. occidentalis</i>	12.7	0.33	3	12.0	0.00	3
<i>E. temexa</i>	12.7	0.61	7	14.8	0.60	7
<i>E. abadona</i>	13.0	0.00	1	14.0	0.00	2
<i>E. tamara</i>	11.7	0.67	3	14.7	0.67	3
<i>E. vitticollis</i>	13.5	0.96	4	17.3	1.73	5
<i>E. unilineata</i>	15.5	0.50	2	19.0	0.00	1
<i>E. monachica</i>	13.0	0.54	8	14.6	0.75	5
<i>E. luteolineata</i>	10.0	1.16	3	11.2	0.37	7
<i>E. leopardina</i>	—	—	—	17.5	0.96	5

<sup>a</sup>Mean of female means.

to pairs in which the male was exposed to the female at an age of one week or less and to the nature of the regression model employed in analysis.

The data are summarized in table 28 and the results of separate analyses of male age and female age at first copulation are given in table 29. Both analyses demonstrate highly significant interaction of taxa and female age at first

exposure to males. The effect of female age at exposure is much less pronounced for males than for females; it does not reach an acceptable level of significance for males. In addition, male age at exposure had a positive effect ( $b = 0.364$ ) on the age of males at first copulation and a negative effect ( $b = -.797$ ) on the age of females. The first relationship seems to be largely an expression of the fact that males were often ready to copulate at first exposure to females. The second relationship indicates that, at least in some taxa, females tend to be stimulated to copulate earlier when exposed to older males than when exposed to younger ones.

The means in table 28 are, for the most part, adjusted for differences in male and female ages at first exposure of partners to each other. This adjustment accounts for means in a few cases being slightly lower than comparable values for age at first courtship (table 15). Comparing these tables, one can conclude that males tend to be capable of copulating as soon as they develop the ability to court. An obvious exception occurred in the case of the single pair of *E. unilineata* studied; the male first courted at the age of 10 days (its partner was a day older) but did not copulate until a month later. This is almost certainly abnormal for the species, although we have no clue as to its cause. The pair subsequently copulated several times,

TABLE 26  
Duration of Copulation in Reared Adults of the Vittata Group  
(Means in table 25 converted to minutes.<sup>a</sup>)

Taxa	First Copulation	Subsequent Copulations
<i>E. vittata</i>		
Typical race	155	—
Lemniscate race	180	188
<i>E. occidentalis</i>	190	180
<i>E. temexa</i>	191	222
<i>E. abadona</i>	195	210
<i>E. tamara</i>	175	220
<i>E. vitticollis</i>	202	260
<i>E. unilineata</i>	232	285
<i>E. monachica</i>	195	219
<i>E. luteolineata</i>	150	169
<i>E. leopardina</i>	—	262

<sup>a</sup>The values are biased downward.

TABLE 27  
Analyses of Variance of Duration of Copulation in Reared Adults of the Vittata Group  
(Time measured in units of 15 minutes. Data summarized in table 25.)

Source	First Copulation		Subsequent Copulations	
	df	MS	df	MS
Among taxa	9	6.65**	9	22.92****
Typical <i>E. vittata</i> vs lemniscate race	1	2.17	—	—
<i>E. vittata</i> (typical race) vs <i>E. occidentalis</i>	1	8.64	—	—
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	0.00	1	16.46*
<i>E. abadona</i> vs <i>E. tamara</i>	1	1.27	1	0.59
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	5.33	1	2.41
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	19.64**	1	33.72**
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	—	—	1	84.17****
Within taxa	25	2.36	33	3.71

TABLE 28  
**Age (Days) of Males and Females at First Copulation, Adjusted for Age of Individuals at First Exposure to Each Other<sup>a</sup>**

(Data restricted to pairs in which males were exposed to females at age of one week or less.)

Taxa	Males			Females			N
	Mean	SE	Range	Mean	SE	Range	
<i>E. vittata</i>							
Typical race	8.0	0.93	6-8	10.3	0.97	10-19	4
Lemniscate race	4.5	0.68	0-7	7.0	0.71	6-9	4
<i>E. occidentalis</i> <sup>b</sup>	7.5	1.50	6-9	4.0	0.0	—	2
<i>E. temexa</i>	10.7	1.92	8-12	13.1	1.98	6-12	6
<i>E. abadona</i> <sup>b</sup>	9.0	0.0	—	9.0	0.0	—	1
<i>E. tamara</i>	10.7	0.76	8-13	13.2	0.79	13-15	3
<i>E. vitticollis</i>	10.1	0.63	9-12	12.7	0.65	8-19	4
<i>E. unilineata</i> <sup>b</sup>	42.0	0.0	—	43.0	0.0	—	1
<i>E. monachica</i>	8.3	0.45	6-19	11.0	0.47	5-27	8
<i>E. luteolineata</i>	6.7	0.48	6-9	10.0	0.49	5-17	8
<i>E. leopardina</i>	9.3	1.11	7-10	12.1	1.15	12-24	3
Mean (unweighted) <sup>c</sup>	8.48			10.24			

<sup>a</sup>Except as noted, means adjusted for initial male exposure age of 3.0 days and initial female exposure age at 5.6 days.

<sup>b</sup>Means not adjusted.

<sup>c</sup>Mean for *E. unilineata* omitted in both cases.

TABLE 29  
**Age (Days) of Males and Females at First Copulation. Analysis of Variance of Multiple Regression Models**  
*Epicauta unilineata* [one pair] Omitted Because of Excessively Long Delay in Copulation After Onset of Courtship  
 (Data summarized in table 28.)

Source	Males		Females	
	df	MS	df	MS
Regression	18	15.62****	18	60.18****
Taxa	9	14.29****	9	12.68****
Female age at exposure	1	0.27	1	496.39****
Male age at exposure	1	28.07****		23.49****
Taxa × female age	7	19.14****		20.83****
Residual	24		24	
Taxa × male age and female age × male age	8	3.31	8	3.93
Error	16	1.55 <sup>a</sup>	16	1.66 <sup>a</sup>
R <sup>2</sup>		0.846		0.949

<sup>a</sup>Used as denominator in all F-ratios determining significance of effects.

and the female's reproductive pattern after first copulation was not unusual.

One other record worth noting is that of a male of the lemniscate race of *E. vittata* that courted and copulated on the first day of its adult life. This is, to our knowledge, the only

case of this kind recorded in any species of the genus *Epicauta*.

In view of the interaction of taxa and female age, we have omitted standard comparisons of taxa, as we did in the case of male age at the onset of courtship. It should be noted that in

each category of behavior summarized in table 28 (as well as that in table 15) the means, being adjusted, are not independently estimated and consequently cannot be compared by the usual procedure of partitioning of the among-taxa sums of squares. Casual inspection suggests that few, if any, of the standard comparisons of taxa do, in fact, involve significant differences.

**FREQUENCY OF COPULATION AND ITS RELATIONSHIP TO OVIPOSITION:** Among the 59 pairs of beetles studied in the paired situation, the number of copulations per pair varied from one to nine, with a grand mean of 3.4 (SE = 0.25). For the ratio of number of copulations per pair per day of exposure of partners, we obtained a mean of 0.051 (SE = 0.003), with a range of 0.021 to 0.167. One-way analysis of variance indicates no significant intertaxa differences in rates of occurrence of copulation ( $F = 1.65$ ,  $df's = 10,48$ ). (An arcsin transformation of square root of rate was used in the analysis.)

The interval between copulations varied considerably, as did the number of ovipositions occurring between copulations. In our analysis of intervals we considered 38 pairs having at least three matings (two intervals) each. In 27 cases, the second interval was longer than the first, in nine shorter, and in two of equal length. A sign test of the changed values indicates that the hypothesis of equality of length of intervals may be rejected at a confidence level of 0.975. In comparisons of subsequent successive intervals, there is no indication of trend. Not enough data are available for standard intertaxa comparisons. The grand mean for time between first and second copulations of adult life (first interval) is 17.8 (SE = 2.41) days. For the remaining intervals, the mean of female means is 24.3 (SE = 1.41).

Associated with the relative shortness of the first intercopulatory interval is a tendency for fewer ovipositions to occur in that interval than in subsequent ones. In tests of independence of frequency distributions of number of ovipositions in successive intervals, we obtained significance only for the test of the first interval with the second ( $X^2_4 = 30.05^{****}$ ). Again, there is no indication of progressive increase or

decrease in number of ovipositions in intervals beyond the second. Percentage distributions of number of ovipositions in the first and combined subsequent intercopulatory intervals are given in table 30. The mean number of ovipositions per interval is 1.2 (SE = 0.15,  $N = 38$ ) in the first interval and 2.7 (SE = 0.15,  $N = 92$ ) in subsequent intervals.

As seen in tables 30 and 31 successive copulations without intervening oviposition were relatively uncommon in any event but much less so in intervals beyond the first. In addition, intervals with only one oviposition were much less common in subsequent intervals than in the first. In instances where only one oviposition occurred in the first interval, only 12 of the 22 egg masses produced hatched. This is an exceptionally low rate of hatching for egg masses in the group and may be taken as strong evidence that successive copulations early in life with one or no intervening ovipositions occur because the female is not, or not adequately, inseminated at first copulation.

Females of the Vittata Group tend to become sexually responsive soon after accomplishing an oviposition. As is shown elsewhere, they do not respond sexually after every

TABLE 30  
Percentage Distribution of Number of Ovipositions in Intervals Between Successive Copulations, Based on Data for 38 Pairs of Adults of the Vittata Group in the Paired Situation

No. ovipositions/ interval <sup>a</sup>	Interval 1	Intervals 2-7
0	18.4	6.5
1	57.9	10.9
2	13.2	30.4
3	7.9	22.8
4	2.6	52.6
5	0.0	4.3
6	0.0	2.2
7	0.0	0.0
8	0.0	1.1
No. ovipositions	38	92

<sup>a</sup>Interval 1 is the period between first and second copulations in adult life, interval 2 the period between second and third copulations, etc.

TABLE 31  
**Temporal Sequences of Copulation and Oviposition in Reared Females Having at Least Four Copulations in the Paired Situation**

Taxa and females	Sequences of copulations (M) and ovipositions (O) <sup>a</sup>
<u>E. vittata</u> (lemniscate race)	
1	MOM●MOM●
<u>E. occidentalis</u>	
1	MM●M000M000M[●]
<u>E. temexa</u>	
1	M●MOM0000M000M000
2	M00M00M000M0000M0000M0
3	MM00M00M00M
4	MMM00M000M000M000M0000000M
5	M●M0000M0000M0M00
<u>E. tamara</u>	
1	MOM000M●00M0●0M●00M●●M000M●
2	M●M0M00M00M0M00M●M●
3	M●M●●M00M●●000M00
<u>E. vitticollis</u>	
1	M●M0●00M0M000
2	M●M00000M000M●M0
3	M●M0000M0000M0000M00M
<u>E. monachica</u>	
1	M0000M0000M000000M000000M00
2	M0M00M000M00
3	M0M0000M00000M[0]
4	M0M●M●M0000
<u>E. luteolineata</u>	
1	MM00M0000M0M0
2	M0M000M000MM000M000MM000M00
3	M000M0000M0000M000
4	MM000M000M0000M0
5	M0M00MM
<u>E. leopardina</u>	
1	MM00M●M000[0]
2	M0M00M00M0

<sup>a</sup>Darkening of the symbol for oviposition indicates that egg mass produced did not hatch. Brackets indicate that oviposition occurred after the death of the male partner.

oviposition, but if a copulation is to occur, it tends to follow closely on oviposition. In the present study, we recorded 128 periods from oviposition to copulation. The mean length of these was 1.9 (SE = 0.25) days, with a range of 0 to 17 days. In 39 (30.5%) of the cases,

copulation occurred on the same day as the oviposition, at first exposure of the female to her male partner following oviposition. In an additional 36 (28.1%) of the cases, it occurred on the day after the oviposition. In contrast, the mean length of the period from copulation to

the next oviposition was 9.1 (SE = 0.48) days, with a range of 1-43 days (N = 172).

With respect to both number and distribution of copulations during adult life, the Vittata Group is rather surprisingly similar to the Albida Group, insofar as the less comprehensive data presented by Selander and Mathieu (1969) permit comparison.

## OVIPOSITION

### DESCRIPTION OF THE BEHAVIOR

As is generally true in Meloinae, females of species of the Vittata Group normally oviposit in burrows which they excavate with the mandibles and legs and subsequently refill. Characteristically, the eggs produced at a given oviposition are deposited in a compact mass over a period of ½ to 1 hour. The eggs themselves are yellow in color and weakly adherent to one another.

Burrows of *E. vittata* excavated in "compact" soil in an insectary in Iowa ranged from ½ to 1 in. in depth (Webster, 1915). Those of *E. occidentalis* (as *E. lemniscata*) were described as being 1½ in. deep and enlarged at the bottom (Ingram and Douglas, 1932). We occasionally noted enlargement of the bottoms of burrows in several species of the group in our laboratory. Gilbertson and Horsfall (1940) figured a completed burrow of *E. "lemniscata"* (*E. vittata* or *E. occidentalis*). The burrow is plugged with soil and is surrounded on the surface of the soil with dried pellets from the excavation. According to these authors, burrows ranged from 1 to 1½ in. in depth. The actual act of excavation of a burrow has not been studied in detail for any of the species of the Vittata Group. In casual observations of the behavior we have not noticed interspecific differences. That such differences may exist, however, is suggested by the work of Church (1967) on species of several genera of Meloinae, including a few of *Epicauta*.

Females in our study were provided with moistened sand in small, cylindrical plastic dishes measuring 5 cm. in diameter and 4 cm. in height. The sand was usually utilized for oviposition, but occasionally (especially in *E. monachica*) eggs were deposited on a leaf or

the floor of the cage. Similar behavior was noted in *E. "lemniscata"* (*E. vittata* and/or *E. occidentalis*) by Riley (1877) and in *E. occidentalis* (as *E. lemniscata*) by Ingram and Douglas (1932). Induction of oviposition by poisoning of females was reported by these last authors, who noted that "few, if any" of the eggs so produced hatched. We have confirmed these observations in several species of Meloidae, although not in any of the present group.

Almost invariably in our study egg masses deposited in sand-filled dishes were placed at the maximum depth possible (4 cm.). Commonly the depth of the burrow was considerably greater than the length of the female excavating it. As a general rule burrows were excavated at the edge of the dish. It is questionable whether females found it easier to excavate against the solid wall of the dish or were somehow stimulated to dig in such situations. A similar tendency has been noted in many other Meloidae in our laboratory.

Egg masses were collected daily and immediately removed from the sand and transferred to individual 3-dram lip vials which had been stoppered with cotton and autoclaved before use. Eggs were incubated in darkness at 27° C. constant temperature and 100 percent RH. For each mass, insofar as possible, we recorded time (days) to hatching, total number of eggs, number of eggs unhatched but containing a recognizable embryo, and number of eggs hatching.

### PATTERNING OF OVIPOSITION DURING ADULT LIFE

As in other Meloinae, females of species of the Vittata Group of *Epicauta* oviposit repeatedly throughout adult life. Contrary to the condition in the Albida Group, however, they do not require copulation for either maturation of eggs or oviposition.

We have chosen to analyze oviposition behavior in terms of oviposition intervals, rate of production of eggs per day of adult life of the female, and number of eggs per mass. Number of ovipositions and total number of eggs produced by a female, measures commonly cited in the older literature, are largely a function of female longevity. Nevertheless, for the record,

we present in table 32 the maximum values recorded for each taxon in these measures. With respect to total number of ovipositions by an individual female, the values for species of the Vittata Group are generally far in excess of maxima recorded in the Albida Group of *Epicauta* (8) by Selander and Mathieu (1969) or the genus *Meloe* (6) by Pinto and Selander (1970).

**THE ONTOGENY OF OVIPOSITON:** For five of the species of the Vittata Group oviposition records were obtained for both mated females and females that remained virgins throughout life.<sup>1</sup> Most females studied, whether in the paired situation or not, first oviposited within two or three weeks of becoming adults. Data for adult age of both mated and virgin females at first oviposition are summarized in Table 33 and analyzed in tables 34-35.<sup>2</sup> The unweighted mean of taxa means for adult age at first oviposition is 25.67 days for mated females and 28.70 for virgins. The earliest age recorded is 10 days, for a female of *E. luteolineata*, and the oldest 66 days, for a female of *E. leopardina*. Ingram and Douglas (1932) indicated that *E. occidentalis* (as *E. lemniscata*) females in Louisiana first oviposited at an adult age of a week or more. In our experience the earliest age at first oviposition in this species was 17 days. Temperature effects on the ontogeny and patterning of oviposition were not investigated by us. As indicated earlier, our females were held at a constant temperature of 25° C.

Analysis of variance of length of the interval from attainment of the adult stage to first oviposition (table 34) shows significant variation among taxa. The principal source of variation is the unusually advanced adult age (mean 53.0 days) recorded in females of *E. leopardina*. Analysis of data for taxa represented by both mated and virgin females, summarized in table 35, indicates that mating status of females had no significant effect on the ontogeny of oviposition behavior. Examination of table 33

<sup>1</sup>Data from the restricted reproductive data set, with the addition of three mated females of *E. abadona*.

<sup>2</sup>Oviposition by a virgin female of *E. monachica* was recorded, but the information obtained was not adequate for inclusion of that female record in the restricted reproductive data set.

shows that the mean for mated females is greater than that for virgins in three species and less in two. Adjustment of means, holding taxa constant and excluding interaction of taxa and

TABLE 32  
Maximum Number of Ovipositions (Egg Masses)  
and Maximum Number of Eggs Per Female  
During Adult Life in Taxa of the Vittata Group

Taxa	Mated Females		Virgin Females	
	Ovi-positions	Eggs	Ovi-positions	Eggs
<i>E. vittata</i>				
(typical race)	8	754	3	389
<i>E. occidentalis</i>	9	1900	3	258
<i>E. temexa</i>	19	3625	6	280
<i>E. tamara</i>	21	2074	7	672
<i>E. vitticollis</i>	15	3639	—	—
<i>E. unilineata</i>	14	2664	—	—
<i>E. monachica</i>	22	2871	—	—
<i>E. luteolineata</i>	18	3517	13	2772
<i>E. leopardina</i>	8	631	—	—

TABLE 33  
Length (Days) of Interval from Attainment of  
Adult Stage to First Oviposition in Females

Taxa	Mean	SE	Range	N
MATED FEMALES				
<i>E. vittata</i>				
Typical race	22.0	0.0	—	1
Lemniscate race	18.4	0.93	17-22	5
<i>E. occidentalis</i>	28.0	4.80	17-37	4
<i>E. temexa</i>	21.7	2.33	15-32	7
<i>E. abadona</i>	33.0	7.21	23-47	3
<i>E. tamara</i>	24.7	2.03	21-28	3
<i>E. vitticollis</i>	24.6	2.52	18-31	5
<i>E. unilineata</i>	28.2	6.49	14-42	4
<i>E. monachica</i>	18.5	1.87	11-28	8
<i>E. luteolineata</i>	17.5	3.71	10-33	6
<i>E. leopardina</i>	53.0	9.30	35-66	3
VIRGIN FEMALES				
<i>E. vittata</i>				
(typical race)	38.5	1.50	37-40	2
<i>E. occidentalis</i>	25.0	3.00	22-28	2
<i>E. temexa</i>	37.0	0.0	—	1
<i>E. tamara</i>	27.8	3.40	19-36	5
<i>E. luteolineata</i>	15.2	2.40	10-24	5

TABLE 34  
**Analysis of Variance of Interval from  
 Attainment of Adult Stage to First Oviposition  
 in Mated Females**  
 (Data summarized in table 33.)

Source	df	MS
Among taxa	10	358.75****
Typical <i>E. vittata</i> vs lemniscate race	1	10.80
<i>E. vittata</i> (typical race) vs <i>E. occidentalis</i>	1	28.80
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	101.03
<i>E. abadona</i> vs <i>E. tamara</i>	1	103.34
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	28.80
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	3.43
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	1	3014.13****
Within taxa	38	68.86

TABLE 35  
**Analysis of Variance of Multiple Regression  
 Model for Length of Interval from Attainment  
 of Adult Stage to First Oviposition for Species  
 Represented by Both Mated and Virgin Females**  
 (Data summarized in table 33.)

Source	df	MS
Taxa	4	4.65**
Mating status	1	1.06
Interaction	4	94.35
Residual	26	50.37

R<sup>2</sup> = 0.377

mating status, provides a value of 22.3 days for mated females and 25.0 days for virgins.

Although it would appear from the above that opportunity to copulate has little if any influence on the ontogeny of oviposition behavior in young females, further analysis indicates that among females exposed to males the age of both males and females at exposure does influence the ontogeny of oviposition. For this analysis we excluded the single pair of *E. unilineata* because of what we have interpreted (above) as an abnormally long delay in the occurrence of first oviposition by the female. In addition, we excluded data for one pair each of *E. vitticollis* and *E. monachica*, females of which actually oviposited before first copula-

tion. These exclusions reduced the data matrix to 38 pairs of beetles, representing 10 taxa.

The multiple regression model adopted for analysis incorporated nine terms for taxa, linear terms for ages of males and females at exposure to their partners, and terms for the interaction of taxa and ages, insofar as possible. In addition, the model contained a linear term representing age of females at first copulation of adult life. The interaction was not significant at the 5 percent level, nor was the covariate fit for age of females at copulation. Adult ages of males and females at first exposure were significant at the 2.5 percent level, with regression coefficients of 1.514 (SE = 0.634) and -2.095 (SE = 0.807), respectively. Delay in exposing females to males tended to delay oviposition slightly, as did exposure to relatively young males. This suggests that courtship behavior received by females affects maturation of egg masses.

#### SUBSEQUENT PATTERNING OF OVIPOSITION

INTERVALS BETWEEN OVIPOSITIONS: Occasionally a female in the paired situation exhibited a marked delay in oviposition. On examination, these cases almost invariably proved to be associated with a doubling or tripling of the number of eggs per mass (over the usual number) when oviposition finally occurred. Clearly, the females skipped one or, very rarely, two ovipositions, finally depositing at a single time what normally would have been two or three egg masses. With the elimination of these cases, whatever their cause, a pattern of impressive consistency emerges with respect both to the temporal spacing of successive ovipositions and the number of eggs constituting a mass.

In summarizing and analyzing the data on intervals between ovipositions and the number of eggs per mass, we have omitted six aberrant intervals of the nature just described. To exemplify the patterning of occurrence of ovipositions during adult life of the female, we present in figure 38 the records for six females of *E. temexa*. The record of a seventh female is omitted entirely; her record is comparable to that of the females shown except that the interval between first and second ovipositions was



about twice that of subsequent intervals and the number of eggs produced at the second oviposition was about 400, or twice the mean value for the species.

Patterning of oviposition during adult life in other species of the group is essentially like that shown in figure 38 for *E. temexa*. Slight irregularities may occur at the beginning of adult life and toward the end. But the striking features of the oviposition pattern are the regularity with which ovipositions succeed each other and, as discussed later, consistency in the number of eggs per mass per female.

Mean length of oviposition-to-oviposition intervals per female is summarized in table 36. A one-way analysis of variance for mated females indicates no significant differences among taxa ( $F_{9,36} = 1.83$ , MS (within taxa) = 15.581). For the five taxa represented also by virgin females, we adopted a multiple regression model incorporating taxa, mating status, and their interaction. Analysis of this model (table 37) yields highly significant effects for both main factors. In four of the taxa (*E. occidentalis* excluded) the mean length of intervals between ovipositions was greatly extended in virgin females, their mean being more than 1½ times that in mated females. The differences in these four taxa are significant at at least the 5 percent

level (table 37). *Epicauta occidentalis* is exceptional in that the mean interval was shorter in

TABLE 36  
Mean Length (Days) Per Female of Oviposition-to-Oviposition Intervals

Taxa	Mean <sup>a</sup>	SE	N Females
MATED FEMALES			
<i>E. vittata</i>			
Typical race	12.0	0.0	1
Lemniscate race	11.2	2.11	5
<i>E. occidentalis</i>	10.0	1.10	4
<i>E. temexa</i>	7.2	0.73	7
<i>E. tamara</i>	8.7	0.31	3
<i>E. vitticollis</i>	11.9	1.59	5
<i>E. unilineata</i>	13.9	3.91	4
<i>E. monachica</i>	12.8	1.64	8
<i>E. luteolineata</i>	7.6	0.79	6
<i>E. leopardina</i>	9.6	2.81	3
VIRGIN FEMALES			
<i>E. vittata</i>			
(typical race)	19.0	1.00	2
<i>E. occidentalis</i>	8.8	2.75	2
<i>E. temexa</i>	13.0	0.0	1
<i>E. tamara</i>	12.9	1.07	5
<i>E. luteolineata</i>	11.6	1.29	5

<sup>a</sup>Mean of female means for each taxon.

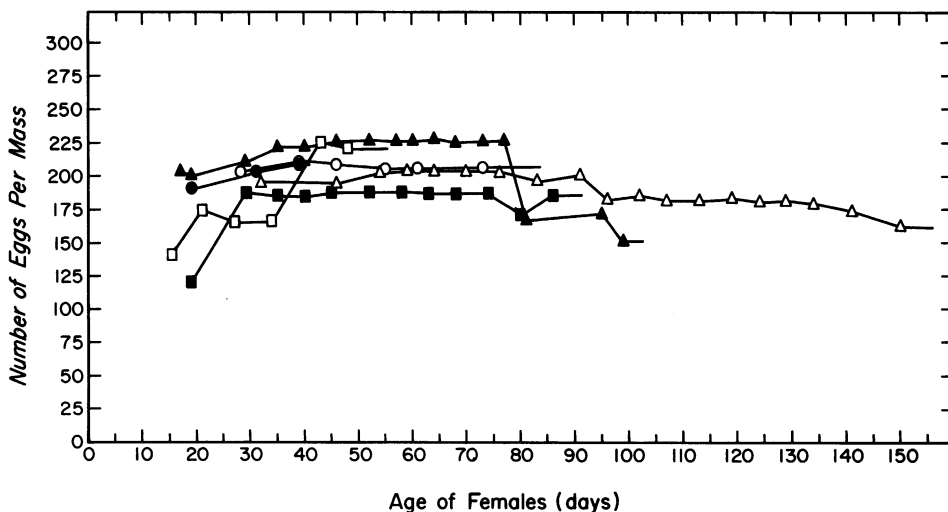


FIG. 38. Oviposition records for six mated females of *Epicauta temexa*. Symbols indicate ovipositions. "Age of females" refers to number of days as an adult.

TABLE 37  
**Analysis of Variance of Multiple Regression  
 Model for Length of Oviposition-to-Oviposition  
 Intervals for Taxa Represented by Both Mated  
 and Virgin Females**  
 (Data summarized in table 36)

Source	df	MS
Taxa	4	27.459***
Mating status	1	95.785****
Interaction	4	11.143
<i>E. vittata</i>	1	32.667*
<i>E. occidentalis</i>	1	1.920
<i>E. temexa</i>	1	29.435*
<i>E. tamara</i>	1	33.075*
<i>E. luteolineata</i>	1	43.636**
Residual	26	4.775

$R^2 = 0.724$

virgins than in mated females; however, the difference is not statistically significant (table 37).

**LAST OVIPOSITION TO DEATH:** This interval is of limited interest but is useful in showing that the pattern of repeated oviposition continues until late in the adult life of the female. The data are summarized in table 38 and analyzed in table 39. As seen in the values for range, females frequently oviposited within the last week of life and in a few cases on the day preceding, or the actual day of death. It is noteworthy that *E. leopardina* females, which began their reproductive cycles unusually late in adult life, continued them, on the average, to a point much nearer death than did females of the other species.

Multiple regression analysis of the interval from last oviposition to death failed to show significant effects for species, mating status, or the interaction of these factors ( $F_{9,35} = 1.804$ , MS (residual) = 7.4983).

**RELATIONSHIP OF COPULATION TO OVIPOSITION:** This subject was discussed in the section on copulation. Reference to figure 38 and table 31 demonstrates clearly the characteristic pattern of several successful ovipositions, interspersed with much less frequent copulations.

## FECUNDITY

**NUMBER OF EGGS PER MASS:** For each female we have calculated both the mean and coefficient of variation of the number of eggs in her egg masses. The latter measure is included to emphasize the relatively low degree of variability in number of eggs per mass in females of most taxa. The data are summarized

TABLE 38  
**Length (Days) of Interval from Last Oviposition  
 to Death in Females**

Taxa	Mean	SE	Range	N
MATED FEMALES				
<i>E. vittata</i> (typical race)	11.0	0.0	—	1
Lemniscate race	15.8	4.73	6-29	5
<i>E. occidentalis</i>	10.5	3.71	1-19	4
<i>E. temexa</i>	5.4	1.17	1-10	7
<i>E. tamara</i>	9.0	1.73	6-12	3
<i>E. vitticollis</i>	9.6	3.37	1-19	5
<i>E. unilineata</i>	17.5	2.90	12-25	4
<i>E. monachica</i>	13.8	2.70	1-24	8
<i>E. luteolineata</i>	18.0	3.22	3-24	6
<i>E. leopardina</i>	4.0	2.31	0-8	3
VIRGIN FEMALES				
<i>E. vittata</i> (typical race)	8.0	7.00	1-15	2
<i>E. occidentalis</i>	3.5	2.50	1-6	2
<i>E. temexa</i>	5.0	0.0	—	1
<i>E. tamara</i>	15.8	4.91	3-29	5
<i>E. luteolineata</i>	15.6	6.33	3-40	5

TABLE 39  
**Analysis of Variance of Interval from Last  
 Oviposition to Death in Mated Females**  
 (Data summarized in table 38.)

Source	df	MS
Among taxa	9	110.30*
Typical <i>E. vittata</i> vs lemniscate race	1	19.20
<i>E. vittata</i> (typical race) vs		
<i>E. occidentalis</i>	1	0.20
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	66.21
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	138.69
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	60.48
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	1	332.44*
Within taxa	36	49.14

in table 40 and analyzed in the following two tables.

Among mated females, taxa means of number of eggs per mass per female range from a low of 86.6 in *E. leopardina* to nearly 200 in *E. temexa* and *E. luteolineata*. The fecundity of the last two species is particularly impressive. Besides excelling those of other taxa in number of eggs per mass, females of these two species began ovipositing relatively early in adult life (adult age at first oviposition was, in fact, minimal for the group in *E. luteolineata*) and had the two lowest means for length of intervals between ovipositions. As shown in table 41 standard comparisons of taxa yielded significant differences only in the case of the South American species. On the average, egg masses of *E. monachica* contained 71 percent as many eggs as those of *E. luteolineata*, and egg masses of *E. leopardina* 62 percent as many as those of *E. monachica*.

Means of coefficients of variation of number

of eggs per mass in mated females ranged from 2.36 in a small sample of the typical race of *E. vittata* to 32.10 in *E. unilineata* (table 40). There is, however, no convincing evidence that real differences exist among taxa (table 41).

Results of analyses of multiple regression models incorporating taxa, mating status, and their interaction for the five taxa in which data for both mated and virgin females were obtained are summarized in table 42. In the case of mean number of eggs per mass, there is significant interaction between taxa and mating status. Individual comparisons for the taxa indicate that in *E. occidentalis*, *E. temexa*, and *E. tamara* mated females laid significantly more eggs per mass, on the average, than did virgin females. The mean for virgins of those species ranges from only 53 percent of that of mated females in *E. tamara* to 72 percent in *E. temexa*. In the other two species, *E. vittata* and *E. luteolineata*, the values for virgins are actually slightly higher than those for mated fe-

TABLE 40  
Mean and Coefficient of Variation of Number of Eggs Per Mass Per Female

Taxa <sup>a</sup>	Mean Number		CV		Females
	Mean <sup>b</sup>	SE	Mean <sup>c</sup>	SE	
MATED FEMALES					
<i>E. vittata</i>					
Typical race	120.0	0.0	2.36	0.0	1
Lemniscate race	137.7	19.86	19.16	6.282	5
<i>E. occidentalis</i>	174.6	12.31	15.80	7.082	4
<i>E. temexa</i>	195.3	4.57	8.90	2.093	7
<i>E. tamara</i>	121.6	22.27	15.18	3.862	3
<i>E. vitticollis</i>	177.0	19.72	12.96	4.359	5
<i>E. unilineata</i>	151.0	19.72	32.10	12.755	4
<i>E. monachica</i>	139.3	9.74	21.27	5.301	8
<i>E. luteolineata</i>	195.5	12.64	13.76	7.510	6
<i>E. leopardina</i>	86.6	5.90	14.25	6.94	3
VIRGIN FEMALES					
<i>E. vittata</i> (typical race)	128.4	1.35	11.94	1.025	2
<i>E. occidentalis</i>	106.8	22.15	38.01	25.950	2
<i>E. temexa</i>	140.0	0.0	46.67	0.0	1
<i>E. tamara</i>	70.3	9.55	21.77	3.065	5
<i>E. luteolineata</i>	212.3	9.11	15.16	4.294	5

<sup>a</sup>Two field-caught females of *E. abadona* laid egg masses containing 81 and 88 eggs, respectively.

<sup>b</sup>Mean of female means for each taxon.

<sup>c</sup>Mean of coefficients of variation of females for each taxon.

TABLE 41  
**Analyses of Variance of Mean and Coefficient of Variation of Mean Number of Eggs Per Mass Per Female**  
 (Data summarized in table 40.)

Source	df	Mean	CV
		MS	MS
Among taxa	9	5209.01****	213.73
Typical <i>E. vittata</i> vs lemniscate race	1	261.08	235.20
<i>E. vittata</i> vs <i>E. occidentalis</i>	1	2384.93	144.61
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	1090.78	121.22
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	1502.22	814.00
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	10828.94***	193.06
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	1	14566.70****	35.79
Within taxa	36	1006.66	209.76

males, although not significantly so. As indicated in table 42, the effect of mating status on variability in number of eggs per mass per female is significant at the 5 percent level. Variability was greater in virgins than in mated females in all taxa studied, although only in *E. temexa* is the difference significant at the 5 percent level.

As indicated by the generally low means of coefficients of variation in table 40 and illustrated for *E. temexa* by individual records in figure 38, there is considerable consistency in the number of eggs in successive masses produced by a female. This consistency is achieved, we believe, by synchronous production of an egg by each ovariole in each oviposition period. Because of their physical condition after death, females maintained in the paired situation and their virgin counterparts were not suitable for ovariole counts. As a result, we cannot assert positively that there is a one-to-one relationship between the number of ovarioles possessed by a female and the number of eggs produced at a single oviposition. There is, however, a strong correlation ( $r = 0.812$ ) between taxa means of number of eggs per mass produced by mated females and number of ovarioles per female, as shown in figure 39.

Taxa means of number of eggs per mass per female in figure 39 are those obtained from reared females in the paired situation (table 40). Taxa means of number of ovarioles per female were obtained from an entirely different set of field-caught and reared females that had

TABLE 42  
**Analysis of Variance of Multiple Regression Models for Mean and Coefficient of Variation of Number of Eggs Per Mass Per Female for Species Represented by Both Mated and Virgin Females**  
 (Data summarized in table 40.)

Source	df	Mean	CV
		MS	MS
Taxa	4	59288.28****	741.52
Mating status	1	4499.37**	970.81*
Interaction	4	2509.79**	1082.42
<i>E. vittata</i>	1	47.04	61.18
<i>E. occidentalis</i>	1	6129.12***	657.71
<i>E. temexa</i>	1	2675.83*	1248.25*
<i>E. tamara</i>	1	4934.42**	81.43
<i>E. luteolineata</i>	1	769.75	5.35
Residual	26	574.36	172.03
R <sup>2</sup>		0.850	0.375

been fixed in alcoholic Bouin's solution and preserved in 70 percent alcohol; these means are given in table 50. Examination of quadratic and cubic components of regression indicates that a simple linear model is adequate. The estimated regression equation is  $\hat{y} = 48.92 + 0.797X$ , where  $\hat{y}$  is mean eggs per mass per female and  $X$  is mean number of ovarioles per female. This model accounts for 66.0 percent of the variation; the regression is significant at less than the 0.5 percent level ( $F_{1,7} = 16.96***$ , MS (error) = 596.45). The use of

separate data sets, although necessary in this case, is undesirable because number of ovarioles is related to female size within taxa (see below).

While the relationship shown in figure 39 does not conform precisely to the hypothesis stated above, it does seem sufficiently in agreement (considering the nature of the data) as to offer support for it.

Previous estimates of number of eggs per mass in species of the Vittata Group are generally lower than ours. Riley (1878) estimated "about 130" eggs per mass for *E. vittata* and *E. pestifera* (as *E. marginata*). It is uncertain whether his *E. vittata* consisted solely of that species or a mixture of it and *E. occidentalis*.

Webster's (1915) mean of 76.9 eggs per mass for 16 masses of *E. vittata* is biased by inclusion of one or more obviously incomplete ovipositions. For *E. occidentalis* in Louisiana Ingram (1927) estimated "about 120" eggs per mass, later modified to "usually over 100" (Ingram and Douglas, 1932). Gilbertson and Horsfall (1940) gave means of 110 and 103 eggs per mass, based on separate samples of 49 and 14 masses, respectively, the latter produced by eight females and the former by an unspecified number. That study was based on mixed samples of *E. vittata* and *E. occidentalis*.

A word of caution is in order with respect to estimates of egg production in taxa or other groups based on the averaging of values for

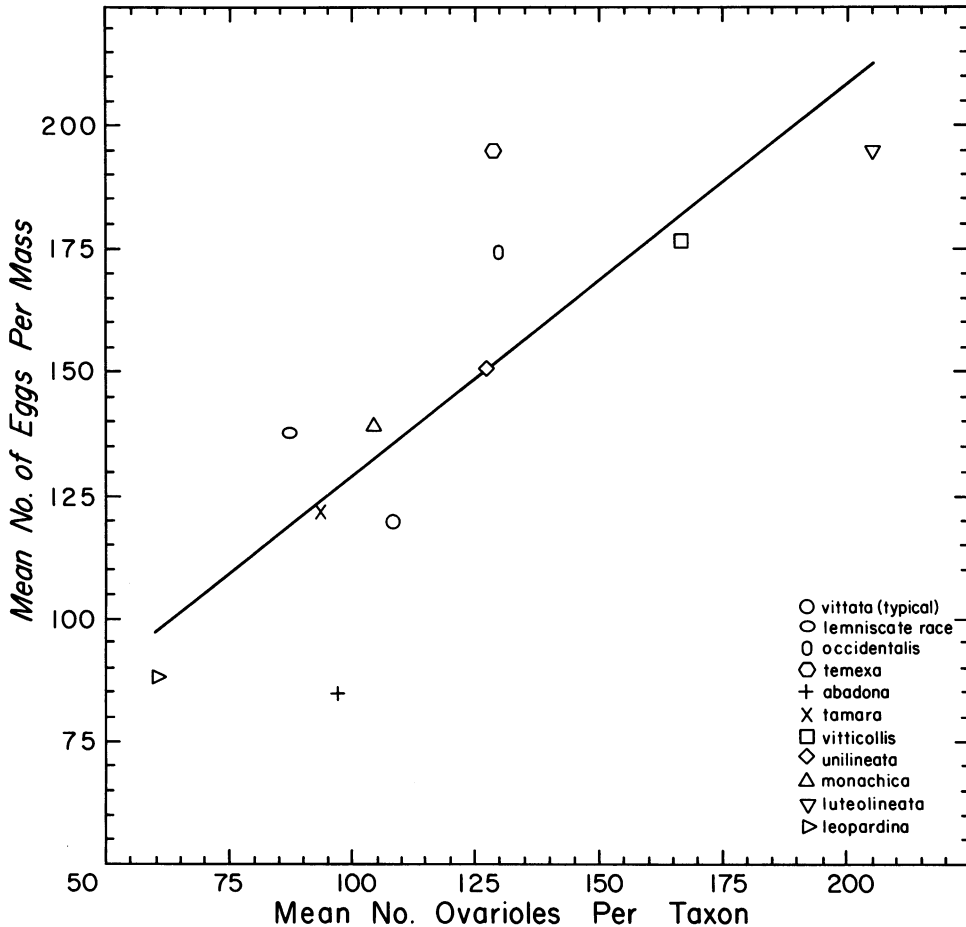


FIG. 39. Relationship of mean number of eggs per mass per female and number of ovarioles per female among taxa of the Vittata Group. Plotted points are taxa means.

egg mass without regard to the number of females producing the masses. In the first place, as we later show, within a given taxon larger females tend to have more ovarioles than smaller females and thus are presumably capable of producing numerically larger egg masses. In addition, inclusion of egg masses produced by unmated females may seriously bias the estimate for a group.

**DAILY RATE OF EGG PRODUCTION:** For each female represented in the restricted oviposition data set we determined daily rate of egg production by dividing the total number of eggs produced by the total number of days the female lived as an adult. The data are summarized in table 43. For mated females there are significant differences between *E. occidentalis* and *E. temexa* and among the three South American species (table 44). *Epicauta temexa* achieves a higher rate than the sympatric *E. occidentalis* by having shorter intervals between ovipositions (table 36) and laying about 20 percent more eggs per mass (table 40). The basis for the superiority of *E. monachica* over *E. luteolineata* is similar. The unusually low rate of egg production in *E. leopardina* reflects, for the most part, delayed ontogeny of oviposition in females (which is not compensated for fully by their tendency to continue oviposition relatively late in life), and the relatively small number of eggs constituting a mass. As shown (table 36), the mean oviposition-to-oviposition interval in *E. leopardina* is longer than in *E. luteolineata* but shorter than in *E. monachica*.

Mean rate of egg production was consistently lower in virgin females than in mated ones in all taxa studied in this regard. In both *E. temexa* and *E. tamara* (table 45) the differences are highly significant. The inferiority of virgin females reflects to varying degrees, depending on species, delayed onset of oviposition, prolongation of the interval between ovipositions, and reduction in the number of eggs per mass.

**EGG SIZE:** In this section we consider the size of individual eggs in the taxa of the Vittata Group and the relationship of the size of eggs to the size and mating status of the females producing them. The data are drawn from records of 82 reared females (50 mated, 32 vir-

gin). Mated females were maintained in the paired situation; virgins were treated similarly but never exposed to males.

As a measure of a female's body size we took the length (mm.) of one of her elytra; measurements were made on dried, pinned specimens. For her egg size we averaged individual estimates of volume in four eggs

TABLE 43  
Eggs Per Day of Adult Life Per Female

Taxa	Mean	SE	N Females
MATED FEMALES			
<i>E. vittata</i>			
Typical race	5.33	0.0	1
Lemniscate race	8.35	0.461	5
<i>E. occidentalis</i>	13.27	1.646	4
<i>E. temexa</i>	22.58	2.339	7
<i>E. tamara</i>	11.58	2.053	3
<i>E. vitticollis</i>	13.09	3.111	5
<i>E. unilineata</i>	10.05	2.951	4
<i>E. monachica</i>	10.77	1.377	8
<i>E. luteolineata</i>	18.14	2.543	6
<i>E. leopardina</i>	5.46	1.286	3
VIRGIN FEMALES			
<i>E. vittata</i> (typical race)	4.49	0.400	2
<i>E. occidentalis</i>	6.68	2.220	2
<i>E. temexa</i>	5.09	0.0	1
<i>E. tamara</i>	4.11	0.657	5
<i>E. luteolineata</i>	16.21	0.982	5

TABLE 44  
Analysis of Variance of Rate of Egg Production  
in Mated Females  
(Data summarized in table 43.)

Source	df	MS
Among taxa	9	135.105****
Typical <i>E. vittata</i> vs lemniscate race	1	7.600
<i>E. vittata</i> vs <i>E. occidentalis</i>	1	50.397
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	220.630**
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	20.632
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	186.229**
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	1	177.182*
Within taxa	36	25.004

TABLE 45  
**Analysis of Variance of Multiple Regression Model for Rate of Egg Production in Taxa Represented by Both Mated and Virgin Females**  
 (Data summarized in table 43.)

Source	df	MS
Taxa	4	190.968****
Mating status	1	251.139***
Interaction	4	48.880
<hr/>		
<i>E. vittata</i> (typical race)	1	0.365
<i>E. occidentalis</i>	1	57.904
<i>E. temexa</i>	1	267.663***
<i>E. tamara</i>	1	104.627**
<i>E. luteolineata</i>	1	10.159
<hr/>		
Residual	26	19.991
<hr/>		
R <sup>2</sup> = 0.666		

sampled randomly from one of her masses. The volume of an egg was estimated by applying the formula for the volume of a cylinder to measurements of egg length and diameter (at the middle). It would be preferable to express both sizes in the same type of units. However, we were hesitant to estimate volume in females because of shrinkage that occurs in the abdomen after death, and a direct measure of volume during life was undesirable because it would be influenced by total egg volume in females. On the other hand, we regard egg volume as more meaningful than either length or diameter in view of differences in the shape of eggs among species.

Estimated egg volumes for mated and virgin females are summarized by taxa in table 46. It is immediately apparent that virgin females, on the average, lay smaller eggs than mated ones and that intertaxa variation is of considerable magnitude.

As a first step in the analysis of the data we considered the relationship of egg volume to female elytral length within taxa for mated females. This entailed fitting a model incorporating 10 terms for taxa, one for elytral length, and 10 for interaction. Significant effects were determined only for taxa (table 47). With interaction dropped from the model the regression of egg volume on elytral length is positive (b

= 0.263, SE = 0.0342). However, there is no convincing evidence that egg volume varies with elytral size *within taxa*. (Intertaxa variation in adult body size is treated elsewhere; because of the strong relationship between adult size and egg size among taxa, shown below,

TABLE 46  
**Volume (mm<sup>3</sup>) of Individual Eggs Produced by Reared Females**

Taxa	Mean	SE	N Females
MATED FEMALES			
<i>E. vittata</i>			
Typical race	0.491	0.140	3
Lemniscate race	0.485	0.460	5
<i>E. occidentalis</i>	0.234	0.021	5
<i>E. temexa</i>	0.387	0.032	7
<i>E. abadona</i>	0.837	0.099	3
<i>E. tamara</i>	0.432	0.050	5
<i>E. vitticollis</i>	0.511	0.018	5
<i>E. unilineata</i>	0.226	0.032	4
<i>E. monachica</i>	0.805	0.048	5
<i>E. luteolineata</i>	0.832	0.080	4
<i>E. leopardina</i>	1.215	0.232	4
VIRGIN FEMALES <sup>a</sup>			
<i>E. vittata</i> (typical race)	0.357	0.057	6
<i>E. occidentalis</i>	0.170	0.033	2
<i>E. temexa</i>	0.237	0.022	7
<i>E. tamara</i>	0.423	0.038	5
<i>E. vitticollis</i>	0.440	0.038	5
<i>E. monachica</i> <sup>a</sup>	0.518	0.019	3
<i>E. luteolineata</i>	0.449	0.031	4

<sup>a</sup>Elytral length was not determined for virgin females of this species.

TABLE 47  
**Analysis of Variance of Multiple Regression Model for Egg Volume as a Function of Elytral Length of Females, Within Taxa**  
 (Data summarized in table 46.)

Source	df	MS
Regression	21	0.1964
Taxa	10	0.3867****
Elytral length	1	0.0170
Interaction	10	0.0218
Residual	28	0.0313
<hr/>		
For model containing only species, R <sup>2</sup> = 0.777.		

there seems to be no purpose in detailed investigation of intertaxa differences in egg size.)

Following the above analysis we regressed taxa means of egg volume on taxa means of elytral length. Quadratic and cubic terms proved to be insignificant, but there is a fairly strong linear relationship ( $r = 0.587$ ) between egg size and female size among taxa (table 48). The taxa means and the estimated linear regression equation are plotted in figure 40. The equation is  $\hat{y} = -1.491 + 0.186X$ , where  $\hat{y}$  is egg volume ( $\text{mm}^3$ ) and  $X$  is elytral length (mm.). *Epicauta leopardina* has unusually large eggs, even considering the large size of the females. *Epicauta occidentalis* and *E. temexa* appear to have disproportionately small eggs. This reflects partially the fact that adults of these last two species are unusually slender. Since their ratio of elytral length to body volume is greater than that of other species of the group, our index of body size tends to make *E. occidentalis* and *E. temexa* appear larger than they "really" are.

Finally, we investigated the difference already noted in the size of eggs produced by mated and virgin females. Initially we fit a model to the data summarized in table 46 that incorporated taxa, mating status, their interaction as well as a linear covariate representing elytral length in females. *Epicauta monachica* was omitted because the size of virgin females of this species was not determined (females were not preserved after death). The partial linear regression of egg volume ( $\text{mm}^3$ ) on elytral length (mm.) is 0.0207, not significantly different from zero at the 5 percent level ( $F_{1,41} = 1.212$ , MS (residual) = 0.0110). We subse-

quently dropped the covariate in the interest of including *E. monachica* in the analysis.

Analysis of the new model (table 49) demonstrates very highly significant effects for mating status and, as expected, taxa, with no significant interaction. In every taxon studied the mean size of eggs from virgins was less than that from mated females, although in the case of *E. tamara* the difference is small. The unweighted mean of taxa means of egg volume for virgins (346.0) is only two-thirds that for mated females (586.8).

**FECUNDITY AND BODY SIZE OF THE FEMALE:** In the preceding section we showed that taxa of large adult body size tend to have large eggs but failed to establish a relationship between adult body size and egg size within taxa. We now ask whether there is a relationship between fecundity and body size (elytral length).

Our measures of fecundity are mean number of eggs per mass per female, rate of egg production per day, and number of ovarioles per female, all highly correlated. For analysis of the first two measures we extracted from the restricted reproductive data set information for 39 mated females for which there were records of number of eggs per mass and eggs per day of adult life as well as of female body size. For the analysis of number of ovarioles we utilized records of some 52 females, 36 of which were field-caught and the remainder reared; these records are summarized in table 50.

**VARIATION AMONG TAXA:** For taxa means of each of the fecundity measures we tested for linear regression on elytral length. In no case

TABLE 48  
Analysis of Variance of Regression of Means of Egg Volume for Taxa on Means of Elytral Length for Taxa  
(Data for mated females only table 46.)

Source	df	MS
Regression (elytral length)	3	0.2314*
Linear term	1	0.5062***
Quadratic and cubic terms	2	0.0890
Residual	7	0.0307

For linear model,  $R^2 = 0.557$ .

TABLE 49  
Analysis of Variance of Multiple Regression Model for Egg Volume as a Function of Taxa and Mating Status of Females  
(Data summarized in table 46.)

Source	df	MS
Regression	13	0.1426
Taxa	6	0.2021****
Mating status	1	0.2741****
Interaction	6	0.0120
Residual	68	0.0153

$R^2 = 0.641$



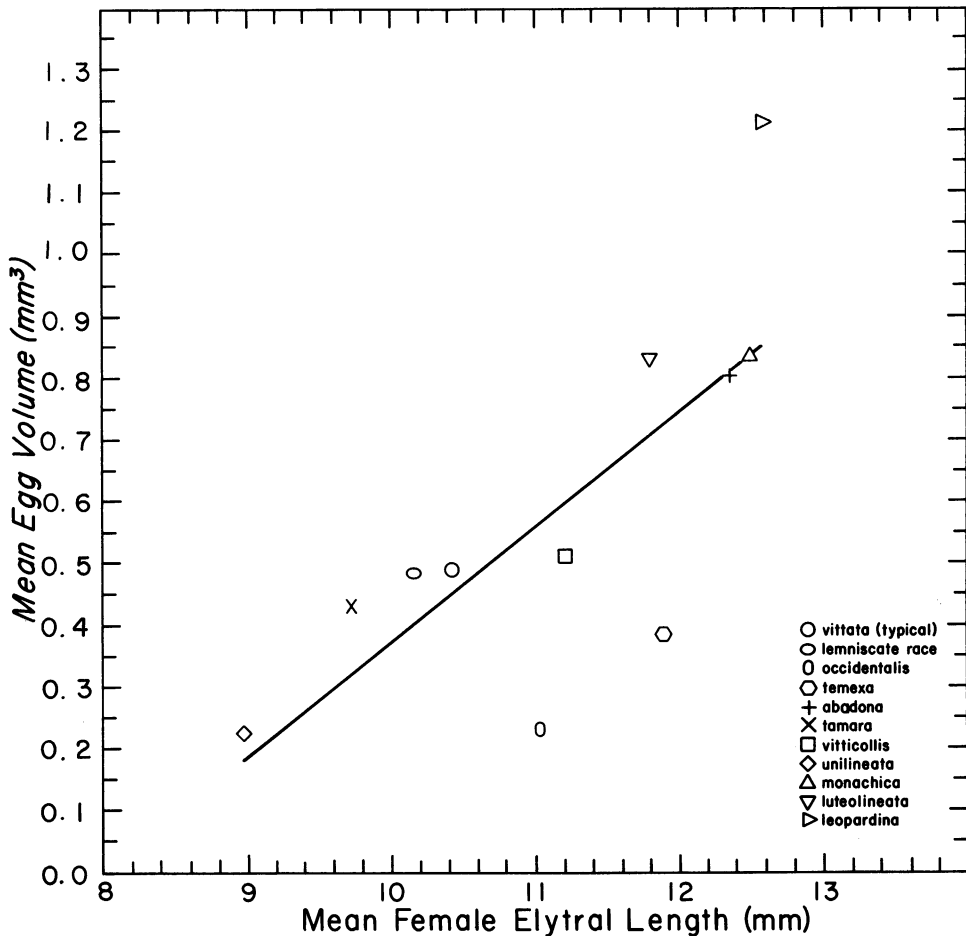


FIG. 40. Relationship of size of eggs and mean elytral length of females producing them among taxa of the Vittata Group. Plotted points are taxa means.

was the regression significant at the 5 percent level (table 51). The regressions of mean number of eggs per mass and number of ovarioles for taxa on mean female elytral length for taxa are graphed in figures 41, 42, respectively. We conclude that there is no simple relationship between these measures of fecundity and body size of the female at the level of taxa.

**VARIATION WITHIN TAXA:** In order to investigate whether fecundity varies with body size within taxa we fit, for each of the three fecundity measures, a multiple regression model incorporating terms for taxa, a linear term for elytral length, and terms for the interaction of

these two factors. The regression models for number of eggs per mass and number of eggs per day (table 52) did not account for significant amounts of variation. However, a significant linear relationship between number of ovarioles and body size was detected, the nature of which varies significantly among taxa (table 53). As shown in figure 43, number of ovarioles increases linearly with elytral length in each taxon, but the slope of the estimated regression line varies greatly among taxa. Lack of significance in the first two measures is attributable, we believe, partially to the smaller size of the sample employed and partially to

TABLE 50  
Number of Ovarioles and Elytral Length (in Millimeters) in Mated Females<sup>a</sup>

Taxa	Number of Ovarioles		Elytral Length		N Females
	Mean	SE	Mean	SE	
<i>E. vittata</i>					
Typical race	108.7	10.70	10.8	0.74	6
Lemniscate race	87.5	1.73	9.9	0.17	6
<i>E. occidentalis</i>	130.0	8.75	11.5	0.34	6
<i>E. temexa</i>	128.8	9.77	11.1	0.42	6
<i>E. abadona</i>	96.8	10.05	12.8	0.63	4
<i>E. tamara</i>	93.8	2.94	8.9	0.26	6
<i>E. vitticollis</i>	167.0	0.0	11.4	0.0	1
<i>E. unilineata</i>	127.3	5.21	8.2	0.24	3
<i>E. monachica</i>	104.7	13.86	12.6	0.64	6
<i>E. luteolineata</i>	205.5	12.50	11.0	0.20	2
<i>E. leopardina</i>	60.5	3.33	12.1	0.62	6

<sup>a</sup>Data for *E. vittata*, *E. occidentalis*, *E. temexa*, *E. monachica*, and *E. leopardina* obtained from field-caught females. Data for *E. abadona* obtained from two reared and two field-caught females. Data for other taxa obtained from reared females.

TABLE 51  
Analyses of Variance of Linear Regression of Taxa Means of Fecundity Measures on Taxa Means of Elytral Length (Mated females only<sup>a</sup>)

Source	df	Eggs per mass	Eggs per day	No. of ovarioles	
		MS	MS	df	MS
Elytral length	1	136.92	41.02	1	58.71
Residual	8	1475.75	36.65	9	1762.91
R <sup>2</sup>		0.012	0.123		0.004
r		0.107	0.350		-0.061

<sup>a</sup>Eggs per mass and eggs per day from 39 females in restricted reproductive data set (*E. abadona* not represented) (Number of ovarioles from data set summarized in table 50.)

the fact that reared females, which constituted the entire sample, are more uniform in size than those in field-caught samples.

To summarize: (1) Egg size is apparently independent of female body size *within* taxa but varies directly with it *among* taxa. (2) Fecundity (as indicated by number of ovarioles per female, at least) varies directly with female body size *within* taxa but bears no simple relationship to it *among* taxa. It is true that *E. leopardina*, with the largest eggs (and larvae) in the group, has the lowest fecundity. But large egg size is not necessarily associated with

low fecundity. Rather, each taxon seems to have made a separate compromise between the size and number of eggs produced.

Lack of correlation between adult body size and egg size within taxa may be explained, perhaps, on the basis that there is an optimal egg (and larval) size for each taxon which is determined by the amount of food available in the pods of the common or favored grasshopper hosts. Under these circumstances, however, larger females could increase their reproductive value by producing more larvae. Whether, like variation in adult body size, variation in fecun-

dity within taxa is controlled by both genetic factors and the amount of food consumed by developing larvae is an interesting question for future investigation.

DEVELOPMENT AND HATCHING OF EGGS

This section is devoted to a summary and analysis of information on the proportion of eggs developing and hatching and the incubation period or time to hatch for eggs maintained

under the physical conditions described in the section on Materials and Methods. Ontogeny beyond the point of eclosion of triungulin larvae from eggs will be treated in a separate work. The data for this section are from the restricted reproductive data set.

EGGS FROM MATED FEMALES

Taxa means of the percentage of eggs developing to a recognizable embryonic stage and the percentage of eggs hatching are given in

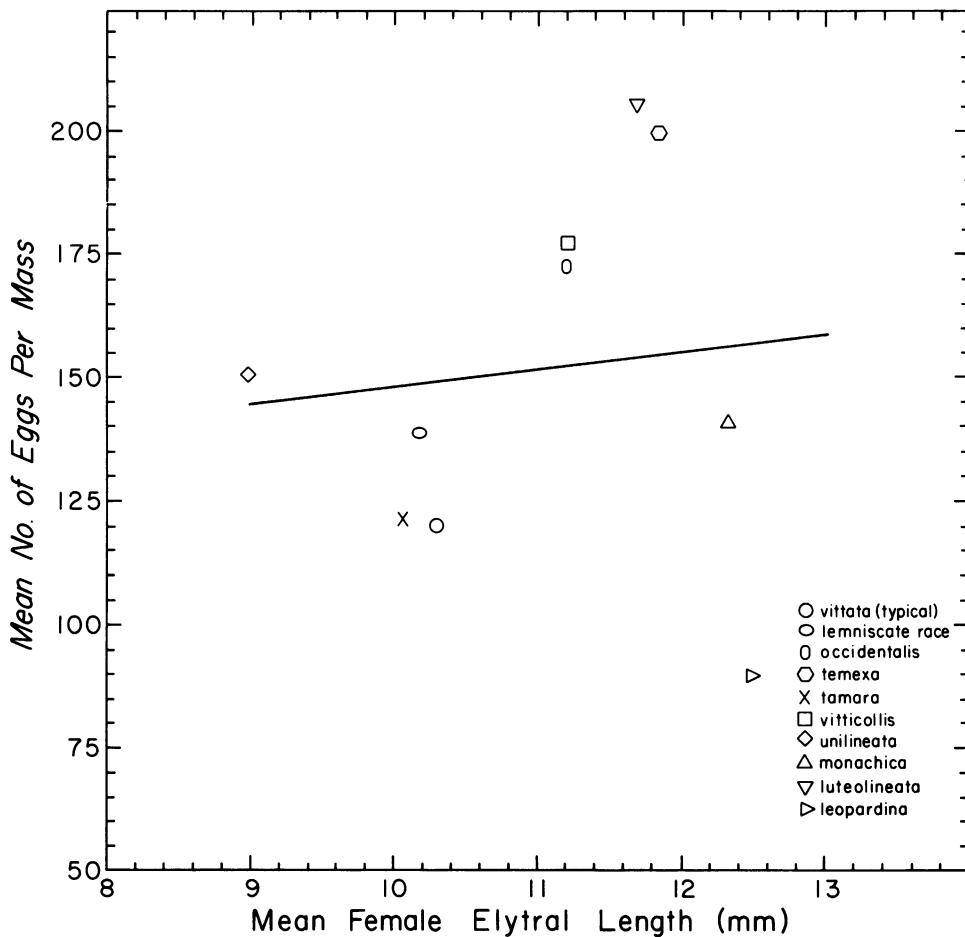


FIG. 41. Relationship of mean number of eggs per female and female elytral length among taxa of the Vittata Group. Plotted points are taxa means. The regression ( $\hat{y} = 113.35 + 3.44X$ ) is not significant at the 5 percent level.

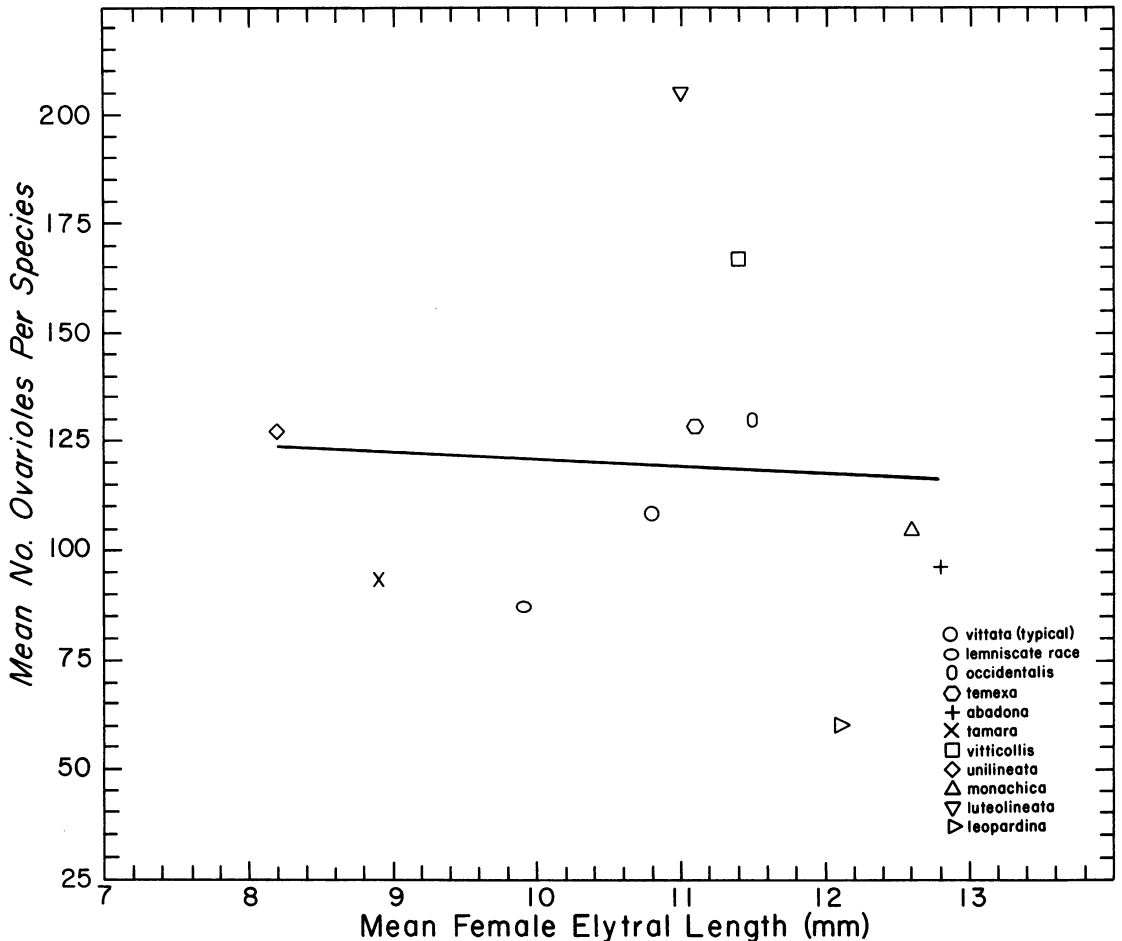


FIG. 42. Relationship of number of ovarioles per female and female elytral length among taxa of the Vittata Group. Plotted points are taxa means. The regression ( $\hat{y} = 137.48 - 1.67X$ ) is not significant at the 5 percent level.

table 54. Analyses of variance indicate that the significance of variation among taxa means is slightly below the 5 percent level for both variables. For percentage developing,  $F_{9,36} = 2.56^*$ , MS (within) = 0.647; for percentage hatching,  $F_{9,36} = 2.82^*$ , MS (within) = 0.099. The analyses were done on proportions transformed as the square root of the arcsin.

Time (days) to hatch is summarized by taxa in table 55 and analyzed in table 56 by means of a nested analysis of variance. Variation among taxa is highly significant, but the signifi-

cance of the variance component for females within taxa does not reach the 5 percent level. Standard single degree of freedom contrasts between taxa show that hatching time is significantly shorter in typical *E. vittata* than in the lemniscate race and highly significantly shorter in *E. vitticollis* than in *E. unilineata*. The latter difference is perhaps the more interesting inasmuch as the species are sympatric and the original stocks of material were obtained from precisely the same locality. It should be remembered, of course, that eggs in our labora-

tory were incubated at a constant temperature (27° C.), and it would not be safe to infer that *E. vitticollis* has a shorter incubation than *E. unilineata* in nature.

PARTHENOGENESIS

In the course of our study we obtained the first records of parthenogenesis in Meloidae. As far as determined, the process is incomplete in the sense that we have not established that larvae emerging from eggs produced by virgin

females are capable of developing to the adult stage. Moreover, only a small proportion of eggs of this sort hatched, and there was a high incidence of defects among emerging larvae. Nevertheless, our discovery raises the distinct possibility of functional parthenogenesis in the present group and perhaps other groups of Meloidae as well.

Development was recorded in eggs of nine (28.1%) of 32 virgin females studied, representing six taxa (table 57). Lack of recorded parthenogenesis in *Epicauta occidentalis* and *E.*

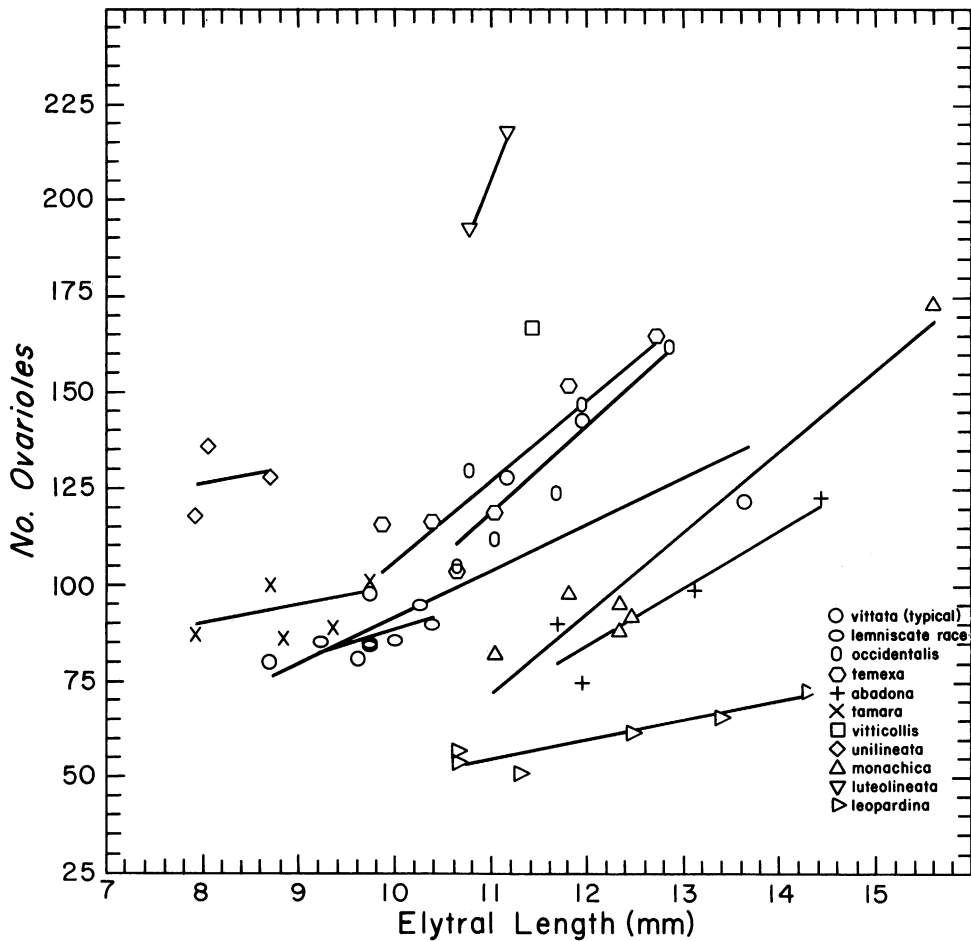


FIG. 43. Relationship of number of ovarioles per female and female elytral length within taxa of the Vittata Group. The lines are loci of adjusted means from evaluation of the estimated regression equation analyzed in table 53.

*monachica* probably reflects inadequacy of the samples of those species. Certainly there is no basis in the present data for concluding that the incidence of parthenogenetic development of eggs varies among taxa. Information on the percentage of eggs developing and hatching is based on the examination, at a magnification of 10X, of some 16,403 eggs from virgin females and about 66,000 eggs from mated females. Eggs were classified as undeveloped (no visible

embryo), developed but unhatched (a recognizable embryo within the egg), or hatched.

The percentage of unfertilized eggs developing to the stage of a recognizable embryo or beyond was 11.6 (1918) and the percentage of eggs hatching was 0.77 (127). Among eggs showing development, the percentage hatching was 6.62. As shown in table 58, the percentage of eggs developing parthenogenetically varied greatly among females, ranging from a low of 0.1 of 1477 eggs for a female of *E. luteolineata* to a high of 89.4 of 113 eggs (one egg mass) for a female of *E. temexa*. An analysis of

TABLE 52  
Analyses of Variance of Multiple Regression Models for Mean Number of Eggs Per Mass Per Female and Number of Eggs Per Day Per Female  
(Mated females only.<sup>a</sup>)

Source	df	Eggs per mass		Eggs per day	
		MS	MS	MS	MS
Regression	18	2751.37**	82.25***		
Taxa	9	3982.98***	125.22****		
Elytral length	1	265.27	17.78		
Interaction <sup>b</sup>	8	1439.86	28.88		
Residual	20	866.09	23.21		
R <sup>2</sup>		0.741	0.761		

<sup>a</sup>Data from 39 females in restricted reproductive data set (*E. abadona* not represented).

<sup>b</sup>*E. vittata* (typical race) omitted from interaction because only one female represented.

TABLE 53  
Analysis of Variance of Multiple Regression Model for Number of Ovarioles Per Female  
(Data summarized in table 50. *E. vitticollis* omitted.)

Source	df	MS
Regression	19	2984.67****
Taxa	9	5779.09****
Elytral length	1	10727.21****
Interaction	9	282.08*
Residual	31	
Quadratic and cubic terms for elytral length	2	185.06
Error	29	106.57 <sup>a</sup>
R <sup>2</sup> = 0.943		

<sup>a</sup>Used as denominator in F-tests of all factors.

TABLE 54  
Development and Hatching of Eggs Produced by Mated Females

Taxa	% developing			% hatching			N females	Mean no. eggs examined/female
	Mean <sup>a</sup>	SE	Range	Mean <sup>a</sup>	SE	Range		
<i>E. vittata</i>								
Typical race	57.0	0.0	—	26.2	0.0	—	1	240.0
Lemniscate race	41.4	8.8	18-63	15.0	5.3	3-30	5	602.2
<i>E. occidentalis</i>	51.7	19.2	20-83	37.9	16.7	0-67	4	1273.8
<i>E. temexa</i>	83.6	7.6	40-99	71.0	11.1	8-97	7	2116.3
<i>E. tamara</i>	76.7	5.7	70-88	60.6	10.6	48-82	3	1729.7
<i>E. vitticollis</i>	60.4	12.6	21-91	41.8	16.2	0-83	5	1508.6
<i>E. unilineata</i>	64.8	11.9	45-97	51.5	16.8	24-96	4	1309.2
<i>E. monachica</i>	84.3	2.4	75-92	75.2	4.6	56-90	8	1480.9
<i>E. luteolineata</i>	83.0	7.1	54-99	70.9	8.6	46-97	6	1775.0
<i>E. leopardina</i>	79.3	0.6	69-89	62.9	1.3	37-80	3	517.0
Mean (unweighted)	68.22			51.30				

<sup>a</sup>Mean of female means.

variance of the proportion of eggs developing (transformed as the square root of the arcsin) fails to establish significant variation among taxa ( $F_{3,5} = 0.73$ , MS (within) = 0.17). Hatching was recorded in three of the four species showing parthenogenesis. The percentage of eggs hatching ranged from 0.3 for single females of *E. vittata* and *E. temexa* to 5.0 percent for a female of *E. luteolineata*. In view of the fact that females were maintained, insofar as possible, under the same conditions with respect to temperature, humidity, light, and food, the great variance among virgin females with respect to incidence of development of

eggs suggests a strong genetic component in the determination of parthenogenesis.

For virgin females 1 and 2 of *E. temexa* (table 58) the percentage of eggs developing to the embryonic stage was greater than the minimum recorded among mated females of that species; indeed, the percentage of developing eggs for virgin female 2 surpassed the mean for mated females. With respect to percentage of total eggs hatching and percentage of developing eggs hatching, comparison of the individual values for virgin females with the taxa means and ranges for mated females should be suffi-

TABLE 55  
Hatching Time (Days) of Egg Masses from Reared, Mated Females Incubated at 27° C., 100% RH, in Darkness

Taxa	Mean <sup>a</sup>	SE	Range	N Masses
<i>E. vittata</i>				
Typical race	11.0	0.00	—	2
Lemniscate race	13.1	0.39	12-15	9
<i>E. occidentalis</i>	9.3	0.22	8-10	12
<i>E. temexa</i>	9.7	0.10	9-13	71
<i>E. tamara</i>	14.9	0.22	13-19	32
<i>E. vitticollis</i>	12.6	0.18	12-15	30
<i>E. unilineata</i>	17.7	0.23	17-21	20
<i>E. monachica</i>	12.4	0.09	11-15	78
<i>E. luteolineata</i>	12.1	0.07	11-14	68
<i>E. leopardina</i>	12.6	0.27	11-16	19
Mean (unweighted)	12.54			

<sup>a</sup>Mean of female means.

TABLE 56  
Analysis of Variance of Hatching Time (Days) of Eggs from Mated Females (Data summarized in table 55.)

Source	df	MS
Among taxa	9	153.37****
Typical <i>E. vittata</i> vs lemniscate race	1	7.22*
<i>E. vittata</i> (typical race) vs <i>E. occidentalis</i>	1	4.95
<i>E. occidentalis</i> vs <i>E. temexa</i>	1	1.64
<i>E. vitticollis</i> vs <i>E. unilineata</i>	1	312.12****
<i>E. monachica</i> vs <i>E. luteolineata</i>	1	3.27
<i>E. monachica</i> and <i>E. luteolineata</i> vs <i>E. leopardina</i>	1	1.94
Females (in taxa)	41	1.52 <sup>a</sup>
Egg masses (in females)	290	0.70

<sup>a</sup>The denominator used in F-ratios testing overall significance of differences among taxa and contrasts of taxa is a synthesized MS for females (in taxa) having the value 1.73, with approximately 34 degrees of freedom.

TABLE 57  
Incidence of Parthenogenesis in Virgin Females of Six Taxa of the Vittata Group

Taxa	No. females studied	% with parthenogenesis	Eggs Examined	
			Total	Mean/female
<i>E. vittata</i> (typical race)	7	14.3	2067	295.3
<i>E. occidentalis</i>	2	0.0	569	284.5
<i>E. temexa</i>	12	33.3	2643	220.2
<i>E. tamara</i>	5	20.0	2623	524.6
<i>E. monachica</i>	1	0.0	109	109.0
<i>E. luteolineata</i>	5	60.0	8392	1678.4
All taxa	32	28.1	16403	512.6

TABLE 58  
Development and Hatching of Eggs Produced by Virgin, Parthenogenetic Females

Taxa and female	Total eggs examined	% developing <sup>a</sup>	% hatching	% of developing eggs hatching
<i>E. vittata</i> (typical race)				
1	773	14.5	0.3	1.8
<i>E. temexa</i>				
1	365	60.6	0.3	0.5
2	113	89.4	0.0	0.0
3	200	8.0	0.0	0.0
4	221	11.8	0.0	0.0
all (unweighted means)	224.8	42.4	0.08	0.12
<i>E. tamara</i>				
1	484	0.2	0.0	0.0
<i>E. luteolineata</i>				
1	1630	39.5	5.0	12.8
2	2528	30.8	1.7	5.7
3	1477	0.1	0.0	0.0
all (unweighted means)	1878.3	23.5	2.23	6.17

<sup>a</sup>To the point of having an embryo recognizable as such by external examination under a dissecting microscope.

cient to indicate that the probability of hatching is drastically reduced in the former case.

Recorded hatching times of eggs produced by virgin females suggest that, on the average, unfertilized eggs require two to four days longer to hatch than fertilized ones. For example, for 11 egg masses from virgin females of *E. luteolineata* the mean recorded hatching time is 15.9 days, with a range of 13-25, which contrasts with a mean of 12.1 and a range of 11-14 days for 68 egg masses from mated females of that species (table 55). However, the data for virgin females are biased. In particular, very light hatching was sometimes not detected on the day that it occurred. Indeed, in a few instances we were not aware that hatching had occurred until preserved egg masses were examined for development. It is perhaps true that hatching time in eggs developing parthenogenetically is somewhat longer and more irregular in length than in normal, fertilized eggs, but it is best not to draw conclusions in this regard at present.

Many of the parthenogenetically produced embryos and larvae exhibited abnormalities in the formation of the mouthparts and sclerites of the body. Among larvae the defects were sometimes sufficiently severe so as to impair loco-

motion. In addition, survival time of larvae without food was shorter than normal. However, a small proportion of larvae had no recognizable defects, either anatomical or behavioral.

At this point it is only fair to state that we have no way of being certain that a given egg mass produced by a mated female was, in fact, fertilized. In fact, some of the variation in hatching success among mated females and among egg masses within mated females may be the result of abnormalities in the fertilization process. However, for the vast majority of egg masses from mated females, the high level of success in hatching and absence of gross anatomical abnormalities in embryos and larvae would argue against the common occurrence of parthenogenesis in females permitted to mate freely.

**ATTEMPTED REARING OF LARVAE:** An unsuccessful effort to rear six larvae that had developed parthenogenetically from an egg mass produced by female 1 of *E. luteolineata* was initiated June 22, 1972. The egg mass contained 278 eggs, of which 118 (42.4%) developed to at least the embryo stage and 30 (10.8%) hatched. Nineteen (63.3%) of the triungulins died on the day of hatching. The rear-



ing procedure, described briefly in Materials and Methods, had been used with great success previously for all taxa of the Vittata Group in the present study as well as for many other species of *Epicauta*. Glass tubes containing individual larvae and 20 grasshopper eggs were held on a daily temperature cycle ranging from a low of 24° C. to a high of 30° C. (mean of 27° C.) at 100 percent RH in darkness.

All six of the parthenogenetically produced larvae died in the first instar, apparently without feeding. At time of death, three of them were four days old, two were eight days old, and the last survivor was 10 days old. The mean survival time, 6.5 days, is well within what may be termed the normal range of variation for unfed larvae produced from fertilized eggs. In a much more extensive counterpart of this rearing involving larvae of *E. luteolineata* from eggs produced by mated females all larvae fed, and there was no mortality in the first four instars.

**DISCUSSION:** We trust that the information given here, meager as it is, will alert other workers to the possibility of functional parthenogenesis in Meloidae. Although our rearing attempt failed, we believe that a more ambitious one will likely lead to successful rearing of parthenogenetically produced larvae to the adult stage. Preliminary examination of em-

bryos suggests that the parthenogenetically produced individuals are diploid. However, this should be verified.

Because parthenogenesis is commonly associated with parasitism, it is interesting to speculate that it has special evolutionary potential in a group such as Meloidae, all species of which are parasitoids in the immature stages. In particular, the wide dispersion of adults developing in scattered nesting burrows of bees might be especially conducive to the evolution of parthenogenesis.

Although this is the first report of parthenogenesis in Meloidae, there is no reason to believe that it is a unique attribute of the Vittata Group. Rather, it seems likely that we have found parthenogenesis in this group simply because we have had the opportunity to incubate large numbers of unfertilized eggs. As a general rule, virgin females of Meloidae do not commonly produce eggs. In the Albida Group of *Epicauta*, for instance, Selander and Mathieu (1969) found that initiation of the egg production cycle in females depends on insemination. Occasionally a female held in the virgin state for a long period of time produced an egg mass, but there was nothing in that group comparable to the nearly normal pattern of repeated ovipositions shown by virgin females of the Vittata Group.

## PATTERNS OF VARIATION IN BIOLOGICAL CHARACTERS

### INTERSPECIFIC VARIATION

What factors determine the particular pattern of geographic variation exhibited by the species of the Vittata Group and, in particular, the degree of geographic overlap or sympatry of the species? Are there differences between sympatric species that are lacking or less marked in allopatric species? Are there ecological correlations of biological characters that help to explain distributional differences between species? These are some of the questions that prompted us to undertake this study. Some progress toward their solution has been made,

although in the main the answers seem as elusive now as when the study began.

Field and laboratory studies reported here establish a high degree of uniformity among the species of the group in all characters except those of male courtship behavior. Furthermore, preliminary analysis of our data indicates comparable homogeneity in the larval and pupal stages. As shown in previous sections, statistically significant interspecific variation occurs in most of the biological characters studied, but in general the range of variation is decidedly limited and in relatively few instances do differences between sympatric species account for

an appreciable or, for that matter, even a statistically significant portion of the variation. As discussed below, differences in courtship behavior are especially marked between sympatric species. Yet in other aspects of reproductive biology as well as in those characters more immediately related to adaptation to the physical environment, such as habitat selection, feeding behavior, seasonal occurrence of the adult stage, and diel periodicity, there is little to suggest how such species are able to partition the environment to an extent sufficient to permit sympatry.

In view of the apparent general homogeneity of the group in biological characters it is not surprising to find that there is a strong tendency for the species to replace one another geographically. As a result, extensive overlap of the range of one species by that of another is exceptional and, even more strikingly, occupancy of an area by more than two species is almost excluded. This pattern is especially well marked in North America. *Epicauta vittata*, which ranges through much of the eastern United States, is replaced by the allopatric *E. temexa* in Texas and southward. *Epicauta occidentalis* is narrowly sympatric with *E. temexa* and broadly so with *E. vittata*; however, there is evidence that even a few decades ago the area of sympatry with the latter species was narrower than at present. Continuing southward, *E. temexa* reaches northern Veracruz, Mexico, where it is replaced by *E. vitticollis* and *E. unilineata*, which are themselves largely allopatric. In middle Central America both of these species are replaced by *E. aragua*, which narrowly overlaps *E. vitticollis* in Honduras and *E. unilineata* in El Salvador. In Venezuela, in turn, *E. aragua* occurs in sympatry with *E. apure*, which replaces it southward. Returning to North America, *E. abadona*, of the West Coast of Mexico and southern Arizona, is widely separated geographically from all other species of the group except *E. tamara*, which occupies the southern half of the range of *E. abadona*, in southern Sonora and Sinaloa, and extends beyond that range into the state of Nayarit.

The Vittata Group is better represented, in

terms of number of species, in southern South America and it would appear that the incidence of sympatry is somewhat higher in that region. Except for *E. monachica* and *E. leopardina*, however, distributional data are so fragmentary as to preclude a meaningful analysis of inter-specific distributional relationships. *Epicauta monachica* and *E. leopardina* are sympatric with each other in northern Argentina, although each has an extensive range in the absence of the other species. The range of *E. luteolineata*, the third species studied from this area, is apparently much smaller than and, so far as known, totally contained within the common range of *E. monachica* and *E. leopardina*.

When sympatric species are compared with respect to characters of male courtship behavior, the interesting fact emerges that, with one exception, species with identical or similar patterns of courtship do not occur together. Consider for example, the position of the male with respect to the female and the occurrence of phases of courtship. *Epicauta occidentalis* differs from both *E. vittata* and *E. temexa* in remaining unmounted throughout courtship. *Epicauta unilineata* differs from the sympatric *E. vitticollis* in partially mounting the female in phase B of courtship. The same difference distinguishes the sympatric *E. monachica* and *E. leopardina*. *Epicauta aragua* differs from *E. vitticollis*, *E. unilineata*, and from *E. apure* in mounting the female fully. In the sympatric *E. abadona* and *E. tamara* the male mounts fully, but the latter species lacks phase A of courtship. The exception alluded to occurs in the case of *E. luteolineata*, which is like the sympatric *E. monachica* in courting entirely from the unmounted position. But even when, as in the last case, sympatric species have the same general pattern of courtship behavior, the behavior is by no means identical. Thus we have shown a number of marked quantitative differences in the behavior of *E. monachica* and *E. luteolineata* as well as one qualitative difference (absence of palpation in phase B in *E. luteolineata*). Conversely, species with identical patterns of male courtship behavior are highly disjunct, occurring, in fact, on different continents. These are, on the one hand, *E. occiden-*

*talis*, of northern North America, and *E. monachica*, of southern South America, and, on the other, the Central American *E. vitticollis* and southern South American *E. luteolineata*.

One can hardly escape the conclusion that the evolution of courtship behavior in the Vittata Group reflects to some extent a history of selection for accentuation of differences among interacting, sympatric populations or, alternately, that marked differentiation in courtship behavior is a prerequisite to sympatry. Some evidence has been obtained suggesting that differences in patterning of courtship behavior serve to reduce interspecific interactions. Whether these differences have any real importance in maintaining the integrity of sympatric species is questionable, since there is no evidence that any of the species of the group are genetically compatible.

#### ECOLOGICAL RELATIONSHIPS OF BIOLOGICAL CHARACTERS

As an adjunct to our investigation of biological differences among species as a function of the presence or absence of sympatry, we examined the possibility of explaining some of the variability in biological characters on the basis of correlation with the geographic position, elevation, precipitation, and temperature of the localities at which our samples of the various taxa were collected.

Initially we obtained long-range monthly means of precipitation and temperature for each locality and entered these, together with elevation, latitude, and longitude, into a principal components analysis. The first component was found to reflect largely variation in temperature and nonsummer precipitation, the second component variation in summer precipitation. Together they accounted for 80 percent of the variation in the ecological variables considered. Because of their heterogeneity, however, we found the principal components to be of relatively little value in making ecological interpretations. We therefore decided on a simpler approach. Specifically, we chose to perform, for each of the biological characters considered, a stepwise multiple regression on latitude and

summer and winter means of precipitation and temperature. Elevation and longitude, which proved superfluous in the principal components analysis, were omitted entirely.

Latitude and long-range means of summer and winter precipitation and temperature for the localities are given in table 59. Correlations between these variables are shown in table 60. Note that south latitude is given a negative value, thus making latitude an absolute measure of distance between localities in a north-south direction. For *E. vittata* (typical race) and *E. occidentalis* we averaged the values for Illinois and Mississippi localities; for *E. temexa* we averaged the values for Frio and Bee-Goliad counties, Texas.

Table 59 shows that South Carolina differs from Illinois-Mississippi principally in having heavier summer precipitation; that Texas and Santiago del Estero are similar except with respect to the seasonal patterning of precipitation; and that Veracruz and Sinaloa are rather comparable climatically except for the extremely heavy summer precipitation in Veracruz.

Because of the few degrees of freedom available, we restricted the model in each analysis to linear terms for the ecological variables. As usual, we used as the error term the residual MS obtained by fitting the "full" model (five independent variables). The results of the study are presented in table 61 in terms of correlations of the biological and ecological variables. Since localities were not sampled randomly, the coefficients of correlation are convenient descriptive statistics only and do not purport to estimate parameters.

Age of males at first courtship, volume of individual eggs, proportion of eggs developing, and proportion of eggs hatching all proved to have significant linear relationships with one or more ecological variables. Age of males at first courtship increases with summer temperature (°C.) according to the equation  $\hat{y} = -30.114 + 1.396X$ . Egg volume decreases from south to north according to the equation  $\hat{y} = 0.697 - 0.87X$ , where X is latitude in degrees (with south latitude given a negative sign). The latter relationship reflects the unexplained fact, mentioned earlier, that mean adult body size, which

TABLE 59  
**Latitude, Precipitation, and Temperature for Principal Localities<sup>a</sup>**

Localities	Species	Lat. (°)	Mean Monthly Precipitation (mm)		Mean Monthly Temperature (°C)		Weather Stations
			Summer	Winter	Summer	Winter	
Illinois (Johnson Co.) and Mississippi (Lee and Itawamba counties)	<i>E. vittata</i> (typical race); <i>E. occidentalis</i>	35.9	95.6	109.9	25.8	4.3	Anna, Ill.; Tupelo, Miss.
South Carolina (Colleton County)	<i>E. vittata</i> (lemniscate race)	32.9	158.7	84.2	26.1	9.1	Walterboro
Texas (Frio, Bee, and Goliad counties)	<i>E. temexa</i>	28.6	47.8	41.1	29.1	12.6	Dilley; Beeville
Sinaloa, Mexico (Culiacán)	<i>E. abadona</i> ; <i>E. tamara</i>	24.8	103.3	19.5	29.1	19.9	Culiacán
Veracruz, Mexico (Cotaxtla)	<i>E. vitticollis</i> ; <i>E. unilineata</i>	19.1	263.3	21.2	27.0	22.3	Veracruz
Santiago del Estero, Argentina (Santiago del Estero)	<i>E. monachica</i> ; <i>E. leopardina</i> ; <i>E. luteolineata</i>	-27.8	88.9	5.9	27.5	14.4	Santiago del Estero

<sup>a</sup>Climatological data for localities in the United States were obtained from Climatological Data, United States Department of Commerce, Annual Summaries, 1951-1970, and for localities in Latin America from United States Naval Weather Service World-wide Airfield Summaries, vols. 6 and 7 (1968). For the United States the means are based on a record of 20 years; for Culiacán, 23 years; for Veracruz, 15 years for precipitation, 10 for temperature; for Santiago del Estero, 7 years for precipitation, 28 for temperature. Values for summer are means of June, July, and August and those for winter are means of December, January, and February in the northern hemisphere; means for the same sets of months, with the seasonal names interchanged, are presented for Santiago del Estero, in the southern hemisphere.

TABLE 60  
**Correlation of Ecological Variables**

	Latitude	Summer Precip.	Winter Precip.	Summer Temp.
Summer Precip.	.216			
Winter Precip.	.742	-.134		
Summer Temp.	-.245	-.288	-.672	
Winter Temp.	-.273	.594	-.814	.546

is positively correlated with egg volume, decreases from south to north.

In the case of proportion of eggs developing

and hatching, there is significant regression on all five ecological variables. Under the conditions of the laboratory, eggs from taxa from hot, arid areas developed and hatched with greater success than those from cooler, more mesic areas. In addition, quite apart from this relationship, there is a significant positive relationship between developmental and hatching success and latitude.

In the laboratory eggs were incubated at a constant temperature of 27°C. This is roughly the mean temperature that eggs might experience in either western Mexico or in Santiago del Estero, although in those areas there would be a 15-20 degree diel fluctuation in temperature, depending on the nature of the ground cover. In other areas eggs would be subjected to a somewhat lower mean temperature and less marked amplitude of diel variation. We can

conjecture that taxa from hot areas did better in the laboratory because the mean temperature or heat load (or both) was more appropriate for them than for the other taxa. On the other hand, the relationship between developmental

and hatching success and precipitation is difficult to interpret. As mentioned previously, the relative humidity of the room in which adults were held was rather low (40-60%). With the cage openings covered and both fresh food and

TABLE 61  
Correlation of Biological Characters with Ecological Variables

Biological Characters	Lat.	Precipitation		Temperature	
		Summer	Winter	Summer	Winter
Female longevity (table 9)	-.294	.281	-.545	.303	.561
Age of adults at first feeding (table 5)	.380	.208	-.097	.328	.395
Proportion of days on which courtship occurred (table 17) <sup>a</sup>	-.269	-.069	-.054	-.124	-.145
Mean interval without courtship immediately after copulation (table 19)	.322	.256	-.086	.364	.358
Mean interval without courtship at other times (table 19)	.424	.056	.365	-.153	.154
Duration of first copulation (table 25)	.151	.622	-.272	.100	.538
Mean duration of subsequent copulations (table 25)	-.059	.579	-.454	.117	.663
Age of males at first courtship (table 15)	-.136	.116	-.694	.776	.754
Age of males at first copulation (table 28)	.085	.610	-.230	.011	.489
Age of females at first copulation (table 28)	-.003	.613	-.324	.060	.546
Age of females at first oviposition (table 33)	-.240	.039	.240	.128	.163
Mean interval between ovipositions (table 36)	.098	.662	.111	-.554	.152
Interval from last oviposition to death (table 38)	-.086	.380	.006	-.379	.077
Mean number of eggs per mass (table 40)	.151	.073	.012	.103	.049
Eggs per day of adult life (table 43)	.017	-.227	-.216	.535	.142
Hatching time of egg masses (table 55)	-.070	.639	-.422	.110	.688
Volume of individual eggs (table 46)	.769	-.353	-.543	.353	.128
Number of ovarioles per female (table 50)	-.116	.225	-.116	-.090	.126
Proportion of eggs developing (table 54) <sup>a</sup>	-.693	-.455	-.763	.785	.372
Proportion of eggs hatching (table 54) <sup>a</sup>	-.680	-.360	-.779	.755	.421

<sup>a</sup>Proportions transformed as arcsin of square root.

moist sand available, however, relative humidity in the beetles' immediate environment was considerably higher. Moreover, measures of longevity and egg production do not suggest that the laboratory conditions particularly favored taxa from dry areas. Further, the possibility of evaporation stress on eggs from the time of deposition until transfer to the incubation chamber seems remote, since with few exceptions, egg masses were deposited in moist sand. Beyond that point all eggs were incubated at 100 percent RH, which could hardly favor taxa from dry areas. The problem of

interpretation is further complicated by lack of knowledge of the extent to which failure to develop reflects failure of the eggs to be fertilized during oviposition.

In summary, little of the variation among taxa in biological characters is explicable on the basis of variation in the physical environment of the taxa, and in those few cases where a relationship between biological characters and environmental variables can be shown, no particularly meaningful interpretations of the relationship seem evident.

## SYSTEMATICS

### COMPOSITION OF THE GROUP

We assign to the Vittata Group 31 New World species of the nominate subgenus of the genus *Epicauta* Dejean. In the adult stage, the group is characterized anatomically as follows:

Palpi, head, pronotum, femora, and tibiae (except spurs) not sexually dimorphic. Antennae slender, tapering distad, sexually dimorphic or not. Male anterior tibiae each with one or two spurs, the anterior one curved or not; male fore or fore and middle tarsi swollen or not. Male abdominal sternum with scattered, erect setae, which are generally lengthened and denser posteriorly (these in addition to the regular, recumbent clothing setae) (exception in *E. philamaeta*). Fifth abdominal sternum medianly impressed or not, sixth distinctly emarginate. Pygidium incised, narrowly emarginate, or entire. Elytra with a basic pattern of three black vittae on a yellow or orange background (fig. 52); middle and outer vittae of each elytron partially or completely fused in some North American species; all three vittae fused apically and with pale areas between them reduced to fine, incomplete lines in some South American species (fig. 62); in *E. leopardina*, the middle vittae interrupted, forming maculae (fig. 63).

A diagnosis of the group on the basis of characters of sexual behavior (insofar as known) has already been given.

MacSwain (1956) found that triungulins (first

instar larvae) of *E. vittata*, *E. occidentalis* (as *E. lemniscata*), and *E. temexa* (as *E. sp. a*) are separable from those of other species of *Epicauta* studied by him by the following combination of characters: Three long setae on segment II of labial palpi; femora with more than the normal number (seven) of lanceolate setae; three long setae at apex of antennal segment II; and terminal antennal setae much shorter than antennal segment II. A comparative study of the triungulin larvae currently being carried out in our laboratory by N. Agafitei indicates that the above diagnosis is valid for nine additional species of the group not studied by MacSwain.

Among the North American species not included in the group, the closest approach, phenetically, is made by *E. nigratarsis* (LeConte) and *E. crassitarsis* Maydell, males of which not only have erect setae on the abdominal sternum but possess modifications of the legs similar to those of many of the species of the Vittata Group. Moreover, male courtship behavior in *E. nigratarsis*, at least, is similar to that of several species of the group. Specifically, the male courts from the unmounted position in Phase A, with moderate antennal curling, and moves to a partially mounted position, with the forelegs grasping the female, during abdominal curvature and genital presentation (Phase B).

We present below a key to the adults of the species of the Vittata Group occurring on the North American continent. It is not feasible at this time to prepare a comparable key for the South American species. Of the three South American species treated in detail in this work, *E. monachica* and *E. leopardina* are easily recognized on the basis of highly distinctive color patterns (figs. 61, 63); there are, however, several South American species with color patterns similar to that of *E. luteolineata* (fig. 62).

The key is followed by accounts for all species currently assigned to the group giving synonymy and distributional information. Accounts of the species occurring in North America are presented first, in the order used generally in this work. These are followed by the accounts of the three South American species studied in detail and, finally, by those of the remaining species of that continent.

KEY TO ADULTS OF THE SPECIES IN NORTH AMERICA

Unless stated otherwise, the coloration described is that of the integument and not the clothing setae,

which frequently produce patterning or otherwise modify the superficial coloration of the adult beetle.

1. Elytra black or brown, finely margined with orange and with two fine, longitudinal orange lines arising from the humerus and extending to about apical third or fourth (i.e., black elytral vittae much enlarged, fused with each other in apical region, reducing pale spaces between them to fine, incomplete lines); head with antennae, palpi, labrum, and clypeus black and with a heavy black mark extending from clypeus along each side of front bordering eye; rest of head orange, unmarked; pronotum entirely black, the clothing setae hardly affecting appearance, not producing a pattern; venter and legs black except trochanters and immediate base of femora orange; antennae and legs very slender; male antennae with ventral edge of basal flagellar segments ridged, bare, shiny; male legs not modified; length 7-12 mm.

..... *E. aragua* (p. 251)  
 Inner black elytral vitta well separated throughout its length from middle and outer vittae (which may be partially or entirely fused with each other); color pattern of head not as above; if pronotum entirely black, then with a distinct pattern (pair of black vittae or median black spot on gray or yellow background) produced by clothing

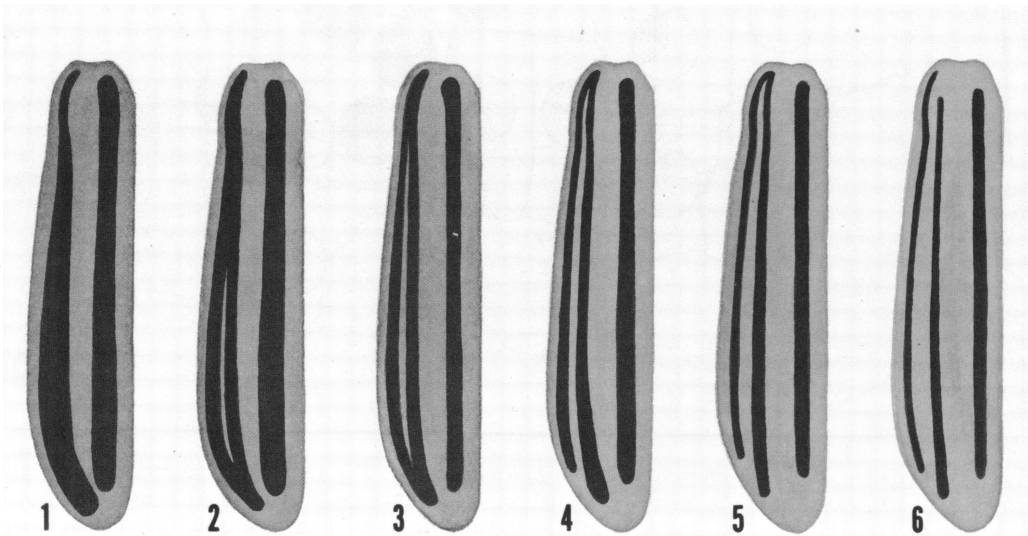


FIG. 44. Classes (1-6) used in analysis of variation in color pattern of elytra in *Epicauta vittata*.

- setae; venter often at least partially yellow or orange; legs more extensively marked with orange than above, varying to entirely orange; male antennae not modified as above. . . . . 2
2. Outer black elytral vitta covered largely or entirely with yellow setae, much narrower and

- much less distinct than middle vitta; head pale, without black markings; male fore tibiae with anterior spur thickened, strongly curved ventrad (fig. 57). Arizona, Sonora, Sinaloa, and Nayarit. . . . . 3
- Outer black elytral vittae covered with black

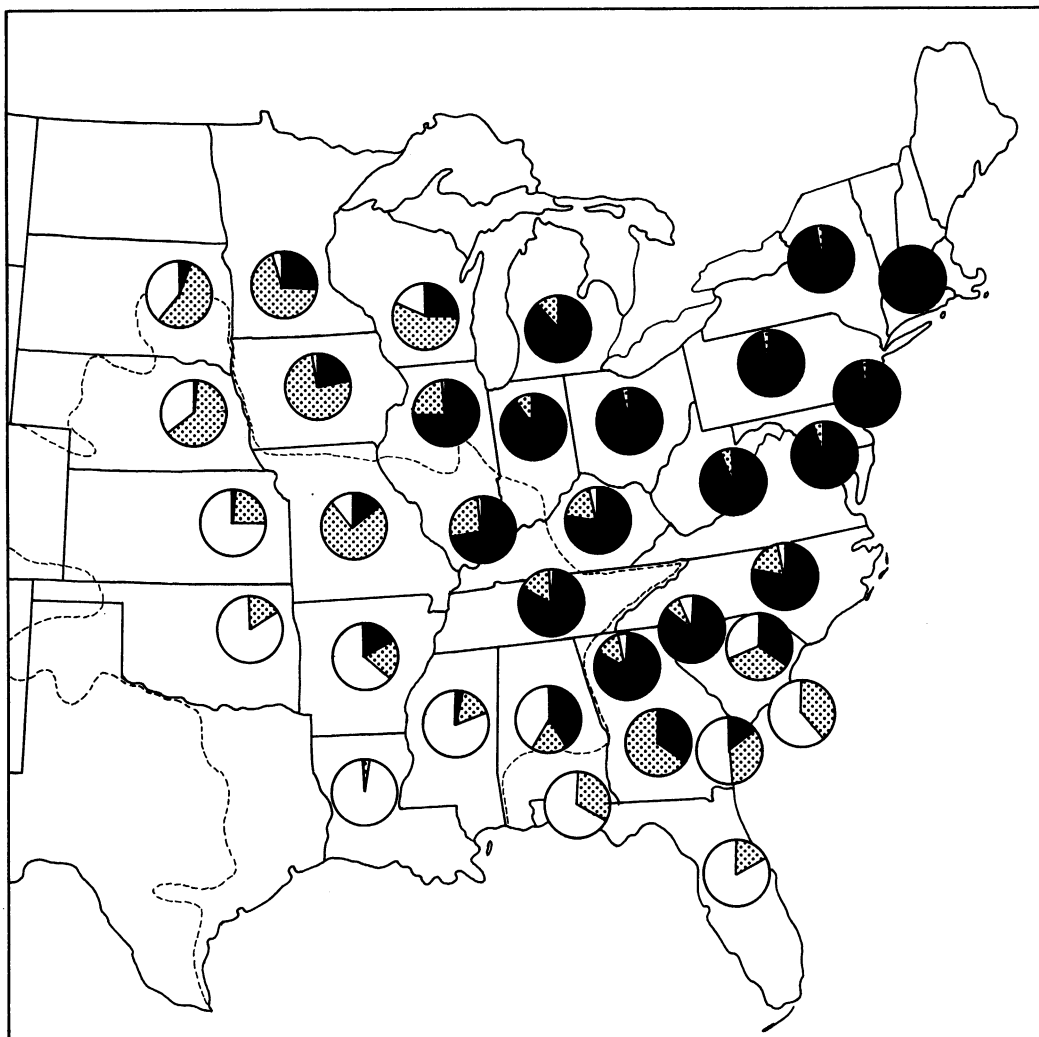
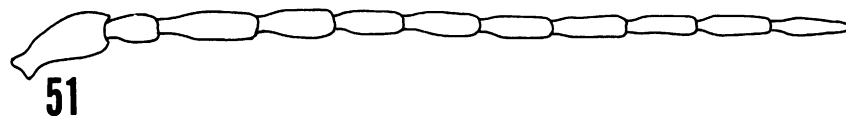
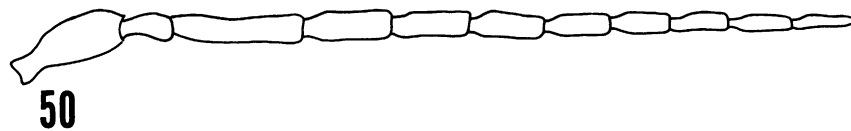
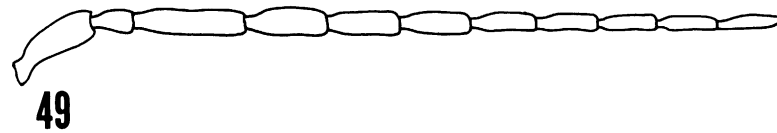
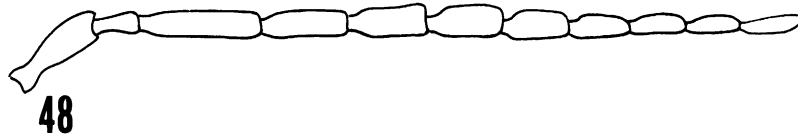
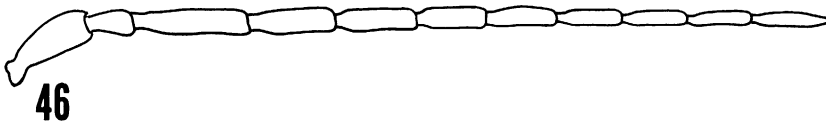


FIG. 45. Variation in color pattern of elytra in *Epicauta vittata*. Diagrams show percentage distribution of specimens in categories formed by pairwise pooling of consecutive color classes (as defined in text). Black area represents classes 1+2 ("two-striped"), dotted area classes 3+4 ("three-striped" but middle and outer black vittae only narrowly separated, tending to fuse at distal ends), clear areas classes 5+6 ("three-striped" with vittae well separated). Sample areas are listed in table 1. Dashed line shows the geographic range of *E. occidentalis*, which is consistently "three-striped" (pattern similar to that of class 5 of *E. vittata*).



- setae, not or only slightly narrower than middle vitta, fully as distinct; head with black markings; male fore tibiae with anterior spur thin, curved or not. Species not occurring in the above region . 4
3. Pale straw yellow above, extensively yellow or orange beneath; antennae, femora, and tibiae orange, without black markings; tarsi reddish brown; pronotum with black markings (two vittae or median blotch) confined largely or entirely to

anterior half; elytral black vittae reduced to fine lines; inner and middle vittae separated by a distance equal to several times the width of inner vitta; antennal segments very elongate, slender; male fore and middle tibiae with anterior spur thickened, strongly curved; male fore tibiae with posterior spur absent or (rarely) vestigial; male hind tibiae with spurs greatly thickened, strongly compressed, flared, and bent; male fore tarsi



FIGS. 46-51. Antennae of some species of the Vittata Group. 46. *Epicauta vittata*, male. 47. Same, female. 48. *E. occidentalis*, male. 49. Same, female. 50. *E. temexa*, male. 51. *E. tamara*, male.

- slender, essentially as in female; male fifth visible abdominal sternum not impressed medianly; length 10-18 mm. . . . . *E. abadona* (p. 249) Orange above, entirely black beneath (or at most small orange areas on metasternum); antennae black; femora orange, tipped distally with black; tibiae nearly entirely black or brown; tarsi black; pronotum black, with a pattern of two heavy, complete black vittae formed by clothing setae; elytral black vittae much wider than above, the inner and middle vittae separated by a distance not much greater than width of inner vitta (figs. 24, 25); antennal segments less elongate (fig. 51); male fore and middle tibiae with posterior spur smaller than anterior one but well developed; male hind tibial spurs not thickened, parallel-sided, straight; male fore tarsi (fig. 58) with first three segments swollen (the first strongly so), clothed with long setae, and with large, dense pads ventrally that extend well onto posterior surface (fig. 59); male fifth visible abdominal sternum (fig. 56) broadly, deeply impressed medianly; length 7-15 mm. . . . . *E. tamara* (p. 249)
4. Elytra with three rather evenly spaced black vittae which are equal in width or nearly so (middle and outer vittae fused at immediate base only, as in fig. 52); male antennae with flagellum noticeably compressed (cf. figs. 48, 49; see also fig. 50); male fifth visible abdominal sternum not impressed (fig. 55).. . . . . 5
- Elytra with middle and outer black vittae at least much closer to each other than middle vitta is to inner one, often fused distally (as well as basally) or throughout their lengths; male antennae not modified, as in female (cf. figs. 46, 47); male fifth visible abdominal sternum impressed medianly or not. . . . . 6
5. Male antennae with flagellum swordlike, very strongly compressed (fig. 49); female antennae moderately compressed (fig. 50); third antennal segment straight in both sexes; elytral black vittae generally very evenly spaced, but with middle vitta sometimes slightly closer to outer one than to inner one (as in fig. 52); length 10-18 mm. Indiana, eastern Tennessee, and Georgia to Colorado and eastern Texas. *E. occidentalis* (p. 246) Male antennae (fig. 16) with flagellum only moderately compressed, not much more so than in female of *E. occidentalis*; female antennae weakly compressed; third antennal segment bowed in both sexes, more strongly so in male; male fore tarsi swollen, especially the first segment, which is distinctly curved in lateral view (fig. 57); middle black elytral vitta consistently closer to outer one than to inner one (figs. 16-19); length 10-15 mm. Texas and northeastern Mexico . . . . . *E. temexa* (p. 248)
6. Labrum, clypeus, and at least sides and undersurface of head black; pronotum entirely black; male fore tibiae with anterior spur straight; male fore tarsi not swollen; male fifth visible abdominal sternum not impressed; length 20-22 mm. South-

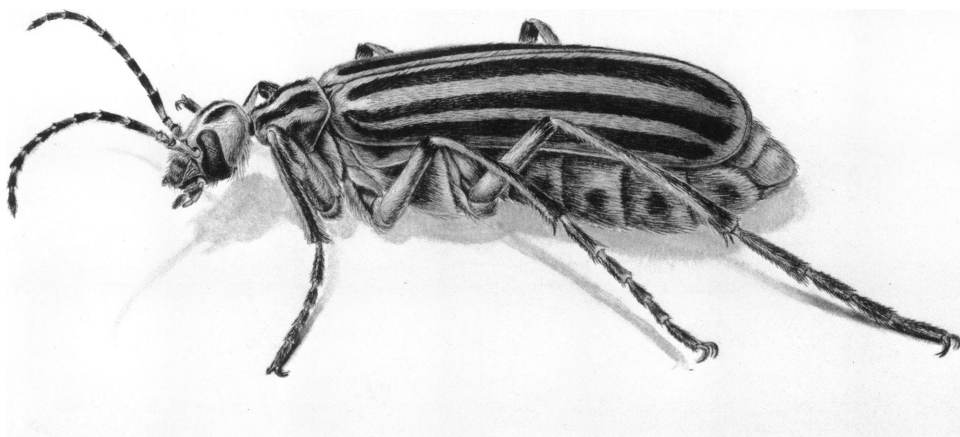
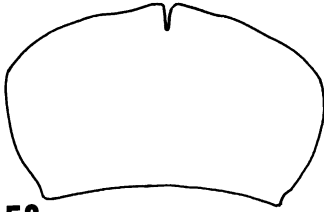


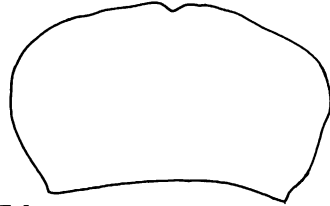
FIG. 52. *Epicauta occidentalis*, female. The middle and outer black vittae are typically more widely separated from each other than in this individual.

ern Mexico and Central America. . . . .  
 . . . . . *E. vitticollis* (p. 250)  
 Labrum, clypeus, and head (except for two me-

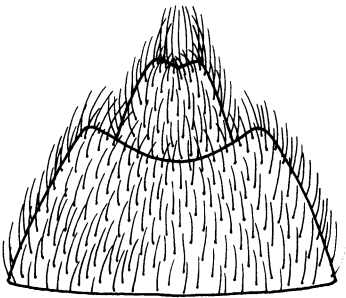
dian black spots on vertex) orange; male fore  
 tarsi swollen. . . . . 7  
 7. Pronotum, metathorax, and tibiae entirely black;



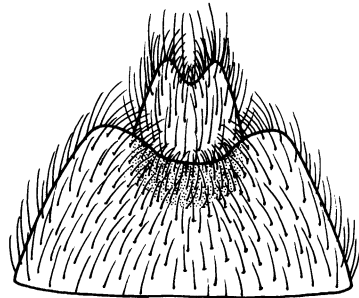
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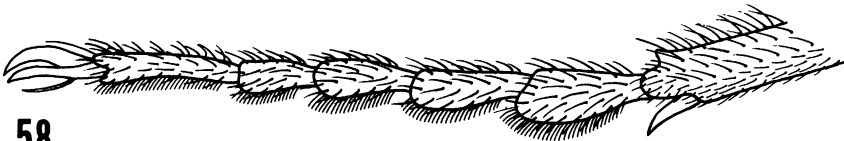
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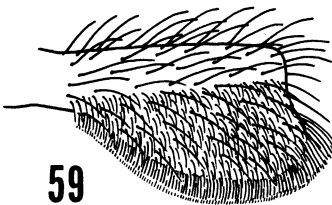
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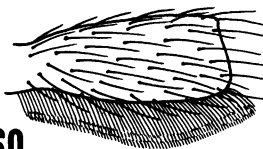
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FIGS. 53-54. Pygidia of males. 53. *Epicauta vittata*, typical race. 54. *E. vittata*, lemniscate race.  
 FIGS. 55-56. Fifth and sixth visible abdominal sterna of males. 55. *E. temexa*. 56. *E. tamara*.  
 FIGS. 57-58. Fore tarsi of males. 57. *E. temexa*. 58. *E. tamara*.  
 FIGS. 59-60. First fore tarsal segment of males. 59. *E. tamara*. 60. *E. unilineata*.

elytra with middle and outer black vittae extensively to entirely fused, separated at most by a fine yellow line which is marked in anterior half by clothing setae only (figs. 20-22); pygidium shallowly, triangularly emarginate; male fore tibiae with anterior spur strongly curved; male fore tarsi with first segment strongly swollen (fig. 60), other segments moderately so; male fifth visible abdominal sternum impressed medianly in posterior half; length 7-13 mm. Southern Mexico and northern Central America. . . . .  
 . . . . . *E. unilineata* (p. 250)

Pronotum and, usually, metathorax and tibiae partially orange; elytra with middle and outer black vittae varying from entirely separate to entirely fused (fig. 44); pygidium deeply incised or triangularly emarginate medianly on posterior margin (figs. 53, 54); male fore tibiae with anterior spur straight; male fore and middle tarsi weakly swollen, nearly as in female; length 10-18 mm. Eastern and central United States and immediately adjacent areas in Canada. . . . .  
 . . . . . *E. vittata* (p. 240)

## SPECIES ACCOUNTS

### *Epicauta vittata* (Fabricius)

#### TYPICAL RACE

*Lytta vittata* Fabricius, 1775, p. 260 [Lectotype, sex undetermined, from "America," designated by Werner (1945, p. 465), in the Hunter Collection, Glasgow University]; 1781, p. 329; 1787, p. 216; 1792, p. 86; 1801, p. 79. Brandt and Ratzeburg, 1883, pp. 123-124. LeConte, 1853, p. 340. Claypole, 1880, p. 245; 1885, p. 119. Zimsen, 1964, p. 129.

*Meloe vittatus*: Thunberg, 1781-1791, p. 109.

*Cantharis* sp., Chapman, 1799, p. 174.

*Meloe Chapmani* Woodhouse, 1800, p. 214 [Syntypes from Bucks County, Pennsylvania, presumably destroyed].

*Epicauta vittata*: Horn, 1873, p. 100. Saunders, 1876, p. 223, fig. 7. Riley, 1877, pp. 8-13, 15-18, fig. (p. 6), pl. 5, figs. 1-8, 10 (at least in part). Hubbard and Schwarz, 1878, p. 663. Forbes, 1880, pp. 110, 132; 1886, p. 19; 1905, pp. 111-112 (at least in part). Hamilton, 1895, pp. 341, 375. Wickham, 1896, p. 34, fig. 3; 1911, p. 35. Forbes and Hart, 1900, p. 448 (at least in part). Ulke, 1902, p. 32. Balduf, 1923, p. 171. Chittenden, 1903, p. 22, fig. 13; 1911, p. 91. Anon., 1908, p. 573 (in part). Blatchley, 1910, p. 1361. Gibson, 1912, p. 86, fig. 5. Sherman, 1913, p. 246. Flint, 1914, p. 477. Webster, 1915, pp. 377-380, figs. 11-13. Britton, 1918, p. 111; 1920, p. 238. Bilsing, 1920, pp. 253, 260. Weiss and Dickerson, 1921, p. 140. Mutchler and Weiss, 1924, p. 10. Davis, 1926, p. 298. Robertson, 1929, p. 30. Brimley, 1938, p. 162. Fenton, 1939, p. 74. Staig, 1940, pp. 139-142, pl. 56. Montgomery and Amos, 1941, p. 254. Werner, 1945, p. 464. Milliron, 1958, p. 8. Gorz, Haskins, and Manglitz, 1971, pp. 1-7.

*Epicauta lemniscata*: Putnam, 1876, p. 173.

Hamilton, 1895, p. 341. Wickham, 1895, p. 40. Ulke, 1902, p. 32. Hendrickson, 1930, p. 98. Carruth, 1931, p. 52 (at least in part). Brimley, 1938, p. 162. Gilbertson and Horsfall, 1940, pp. 10-14, figs. 4, 5B (at least in part). Montgomery and Amos, 1941, p. 254. Horsfall, 1943, pp. 32-37 (in part). Löding, 1945, p. 55 (at least in part). Werner, 1945, p. 463 (in part). Kirk, 1969, p. 63 (in part).

*Epicauta lemnistica* [sic]: Hamilton, 1895, p. 375.

*Epicauta (Epicauta) vittata*: MacSwain, 1956, p. 49, pl. 9. Kirk, 1970, p. 61 (in part).

#### LEMNISCATE RACE

*Lytta lemniscata* Fabricius, 1801, p. 79 [Holotype or syntype, male, from "Carolina," in the Universitetes Zoologiske Museum, Copenhagen, examined; if other material exists, it is presumably in the Bosc Collection, Museum National d'Histoire Naturelle (Paris)]. LeConte, 1853, p. 341. Zimsen, 1964, p. 129.

*Cantharis lemniscata*: Fischer, 1827, p. 19.

*Epicauta lemniscata*: Schwarz, 1878, p. 464. Chittenden, 1903a, p. 115; 1903, p. 23 (in part). Swingle and Mayer, 1944, p. 141. Frost, 1964, p. 140. Kirk, 1969, p. 63 (in part).

*Epicauta vittata*: Watson, 1917, p. 64R.

*Epicauta (Epicauta) vittata*: Kirk, 1970, p. 61 (in part).

**ASSIGNMENT OF REFERENCES:** Compilation of the synonymy of this species has been difficult because previous authors so commonly confused the species with *E. occidentalis* and *E. temexa*. The following references are included on the basis of examination of material studied by the respective authors: References to "*E. vittata*": Hubbard and Schwarz (1878), Blatchley (1910), Wickham (1911), Sherman

(1913) [Newton and Beaufort, North Carolina, material only], Robertson (1929), Hendrickson (1930), Brimley (1938), Montgomery and Amos (1941), and Kirk (1970). References to "*E. lemniscata*": Fabricius (1801), Wickham (1895), Ulke (1902), Carruth (1931) [Canton and Tyn-dall, North Dakota, material only], Brimley (1938) [Belhaven and Chadbourn, North Carolina, material only], Gilbertson and Horsfall (1940) [Canton, South Dakota, material only], Montgomery and Amos (1941), Horsfall (1943) [reared material includes both *E. vittata* and *E. occidentalis*], Löding (1945) [Etowah County, Alabama, material only], and Kirk (1969) [Florence and Georgetown, South Carolina, material only].

For all other references included in the synonymy we have relied on descriptive information given by authors and the fact that through much of its geographic range in the central and eastern United States *E. vittata* occurs in allopatry with all other species of the Vittata Group.

A number of additional references may pertain to *E. vittata*, *E. occidentalis*, *E. temexa*, or a combination of these species. References to "*E. vittata*" in this category are those of Popenoe (1877), Bruner (1891), Sanderson (1905), Sanborn (1916), Wolf (1916), Böving and Craighead (1931), Löding (1945), Smith and Franklin (1961), Maxwell, Lefever, and Jenkins (1965), and Murray, Verhalen, and Bryan (1972). Referenced to "*E. lemniscata*" in this category are those of Popenoe (1879), Townsend (1885), Sanderson (1905), Chittenden (1903), Anonymous (1908), Beal (1912), Swenk (1913), Sanborn (1916), Baerg (1925), Carruth (1931) [In part: Springfield, South Dakota], Whelan (1939), Gilbertson and Horsfall (1940) [In part], Horsfall (1942), Brett (1946), Dorman (1946), Gertler (1946), Dillon (1952) [In part: College Station, Victoria, Victoria County, Brownsville, all in Texas], Fenton and Howell (1957), Smith and Franklin (1961), Arurkar and Knowles (1967), and Blickenstaff and Huggins (1974).

Because of the historical importance of Riley's (1877) pioneering study of the ecology and ontogeny of "*E. vittata*", it is especially unfortunate that his material was apparently not preserved. From a careful study of his article

we are convinced that most, if not all, information that it contains refers to the typical race of *E. vittata*. However, the rearings reported by him were accomplished with material collected in the St. Louis, Missouri area, and it is possible that individuals of *E. occidentalis* were included in his samples, as in the case of Horsfall's (1943) study of "*E. lemniscata*."

Finally, we note that Knowlton's (1930-1931) records of "*E. vittata*" from Utah are based on two specimens labeled as collected by E. G. Titus at Richmond, Kansas and three specimens labeled "Logan, E. G. Titus" are presumably from Kansas also. Knowlton's material is in the Utah State University, where it was examined by Selander several years ago.

#### GEOGRAPHIC VARIATION

**COLOR PATTERN:** The color pattern of this species is highly variable geographically. At one phenetic extreme the occiput is heavily spotted with black on each side of the midline; the pronotum is largely black, with the clothing setae producing a pair of heavy, complete black vittae; the middle and outer black elytral vittae are fused, producing a "two-striped" pattern, and the inner black vitta is heavy; the venter is entirely black or nearly so; the distal ends of the femora are broadly tipped with black; the tibiae are largely black or brown; and the tarsi are black. At the other extreme the black occipital spots are faintly marked, being produced by clothing setae only; the pronotum is orange, with the black vittae marked on the integument and by clothing setae only in the apical half; the elytra are finely "three-striped" (much as in *E. abadona*), with all three vittae well separated; the metathorax is largely orange; the femora are finely tipped with brown; the tibiae are largely orange, and the tarsi are reddish brown.

Because strength of development of black coloration of the integument on different parts of the body and on the appendages is strongly correlated, it seems sufficient to analyze only one part in detail. We have chosen the elytral color pattern, which is, superficially, the visually dominant component of the beetles' general aspect. Although variation in the elytral color (and that of other areas) is continuous, it

is useful to treat it as discontinuous. Preliminary study indicated that it was both feasible and adequate to define six color classes to which we have assigned ordinal values (1 to 6) reflecting progressive narrowing (and increasing separation) of the middle and outer black vittae (fig. 44).

The elytral color classes are as follows:

1. Middle and outer black vittae entirely fused.

2. Middle and outer vittae fused except for a very thin, indistinct, median yellow line marked mainly or entirely by pale clothing setae and not reaching base or distal end of fused vittae.

3. Middle and outer vittae fused broadly basally and distally, elsewhere separated by a thin yellow line marked both on integument and by pale clothing setae; yellow line narrower than outer black vitta.

4. Yellow line about as wide as outer black vitta, separating middle and outer vittae except at humerus, often narrowed at distal end, so that the vittae closely approach or touch each other.

5. Yellow line about 1½ times as wide as outer black vitta, not appreciably narrowed at distal end.

6. Yellow line at least twice as wide as outer black vitta, extending to humerus and thus entirely separating middle and outer vittae.

The geographic pattern of variation in the elytral color pattern can best be appreciated by examining the frequency distributions in table 62 and the graphic representation of these data in figure 45. In the preparation of figure 45 we found it expedient to pool consecutive color classes pairwise. The definition of sample areas reflects, in part, particular concern with the possibility of mimicry between *E. vittata* and *E. occidentalis* and segregation of the Florida-southeastern Coastal Plain population of *E. vittata* as a geographic race (see below).

As seen in figure 45 adults in populations in the northeastern United States are consistently heavily marked. In this region the elytra are for the most part "two-striped" (classes 1-2) or at least show considerable narrowing of the space between the middle and outer black vittae (classes 3-4). From Indiana, Kentucky, and

North Carolina west there is a gradual decrease in the strength of the black markings. A similar but more abrupt gradation occurs from Illinois and Tennessee south and southwest to Texas and Georgia. Finally, there is an especially abrupt lightening of the color pattern as one moves from the Piedmont to the Coastal Plain in South Carolina and Georgia.

Before the present analysis was made we had entertained the hypothesis that geographic variation in the elytral color pattern of *E. vittata* was conditioned by mimicry (presumably Müllerian) with *E. occidentalis*. The latter species, which is consistently "three-striped," has the three black elytral vittae evenly spaced, whereas in *E. vittata* the middle vitta is much closer to the outer one than to the inner one in even the least heavily marked class (6). Apart from this, however, the color pattern of *E. occidentalis* does not differ greatly from that of "three-striped" individuals of *E. vittata* and, in particular, those of class 5. Since, in the past, human observers have almost invariably failed to discriminate properly between "three-striped" *E. vittata* and *E. occidentalis*, the possibility of a mimetic relationship cannot be discounted entirely. Whether such a relationship is in any way responsible for the variation in *E. vittata* is another question.

In examining figure 45 where the range of *E. occidentalis* is outlined, one finds support for a causative hypothesis of mimicry in two points. The first is the sharp shift toward the "three-striped" condition as one moves west from Georgia and enters the range of *E. occidentalis* in Alabama. The second is the high incidence of the "three-striped" pattern (specifically classes 5-6) in populations within the range of *E. occidentalis* in South Dakota and Kansas, as compared with *E. vittata* populations occurring alone in Minnesota and Iowa.

On the negative side, we see first that in moving south from Iowa into the range of *E. occidentalis* in Missouri there is relatively little change in the mean value of the pattern of *E. vittata*. Second, populations in southern Illinois, southern Indiana, and western Kentucky and Tennessee, which do not differ significantly from one another and are sympatric with *E. occidentalis*, do not depart appreciably from

adjacent, allopatric populations in northern Illinois, northern Indiana, eastern Kentucky, North Carolina, South Carolina, and northern Georgia. Third, *E. vittata* varies to the fully

“three-striped” form in the complete absence of *E. occidentalis* along the southeastern Coastal Plain and into Florida.

In the section Geographic Distribution we

TABLE 62  
Variation in Color Pattern of Elytra in *Epicauta vittata* Expressed as Percentage Distributions of Specimens in Color Classes Defined in Text  
(Sample Areas of Sympatry with *E. occidentalis* are marked with an asterisk \*.)

Sample area	Color Classes						Mean	N
	1	2	3	4	5	6		
NORTHEASTERN RANGE								
Conn., Mass., R.I.	97.7	2.3	0.0	0.0	0.0	0.0	1.0	43
Ontario, New York	97.3	1.4	0.0	0.0	0.0	0.0	1.0	73
New Jersey	91.1	7.1	0.0	1.8	0.0	0.0	1.1	56
Pennsylvania	94.1	2.9	0.0	2.9	0.0	0.0	1.1	102
Md., Del., D.C.	93.8	1.0	2.1	3.1	0.0	0.0	1.2	96
West Virginia, Virginia	89.7	4.4	4.4	1.5	0.0	0.0	1.2	68
Ohio	93.5	3.2	0.0	3.2	0.0	0.0	1.1	31
Michigan	83.7	4.7	4.7	7.0	0.0	0.0	1.4	43
Wisconsin	25.0	0.0	25.0	31.3	18.8	0.0	1.6	16
North and central Indiana	75.8	15.8	1.7	6.7	0.0	0.0	1.4	120
Eastern and central Kentucky	75.0	7.1	7.1	7.1	3.6	0.0	1.6	28
Northern Illinois	63.7	9.8	3.9	21.6	1.0	0.0	1.9	102
S Ill. and Ind., W Kentucky <sup>a</sup>	54.1	17.0	8.0	19.2	1.7	0.0	2.0	640
NORTHWESTERN RANGE								
Minnesota	21.1	5.3	0.0	68.4	5.3	0.0	3.3	19
South Dakota*	0.0	6.7	1.1	56.3	35.9	0.0	4.2	446
Iowa	18.2	4.1	3.4	71.6	2.7	0.0	3.4	148
Nebraska*	0.0	2.2	2.2	60.9	34.8	0.0	4.3	46
Missouri*	10.7	4.2	6.1	68.2	10.7	0.0	3.6	214
Kansas*	0.7	0.7	0.7	23.6	74.3	0.0	4.7	144
SOUTHWESTERN RANGE								
Arkansas*	14.3	2.4	9.5	9.5	64.3	0.0	4.1	42
Oklahoma*	0.0	0.0	0.0	16.7	83.3	0.0	4.8	18
Louisiana*	0.0	0.0	0.0	2.6	94.7	2.6	5.0	38
Mississippi*	4.9	0.0	4.9	9.8	78.0	2.4	4.6	41
SOUTHEASTERN RANGE								
Alabama*	41.7	0.0	4.2	12.5	33.3	8.3	3.2	24
Tennessee*	63.0	20.0	4.0	12.0	1.0	0.0	1.7	100
North Carolina	60.2	17.0	14.8	4.5	3.4	0.0	1.7	176
South Carolina <sup>b</sup>								
Northwestern	72.9	13.6	3.4	5.1	5.1	0.0	1.6	59
Central	23.1	11.5	11.5	23.1	30.8	0.0	3.3	26
Coastal (lemniscate race)	0.0	0.0	1.3	37.7	59.7	1.3	4.6	77
Georgia <sup>c</sup>								
Northern	61.6	21.9	6.8	5.5	4.1	0.0	1.7	73
Central southern	37.5	0.0	25.0	37.5	0.0	0.0	2.6	8
Southern (lemniscate race)	2.9	11.4	8.6	25.7	51.4	0.0	4.1	35

TABLE 62 — (Continued)

Sample area	Color Classes						Mean	N
	1	2	3	4	5	6		
Florida <sup>d</sup>								
Northwestern border	0.0	0.0	4.3	29.8	57.4	8.5	4.7	47
Rest of state (lemniscate race)	0.0	0.0	0.0	16.6	74.2	9.2	4.9	229

<sup>a</sup>This area encompasses the southern half of Illinois (Adams and Vermilion counties southward), the southwestern fifth of Indiana (Parke, Putnam, Lawrence, Orange, and Spencer counties), and the western fourth of Kentucky (Henderson and Trigg counties westward).

<sup>b</sup>The northwestern area is Oconee, Pickens, Anderson, and Abbeville counties; the central area Kershaw, Florence, Richland, Clarendon, Orangeburg, Barnwell, Bamberg, and northern Dorchester counties; and the coastal area Georgetown and southern Dorchester counties south to Beaufort County.

<sup>c</sup>The northern area is the northern half of the state (Chattahoochee, Schley, Houston and Jefferson counties northward); the central southern area extends from Terrell, Lee, and northern Dougherty counties east to Screven, northern Bryan, Wayne counties; and the southern area extends from southern Dougherty and Thomas counties east to Glynn County and thence north along the coast to southern Bryan and Chatham counties.

<sup>d</sup>The northwestern border area includes Escambia and Jackson counties only.

presented evidence suggesting that *E. occidentalis* has extended its geographic range from the Great Plains east in relatively recent times. It is possible, then, that failure of *E. vittata* to vary markedly toward the "three-striped" pattern of *E. occidentalis* in the northeastern part of the range of the latter simply reflects recency of sympatry in that area. However, on the whole, the data do not present convincing evidence that mimicry of *E. occidentalis* affects geographic variation in the color pattern of *E. vittata*.

**RECOGNITION OF RACES:** During the present study we determined that populations on and near the southeastern Coastal Plain, from the southern border of North Carolina south through South Carolina and Georgia, and on the Florida peninsula, are differentiated from adjacent populations on the basis of both color pattern, as just discussed, color of the clothing setae of the venter of the body, and the form of the pygidium. In addition, as already described previously, we detected minor differences in the male courtship of samples from South Carolina and those from the central United States. Examination of Fabricius' type of "*E. lemniscata*" made it clear that the specimen was drawn from the coastal population, and for some time we carried this population in our records as a separate species. Later we found definite intergradation between *E. vittata* and

"*E. lemniscata*" in the pygidial character as well as coloration and also established that South Carolina and Illinois populations are not reproductively incompatible, at least in the laboratory. Although, in general, we are reluctant to recognize races, even if named only in the vernacular, we feel that the differentiation between populations is sufficiently great and the zone of intergradation sufficiently narrow that the subspecies concept has some utility in this case. We propose, then, to refer to the southeastern coastal and Floridian population of *E. vittata* as the lemniscate race and the remainder of the species as the typical race. We use the terms race and subspecies synonymously.

In addition to the behavioral characters already described, the lemniscate race is distinguished from the typical race as follows: Coloration as described above for the lightly marked extreme or nearly so, the elytra generally "three-striped," with color category 5+6 at least predominating; clothing setae of venter of body golden yellow in color; pygidium not incised but rather with posterior margin triangularly emarginate at middle, much as in the other North American species of the Vittata Group (cf. figs. 53, 54).

Intergradation between the two races is confined almost entirely to a narrow area bordering the edge of the Piedmont in South Carolina and Georgia. The principal localities at which inter-



gradation occurs are in Columbus County, North Carolina; Florence and Richland counties, South Carolina; and Bryan and Berrien counties, Georgia. Most intergrade series consist entirely of intermediates, but in a few cases there are, in addition, one or more specimens indistinguishable from typical representatives of the typical race or the lemniscate race. Unfortunately, relatively little material is available from the general area in which intergradation has been found.

In recording localities and mapping the distributions of the races, we assigned intergrade samples to the race which, on the average, they more closely approach phenetically.

In the laboratory we found that field-caught males of the lemniscate race of *E. vittata* from Colleton County, South Carolina, mated freely with reared, virgin females of the typical race from Illinois. Hybrid progeny from several such matings were reared and these reproduced successfully after mating among themselves. The data indicate neither lessened fertility from hybrid matings or in hybrid females nor impairment of ontogenetic development in hybrid individuals. However, the data are competent to detect only very marked effects.

#### LOCALITY RECORDS

We have examined 3428 specimens. For the United States we list only county names.

**TYPICAL RACE:** CANADA: *Ontario*: Napanee. *Quebec*: Saint Hyacinthe (Gibson, 1911).

**UNITED STATES (counties):** *Alabama*: Barbour; DeKalb; Etowah; Houston; Limestone; Madison; Mobile; Shelby; Sumter; Washington. *Arkansas*: Arkansas; Conway; Hempstead; Lawrence; Mississippi; Pulaski; Washington. *Connecticut*: Fairfield; Hartford; New Haven. *Delaware*: Kent; New Castle; Sussex. *District of Columbia*: Washington. *Florida*: Escambia; Jackson. *Georgia*: Bartow; Bryan; Bulloch; Catoosa; Chattahoochee; Chattooga; Clarke; Cobb; Dade; Dougherty; Fannin; Fulton; Gordon; Haralson; Hart; Houston; Jackson; Jefferson; Lee; Macon; Madison; Morgan; Muscogee; Oconee; Paulding; Polk; Schley; Screven; Talbot; Taylor; Terrell; Towns; Wayne; Whitfield;

Wilkes. *Illinois*: Adams; Alexander; Champaign; Clay; Cook; De Kalb; Du Page; Edgar; Effingham; Franklin; Fulton; Gallatin; Greene; Henry; Jackson; Jo Daviess; Johnson; Kankakee; Lake; McHenry; Macon; Macoupin; Marion; Mason; Morgan; Peoria; Perry; Piatt; Pope; Putnam; Rock Island; Saint Clair; Saline; Sangamon; Union; Vermilion; Wabash; Warren; Washington; White; Will; Williamson. *Indiana*: Clark; Franklin; Gibson; Hamilton; Harrison; Hendricks; Jefferson; Knox; Lake; Lawrence; Marion; Orange; Parke; Porter; Posey; Putnam; Spencer; Starke; Tippecanoe; Vanderburgh; Vigo; Wayne. *Iowa*: Adams; Cherokee; Clayton; Crawford; Davis; Decatur; Dickinson; Dubuque; Floyd; Henry; Iowa; Johnson; Lee; Marshall; Monona; Muscatine; Page; Polk; Sac; Scott; Story; Winneshiek; Woodbury. *Kansas*: Chase; Dickinson; Doniphan; Douglas; Franklin; Linn; Miami; Pottawatomie; Reno; Riley; Rooks; Shawnee; Wyandotte. *Kentucky*: Bell; Campbell; Edmonson; Fulton; Graves; Green; Henderson; Jefferson; Mercer; Oldham; Rowan; Spencer; Trigg; Wayne. *Louisiana*: Avoyelles; East Baton Rouge; Jefferson; Livingston; Madison; Orleans; Saint Mary; Saint Tammany; Union. *Maryland*: Baltimore; Baltimore City; Carroll; Charles; Dorchester; Frederick; Harford; Montgomery; Prince Georges; Washington; Worcester. *Massachusetts*: Hampden; Hampshire; Middlesex; Suffolk; Worcester. *Michigan*: Berrien; Kent; Muskegon; Saginaw; Van Buren; Washtenaw; Wayne. *Minnesota*: Carlton; Faribault; Jackson; Martin; Nicollet; Olmsted; Rock. *Mississippi*: Coahoma; Copiah; De Soto; Franklin; George; Itawamba; Lee; Leflore; Oktibbeha; Warren. *Missouri*: Atchinson; Barry; Boone; Buchanan; Callaway; Carter; Clinton; Cooper; Franklin; Holt; Jackson; Jefferson; Johnson; Lafayette; Lincoln; Linn; Livingston; Mississippi; Newton; Pike; Polk; Saint Charles; Saint Louis; Saint Louis (city); Scott; Vernon. *Nebraska*: Burt; Colfax; Dakota; Douglas; Lancaster; Seward. *New Jersey*: Bergen; Burlington; Cape May; Cumberland; Gloucester; Middlesex; Morris; Ocean; Passaic. *New York*: Bronx; Cattaraugus; Columbia; Erie; Greene; Kings; Nassau; Ontario; Queens; Suffolk; Tompkins; Westchester. *North Carolina*: Avery; Beaufort; Bladen;

Brunswick; Caldwell; Carteret; Catawba; Chowan; Cleveland; Columbus; Currituck; Duplin; Durham; Edgecombe; Gates; Graham; Granville; Harnett; Hyde; Iredell; Johnston; Jones; Macon; Moore; New Hanover; Onslow; Pasquotank; Sampson; Scotland; Swain; Union; Wake; Watauga; Wilson. *Ohio*: Athens; Auglaize; Clinton; Erie; Franklin; Greene (Claypole, 1880); Lucas; Morgan; Muskingum; Summit (Claypole, 1885); Williams. *Oklahoma*: Craig; Kay; Mayes; Ottawa; Pawnee; Sequoyah; Washington. *Pennsylvania*: Adams; Allegheny; Armstrong; Bucks; Chester; Centre; Delaware; Lancaster; Lycoming; Philadelphia; Snyder; York. *Rhode Island*: Washington. *South Carolina*: Abbeville; Anderson; Barnwell; Clarendon; Darlington; Dorchester; Florence; Kershaw; Oconee; Orangeburg; Pickens; Richland. *South Dakota*: Brookings; Bon Hommes; Clay; Hutchinson; Lincoln; Minnehaha; Sully; Union; Yorktown. *Tennessee*: Anderson; Benton; Blount; Claiborne; Davidson; Franklin; Greene; Hamilton; Hardeman; Henderson; Knox; Marion; Marshall; Monroe; Montgomery; Morgan; Obion; Sevier; Shelby; Sullivan; Warren; Weakley. *Virginia*: Accomack; Arlington; Augusta; Fairfax; Falls Church (city); Fauquier; Isle of Wight; Loudon; Montgomery; Nansemond; Nelson; Norfolk; Northampton; Pittsylvania; Prince William; Richmond (city); Virginia Beach (city). *West Virginia*: Greenbrier; Mineral. *Wisconsin*: Dane; Door; Grant; La Crosse; Winnebago; Wood.

**LEMNISCATE RACE: UNITED STATES** (counties): *Florida*: Alachua; Baker; Bradford; Broward; Calhoun; Clay; Collier; Columbia; Dade; DeSoto; Duval; Gilchrist; Hernando; Highlands; Jefferson; Lake; Leon; Levy; Marion; Nassau; Okaloosa; Okeechobee; Orange; Osceola; Palm Beach; Polk; Pasco; Putnam; Saint Johns; Saint Lucie; Sarasota; Seminole; Taylor; Volusia. *Georgia*: Berrien; Bryan; Chatham; Dougherty; Glynn; Lowndes; McIntosh; Thomas. *South Carolina*: Beaufort; Charleston; Colleton; Dorchester; Georgetown; Jasper.

*Epicauta occidentalis* Werner

*Epicauta occidentalis* Werner, 1944, p. 69  
[Holotype, male, from Cambridge, Nebraska, in

the Museum of Comparative Zoology, Harvard University, No. 26069, examined]; 1945, p. 465, fig. 10. Dillon, 1952, p. 399.

*Epicauta lemniscata*: Horn, 1873, p. 100. Ortenburger and Hatch, 1926, p. 144. Ingram, 1927, pp. 1-5, figs. 1-2. Ingram and Douglas, 1932, pp. 71-74. Horsfall, 1943, pp. 32-37 (in part). Douglas, 1935, p. 686. Werner, 1945, p. 463 (in part). Dillon, 1952, p. 398 (in part).

*Epicauta vittata*: Bruner, 1891, p. 15 (at least in part). Cockerell and Harris, 1925, p. 31, fig. 4. Tafanelli and Bass, 1968, pp. 51-54 (at least in part).

*Epicauta (Epicauta) lemniscata*: MacSwain, 1956, p. 60, pl. 9.

**ASSIGNMENT OF REFERENCES:** The extent to which this species has been confused with *E. vittata* and *E. temexa* by previous workers would be almost amusing if it were not for the fact that several studies containing valuable biological information are involved, including the ontogenetic investigations of Riley (1877) and Horsfall (1943). To make matters worse, authors frequently have not preserved or properly labeled their material.

In only a few cases have we been able to determine with any degree of confidence whether a given reference to "*E. vittata*" or "*E. lemniscata*" involving material from within the geographic range of *E. occidentalis* does, in fact, pertain to *E. vittata*, the present species, or a mixture of the two. In addition, there are a few cases in which a reference to "*E. lemniscata*" may actually pertain to *E. occidentalis* or *E. temexa* or both. In the following paragraphs we outline the basis for the synonymy of *E. occidentalis* presented above.

By examining the material on which their studies were based, we have determined the following: Horsfall's (1943) account of the ontogeny of "*E. lemniscata*" was based on mixed samples of *E. vittata* and *E. occidentalis*. Werner (1945) mistakenly assigned females of *E. occidentalis* to *E. vittata*. Dillon's (1952) treatment of *E. occidentalis* was also based on males, females being confused with those of *E. temexa* under the name *E. lemniscata*. Tafanelli and Bass' (1968) reference to "*E. vittata*" was based at least partially on observations of *E. occidentalis*.

In a few cases it is evident from the geographic location of the study or descriptions

given by authors that *E. occidentalis* was the species involved: Horn (1873) was clearly referring to *E. occidentalis* in describing the appearance of adults of "*E. lemniscata*" in the southern United States. Ingram (1927) and Ingram and Douglas' (1932) references to "*E. lemniscata*" are assignable to *E. occidentalis* on the basis of consideration of both the region involved (southwestern Louisiana) and the description and figures given by Ingram (1927). Ortenburger and Hatch's (1926) record of "*E. lemniscata*" from Choctaw County, Oklahoma; Cockerell and Harris' (1925) description of the hind wing of "*E. vittata*" (based on material from Anahuac, Texas); and Douglas' (1935) report of damage to *Crotalaria* at Crowley, Louisiana, are referable to *E. occidentalis* on the basis of geographic considerations. Bruner's (1891) reference to "*E. vittata*" at Ogallala, Nebraska, almost certainly was based on *E. occidentalis*, although other information in the paper may refer to either that species or *E. vittata* or both.

Finally, comparison of triungulin larvae obtained in our study with MacSwain's (1956) detailed description leaves no doubt but that his larval material of "*E. lemniscata*" from Lawrence, Kansas, actually represents *E. occidentalis*.

#### LOCALITY RECORDS

We have examined 2506 specimens of this species. In addition to the material on which our map (see Geographic Distribution, fig. 2) and the following list of records of *E. occidentalis* are based, we have tentatively assigned two females from Walker County, Texas, and individual females from Bosque and Red River counties, Texas, and Quay, New Mexico, to this species.

UNITED STATES (counties): *Alabama*: Calhoun; Colbert; Dekalb; Greene; Jefferson; Limestone; Montgomery; Russell; Shelby; Sumter; Tuscaloosa. *Arkansas*: Arkansas; Ashley; Benton; Chicot; Crittenden; Franklin; Garland; Greene; Hempstead; Jackson; Lawrence; Logan; Mississippi; Monroe; Pope; Prairie; Pulaski; Washington. *Colorado*: Alamosa; El Paso; Larimer (Werner, 1944); Otero; Yuma (Werner, 1944). *Georgia*: Chattahoochee. *Illinois*: Alex-

ander; Champaign; Clay; Effingham; Fayette; Hamilton; Hardin; Jackson; Jersey; Johnson; Marion; Perry; Pike; Pope; Pulaski; Richland; Saint Clair; Saline; Union; Wabash; Wayne; White; Williamson. *Indiana*: Lawrence; Spencer. *Kansas*: Allen; Barber; Barton; Brown; Cherokee; Cheyenne; Clay; Cloud; Cowley; Crawford; Decatur; Dickinson; Douglas; Ellis; Finney; Ford; Franklin; Geary; Gray; Hamilton; Harvey; Jewell; Kearny; Labette; Lane; Lincoln; Linn; McPherson; Osborne; Ottawa; Pottawatomie; Pratt; Reno; Rice; Riley; Rush; Russell; Saline; Scott; Sedgwick; Shawnee; Sherman; Smith; Stafford; Sumner. *Kentucky*: Butler; Henderson; Trigg; Warren. *Louisiana*: Acadia; Avoyelles; Boosier; Caddo; Calcasieu; East Baton Rouge; Evangeline; Franklin; Iberia; Jefferson; Lafourche; Natchitoches; Orleans; Ouachita; Rapides; Saint Charles; Saint Landry; Saint Tammany; Vermilion. *Mississippi*: Claiborne; Coahoma; De Soto; Forrest; Harrison; Lee; Hinds; Jones; Itawamba; Lafayette; Lee; Leflore; Lauderdale; Newton; Smith; Washington; Winston. *Missouri*: Barry; Benton; Boone; Buchanan; Butler; Callaway; Cape Girardeau; Carroll; Clinton; Cole; Cooper; Dent; Dunklin; Franklin; Jackson; Jasper; Jefferson; Johnson; Laclede; Lawrence; Linn; Madison; Miller; Oregon; Pemisnot; Pettis; Phelps; Pike; Polk; Pulaski; Saint Louis; Saint Louis (city); Scott; Stoddard; Vernon; Warren; Wayne. *Nebraska*: Adams; Buffalo; Cherry; Clay; Colfax; Dodge; Douglas; Fillmore; Franklin; Furnas; Gage; Howard; Kearney; Keith (Bruner, 1891); Lancaster; Lincoln; Merrick; Phelps; Polk; Saunders. *Oklahoma*: Adair; Atoka; Beckham; Bryan; Caddo; Canadian; Carter; Delaware; Cherokee; Choctaw (Ortenburger and Hatch, 1926); Cleveland; Comanche; Cotton; Craig; Garvin; Grady; Harper; Haskell; Jackson; Kay; Le Flore; Logan; Major; Marshall; Mayes; McCurtain; Noble; Nowata; Oklahoma; Osage; Ottawa; Pawnee; Payne; Rogers; Sequoyah; Stephens; Tulsa; Wagoner; Washington; Washita. *South Dakota*: Bon Homme; Brookings; Brule; Buffalo; Hyde; Jerauld; Turner. *Tennessee*: Benton; Dyer; Franklin; Gibson; Greene; Henderson; Jefferson; Knox; Lawrence; Maury; McMinn; Montgomery; Rutherford; Robertson; Shelby; Warren. *Texas*: Brazoria; Brazos; Calhoun;

Cameron; Cass; Chambers; Colorado; Dallas; Denton; Frio; Fort Bend; Galveston; Grayson; Gregg; Grimes; Harris; Hunt; Jackson; Jefferson; Kaufman; Leon; Liberty; Lubbock; Madison; Matagorda; Oldham; Panola; Randall; Robertson; San Patricio; Titus; Victoria; Wharton; Willacy.

### ***Epicauta temexa*, new species**

*Epicauta vittata*: Dugès, 1889, p. 87.

*Epicauta lemniscata*: Champion, 1891-1893, p. 415. Snow, 1906, p. 149. Dillon, 1952, p. 398 (in part). Hernández, 1960, p. 65.

*Epicauta (Epicauta) sp. A*, MacSwain, 1956, p. 51, pl. 9.

ETYMOLOGY: *temexa*, from the state Texas and country Mexico.

TYPE DESIGNATION: Holotype, male, from Pearsall, Frio County, Texas, October 7, 1971, at light, R.B. Selander, Notes 43-71, in the American Museum of Natural History.

See the key for the diagnostic characters of this species.

ASSIGNMENT OF REFERENCES: Dugès' (1889) record of "*E. lemniscata*" from the Hacienda de Santa Clara, Huasteca Potosina, Mexico, is assigned to the present species on the basis of his description and the fact that *E. temexa* is the only species of the group known to range into the Huasteca Potosina, which is the mountainous eastern part of the state of San Luis Potosí (Selander and Vaurie, 1962). Similarly, there is no doubt but that the information given by Hernández (1960) for "*E. lemniscata*" in the Monterrey region of Nuevo León, Mexico actually refers to *E. temexa*. We have seen part of his material and have collected *E. temexa* commonly in and around Monterrey. A report of "*E. lemniscata*" from the Distrito Federal (Calvino et al., 1920) possibly refers to *E. temexa*, but we are inclined to believe that it was not based on a species of meloid of the Vittata Group.

Snow's (1906) record of "*E. lemniscata*" from Brownsville, Texas, and Dillon's (1952) records from Dimmit County, Hidalgo County, Carrizo Springs, Del Rio, Roma, Burleson, Temple, Pearsall, Alice, and the Big Bend region, all in Texas, were based on specimens of

*E. temexa* that we have examined. On the basis of range, Dillon's record of "*E. lemniscata*" from Hays County, Texas, is probably referable to *E. temexa* also. Finally, we note that the triunglin larva found in soil in an orchard and described by MacSwain (1956) as *Epicauta* "sp. A" clearly belongs to *E. temexa* on the basis of his description.

SPECIFIC IDENTIFICATION: The only species with which *E. temexa* is apt to be confused is *E. occidentalis*, which broadly overlaps it geographically in Texas. Specific separation of males presents no problem because of marked differences in the form of the antennae in the two species (cf. figs. 48, 50). With a little experience it is not particularly difficult to distinguish between females of the species, especially if comparative material is available. In the present study we have been able to assign confidently all but a handful of females from Texas to one or the other of these species.

### LOCALITY RECORDS

We have examined 850 specimens. In preparing the following list of localities we have excluded four records which, if valid, would extend the established range of *E. temexa* in the United States beyond the border of Texas. The material involved consists of a male labeled as from Albuquerque, New Mexico; two females from localities in southern New Mexico tentatively assigned to the species; and a male labeled as from Calcasieu Parish, Louisiana. Verification of the occurrence of *E. temexa* in New Mexico and Louisiana is desirable.

MEXICO: *Coahuila*: 12 mi. N Jiménez [not mapped]; Las Rusias, Muzquiz. *Nuevo León*: Apodaca; Allende; Linares; Montemorelos; Monterrey and vicinity; Sabinas Hidalgo. *San Luis Potosí*: Ciudad Valles and vicinity; El Salto; Guerrero; Hacienda de Santa Clara, Huasteca Potosina (Dugès, 1889) [not mapped]. *Tamaulipas*: Ciudad Mante; Ciudad Victoria; El Limón and vicinity; Nuevo Laredo; Tampico. *Veracruz*: Alazán; El Naranjo, 900 ft. [not mapped]; 4 mi. SW Panuco.

UNITED STATES: *Texas* (counties): Atascosa; Bastrop; Bee; Bell; Bexar; Brazos;

Brewster; Brown; Burleson; Burnet; Cameron; Colorado; Comanche; Coryell; Dallas; DeWitt; Dimmitt; Fort Bend; Frio; Gillespie; Goliad; Gonzales; Harris; Hidalgo; Jeff Davis; Jim Wells; Jones; Karnes; Kerr; Kimble; Kinney; Kleberg; LaSalle; Lee; Live Oak; Maverick; McCulloch; McLennan; Medina; Nueces; Nolan; Pecos; Presidio; Reeves; Robertson; San Patricio; Starr; Taylor; Tom Green; Travis; Uvalde; Val Verde; Victoria; Ward; Washington; Webb; Wharton; Willacy; Williamson.

*Epicauta abadona* Skinner

*Epicauta abadona* Skinner, 1904, p. 217 [Holotype, male, from Phoenix, Arizona, in the collection of the Academy of Natural Sciences of Philadelphia, no. 8068, examined]. Snow, 1906, p. 174. Werner, 1945, p. 435. Werner, Enns, and Parker, 1966, p. 37, fig. 64.

*Epicauta abandona, lapsus calami*, Maydell, 1934, p. 331.

*Epicauta mutchleri* Maydell, 1934, p. 331 [Holotype, male, from Phoenix, Arizona, in the American Museum of Natural History, examined].

LOCALITY RECORDS

MEXICO: *Sinaloa*: Concordia, 5; Culiacán and vicinity, 142; 57 mi. N Culiacán, 3; Los Mochis (Werner, Enns, and Parker, 1966); Mazatlán and vicinity, 24; 20 mi. N Pericos, 2; Puente de que Malo [not found], 4; Venedio [not found] (Werner, Enns, and Parker, 1966). *Sonora*: Álamos, 1; 20 mi. SE Agua Prieta, 1; Ciudad Obregón (Werner, Enns, and Parker, 1966); Hermosillo, 3; 40 mi. N Hermosillo, 4.

UNITED STATES: *Arizona*: Agua Fria River (Werner, 1945) [not mapped]; Cashion, Florence, and Gillespie Dam (Werner, Enns, and Parker, 1966); Douglas, 1; Mesa, 3; Nogales and Patagonia (Werner, Enns, and Parker, 1966); Phoenix, 12; San Bernardino Ranch, 18 mi. E Douglas (Snow, 1906); Tempe (Werner, Enns, and Parker, 1966); Tucson, 1.

*Epicauta tamara*, new species

*Epicauta dugesi*: Werner, 1957, pp. 107-108.

ETYMOLOGY: *tamara*, from the female name Tamar.

TYPE DESIGNATION: Holotype, male, from Culiacán, Sinaloa, Mexico, September 26/27, 1972, at light, R.B. Selander and A. Berríos, Notes 301-72, in the American Museum of Natural History.

See the key for the diagnostic characters of this species.

NOMENCLATURE HISTORY: There has been an inordinate amount of confusion associated with the name *dugesi*, which Werner (1957) incorrectly applied to this species. The name *Epicauta dugesi* Beaugard (1889) is a *nomen nudum* proposed, unnecessarily, as a replacement for "E. vittata Eug. Dug.," itself a *nomen nudum* appearing in a list of Meloidae published by Dugès in 1886. Werner's (1957) application of Beaugard's *dugesi* to specimens of the present species from the West Coast of Mexico (Sinaloa and Nayarit), although accompanied by descriptive material, does not validate that name for purposes of zoological nomenclature.

An apparent complication arises from Werner's (1957) citation in his synonymy of "*Epicauta vittata* Duges" of Dugès' (1889) subsequent reference to an "*Epicauta vittata*." Thus Werner's readers may conclude, erroneously, that Dugès validated *E. vittata* Dugès in 1889 and that Beaugard, recognizing the priority of *Epicauta vittata* (Fabricius, 1775), was correct in proposing a replacement name. However, it is explicit in Beaugard's paper that *dugesi* was intended as a replacement for *E. vittata* Dugès (1886), not *E. vittata* of Dugès (1889), wherein *vittata* is credited to Fabricius. In point of fact, Dugès in 1889 did no more than identify and describe material from San Luis Potosí as *E. vittata* Fabricius, and it is now apparent, from the locality involved and the description, that this was a misidentification of *E. temexa*. In any event, the identity of Dugès' (1889) material has no bearing on the nomenclatural status of *E. dugesi* Beaugard.

LOCALITY RECORDS

We have examined all the material of this species studied by Werner (1957) except for one specimen from Tepic, Nayarit.

MEXICO: *Sinaloa*: Concordia, 10; Culiacán and vicinity, 110; 3 mi. E Culiacancito, 1; Los Mochis, 35; Mazatlán and vicinity, 26; Presidio River, near [Villa] Unión, 1; Rosario, 2; Venedio [not found], 1. *Sonora*: Cocorit, 5; [Presade] Mocúzari, 1; 18 mi. E El Puerto [not found], 2. *Nayarit*: 24 mi. N Acaponeta, 2; 3 mi. NW Las Varas, 12; San Blas and vicinity, 2; Tepic, 4.

*Epicauta vitticollis* (Haag-Rutenberg)

*Lytta vitticollis* Haag-Rutenberg, 1880, p. 52 [Syntypes from San [=St.] Juan del Norte, Nicaragua; Guatemala; and Mexico, "Mus. Bruxell., Helsingfors, Bates, Haag."]

*Epicauta canoi* Dugès, 1889, p. 86 [Type material from Veracruz, Mexico, presumably lost].

*Epicauta vitticollis*: Champion, 1891-1893, p. 414, pl. 19, fig. 11.

ASSIGNMENT OF REFERENCES: Champion (1891-1893) sank *E. canoi* under *E. vitticollis* without comment. Dugès' (1889) description, based perhaps on a single specimen, leaves no doubt but that Champion was correct.

GEOGRAPHIC VARIATION: As noted by Champion (1891-1893), the color pattern of this species is geographically variable. In specimens least heavily marked with black the vertex of the head is dark orange; the orange frontal spot of the head is relatively large, occupying most of the area between the eyes; the elytra each have three separate black vittae, producing a pattern like that of class 4 of *E. vittata* (fig. 44) and the trochanters and basal half to two-thirds of the femora are orange. The most heavily marked specimens have no orange on the head except for the frontal spot, which is only half as wide as the area between the eyes; the inner black elytral vitta is much broadened and the middle and outer vittae are completely fused to each other, producing a pattern like that of class 1 of *E. vittata* (fig. 44) except that the inner vitta is even broader, so that the yellow area between it and the fused middle and outer vittae is reduced to a thin line; and the orange areas of the femora are confined to the basal one-third or less. Intermediate elytral patterns, corresponding to classes 2 and 3 of *E. vittata* also occur; as in that species, specimens with

such patterns show intermediate development of orange markings on the head and femora.

The geographic pattern of the variation is indicated in table 63. It will be seen that the average pattern becomes more melanistic as one moves from Veracruz and Oaxaca, where the population is evidently largely three-striped eastward to Honduras, where the entire sample is of the two-striped form. It is perhaps worth mentioning that the color pattern of *E. vitticollis* least resembles that of *E. unilineata* (two-striped) in the area of known sympatry of these species (Veracruz).

LOCALITY RECORDS

BELIZE: *Corozal*: Río Hondo (Champion, 1891-1893). *Orange Walk*: Orange Walk, 3. *Toledo*: Punta Gorda, 5.

GUATEMALA: *Alta Verapaz*: Chiacam and Gubilquitz [=Cubilquitz] (Champion, 1891-1893); Panzos, 2; Trece Aguas, 2. *El Petén*: Tikal, 5. *Izabel*: (Champion, 1891-1893); Quiriguá, 2. *Department Unknown*: Sayuga, 2.

HONDURAS: *Atlantida*: La Ceiba, 49; Tela, 4. *Colón*: Corocito, 2; Olanchito, 1. *Francisco Morazán*: Tegucigalpa, 2. *Yoro*: La Lima and vicinity, 2. *Department Unknown*: Carmelina, 3; Lombardia, 2; Monchita Mine Road, 1.

MEXICO: *Chiapas*: Colonia Chupa, 600 ft., 5 mi. S Palenque, 2. *Oaxaca*: Donaji [not found], 2; Tuxtepec, 5. *Quintana Roo*: 15 mi. W Chetumal, 2. *Tabasco*: 5 km. E Cárdenas, 1; Tepas and vicinity, 3; Villahermosa, 1. *Yucatán*: Pisté, 1. *Veracruz*: 2 mi. W Ciudad Alemán, 2; Córdoba, 1; Cosamaloapan (Champion, 1891-1893); Cotaxtla, 80; 31 km. WNW [El] Potrero [ambiguous, not mapped], 1; 10 mi. W Tezonapa, 1; Veracruz, 8; state label only, 2.

NICARAGUA: *Río San Juan*: San Juan del Norte (Haag-Rutenberg, 1880).

*Epicauta unilineata* Champion

*Epicauta unilineata* Champion, 1891-1893, p. 415, pl. 19, fig. 13 [Syntypes from near the city [of Guatemala] and from San Jerónimo [=San Geronimo], Guatemala; lectotype, male, from San Jerónimo, Guatemala, in the collection of the

TABLE 63  
Variation in Color Pattern of Elytra in *Epicauta vitticollis* Expressed as Percentage Distributions of Specimens in Color Classes

(Color classes correspond closely to those defined for *E. vittata* and shown in figure 44.)

Sample area	Color Classes				Mean	N
	1	2	3	4		
Veracruz, Oaxaca	0.0	1.2	9.2	89.7	3.9	87
Tabasco, Chiapas	0.0	14.3	42.9	42.9	3.3	7
Yucatán, Quintana Roo, Belize	93.3	0.0	16.7	0.0	1.3	6
Guatemala	72.2	11.1	16.7	0.0	1.4	18
Honduras	100.0	0.0	0.0	0.0	1.0	62

Academy of Natural Sciences of Philadelphia (examined), hereby designated.]

#### LOCALITY RECORDS

EL SALVADOR: *La Unión*: Santa Rosa, 4. *San Salvador*: San Salvador, 2. *Santa Ana*: Candelaria, 1.

GUATEMALA: *Baja Verapaz*: San Jerónimo, 1. *Guatemala*: near Guatemala (Champion, 1891-1893).

MEXICO: *Chiapas*: Suchiapa, 4. *Oaxaca*: Juchitán, 1; Tehuantepec, 4. *Puebla*: Cacaloapan, 1. *Veracruz*: Cotaxtla, 62; La Granja [not located], 7; 10 mi. W Tezonapa, 1; 5 mi. NE Tinajas [not located], 11; Veracruz, 1.

#### *Epicauta aragua*, new species

*Epicauta grammica*: Denier, 1933, p. 39 (in part); 1935, p. 20 (in part). Martorell, 1939, p. 197. Virkki, 1962, p. 7.

ETYMOLOGY: *aragua*, from the Venezuelan state Aragua.

TYPE DESIGNATION: Holotype, male from Maracay, Aragua, Venezuela, July 30, 1975, R.B. Selander and J.K. Bouseman, in the American Museum of Natural History.

REMARKS: This species is easily distinguished from all other members of the Vittata Group by the fact that the ventral edge of the third to eighth antennal segments is ridged, bare, and shiny in the male. In the course of courtship behavior (to be described in detail elsewhere), this edge of the segments is rubbed vigorously on the elytra of the female.

Martorell (1939) described this species as "very abundant in the surroundings of La Providencia and Saman de Guere," both in the state of Aragua, Venezuela, on weeds and grasses. A specimen examined from Guaparo, Carabobo, Venezuela, is labeled as feeding on *Solanum tuberosum*. We found adults feeding on *Amaranthus* sp., *Portulaca* sp., and *Trianthema portulacastrum* (Portulacaceae) in great numbers along the edges of fallow agricultural fields near Maracay, Aragua, in 1975. At San Fernando, Apure, we collected 25 adults, together with six adults of *E. apure*, on *Kallstroemia* sp., but adults of neither species ate this plant in captivity.

Adults have been collected in every month of the year. The percentage distribution, by months, of records is bimodal: January, 7.0; February, 5.5; March, 4.7; April, 10.2; May, 18.0; June, 10.9; July, 11.7; August, 8.6; September, 5.5; October, 4.7; November, 9.4; December, 7.0. Several of the specimens examined from Central America are labeled as collected at light; however, it was our experience in Venezuela that the adults of *E. aragua*, unlike those of the sympatric *E. apure*, are relatively inactive at night and unlikely to be found at lights even in areas of heavy population density.

#### LOCALITY RECORDS

We have examined nearly 500 specimens.

COLOMBIA: *Magdalena*: Tamalameque. *Meta*: Villavicencio. *Santander*: La Cimitarra, about 80 km. NW Veléz. *State Unknown*:

“Amero, Santuario & Cauca Valley”; Río Frio.

COSTA RICA: *Guanacaste*: Bagaces; Finca Jiménez, near Taboga [not found]; Santa Elena. *Puntarenas*: Coronado, 1400-1500 m. *San José*: Higuito; San José. *Province Unknown*: Coyolar.

EL SALVADOR: *La Libertad*: Quezaltepique and vicinity. *San Salvador*: San Salvador.

HONDURAS: *Copán*: Copán. *Francisco Morazán*: Zamorano [not found].

PANAMA: *Canal Zone*: Alhajulla; Ancón; Balboa; Barro Colorado Island; Cabima; Ciricito; Coco Solo; Corozal; Fort Kobbe; Gatún; Juan Minas; Las Cascadas; Madden Dam; Margarita; Paraíso, Tabernilla. *Chiriquí*: Bugaba; David; Rovira [not found]. *Coclé*: Río Hato. *Panamá*: La Chorrera; Río Trinidad.

VENEZUELA: *Apure*: San Fernando. *Aragua*: Cagua; El Castaño; El Limón; Las Delicias; La Providencia; Ocumare de la Costa; Rancho Grande; Maracay; Saman de Guere (Martorell, 1939); Villa de Cura. *Bolívar*: El Pao; Guaniamito [not found]; Santa Elena. *Carabobo*: Guaparo; Las Trincheras; Las Vueltas; Milagro. *Distrito Federal*: Caracas and vicinity; El Valle. *Guarico*: [Hato] Las Lajes [not found]. *Miranda*: Baruta; Tacariguá. *Monagas*: Caripito; Hacienda Las Acasias, Caripe. *Portuguesa*: Baronero [not found]; San Nicolas, 180 m. *Sucre*: Cumanocoa. *Trujillo*: Km 80, carr [etera between] Valera and Maracaibo; Valera. *Zulia*: [San Juan de] Colón; Kasmara, Sierra de Perija, 250 m. [not found]; Tucuco, 420 m.

*Epicauta monachica* (Berg)

*Lytta monachica* Berg, 1883, p. 68 [Lectotype, female, from Rodeo del Medio, Mendoza, Argentina, in the Berg Collection, Museo de La Plata, La Plata, Argentina, hereby designated (examined)].

*Epicauta monachica*: Blanchard, 1891, p. 495. Bosq, 1934, p. 327; 1943, p. 11. Denier, 1935a, p. 157; 1939, p. 562. Hayward, 1942, p. 54; 1960, p. 23. Martínez, 1952, p. 254.

REMARKS: We have seen nothing from South America that might be confused with this species, which is characterized by a highly distinctive color pattern (fig. 61).

LOCALITY RECORDS

ARGENTINA: *Catamarca*: (Bosq, 1934). *Chaco*: Villa Angela, 2. *Córdoba*: (Bosq, 1943). *La Rioja*: La Rioja, 3; Patquia, 2. *Mendoza*: Rosario del Medio, 2. *Salta*: El Morenillo, Rosario de la Frontera, 1; Tartagal, 1. *San Luis*: (Bosq, 1934). *Santiago del Estero*: El Charco, 2; Fernández, 20; Icaño, 1; Mal Pozo [not found], 1; Santiago del Estero and vicinity (including La Banda and Las Termas), 230. *Tucumán*: Amaicha del Valle, 1978 m., 10; Carmendia [not found], 1; Concepción, 1; Tacañas, 3; Tucumán, 3. *Province Unknown*: Siambón, 1.

BOLIVIA: *Santa Cruz*: Lagunillas, 5; Santa Cruz, 12.

*Epicauta luteolineata* Pic

*Epicauta luteolineata* Pic, 1933, p. 25 [Syntypes from “Río Salado,” Argentina, presumably in the Museum National d’Histoire Naturelle (Paris)]. Denier, 1940, p. 421.

*Epicauta missionum* var. *luteolineata*: Denier, 1935a, p. 157.

REMARKS: There are several South American species of *Epicauta* that resemble *E. luteolineata* (fig. 62) with respect to color pattern. We are, however, fairly confident that we have identified this species correctly.

The “forma typica” of this species and the varieties *E. luteolineata* var. *discolineata* and *E. l.* var. *brevebasalis* were described by Pic (1933) from “Río Salado,” Argentina, which we interpret as the river of that name arising in Salta Province and flowing through Santiago del Estero and Santa Fé provinces to empty into the Río Paraná at Santa Fé. The two varieties were assigned to *E. clericalis* (Berg) by Denier (1935, p. 23).

LOCALITY RECORDS

ARGENTINA: *Santiago del Estero*: Fernández, 20; Santiago del Estero and vicinity, 12. *Province Unknown*: Río Salado (Pic, 1933).

*Epicauta leopardina* (Haag-Rutenberg)

*Lytta leopardina* Haag-Rutenberg, 1880, p. 30



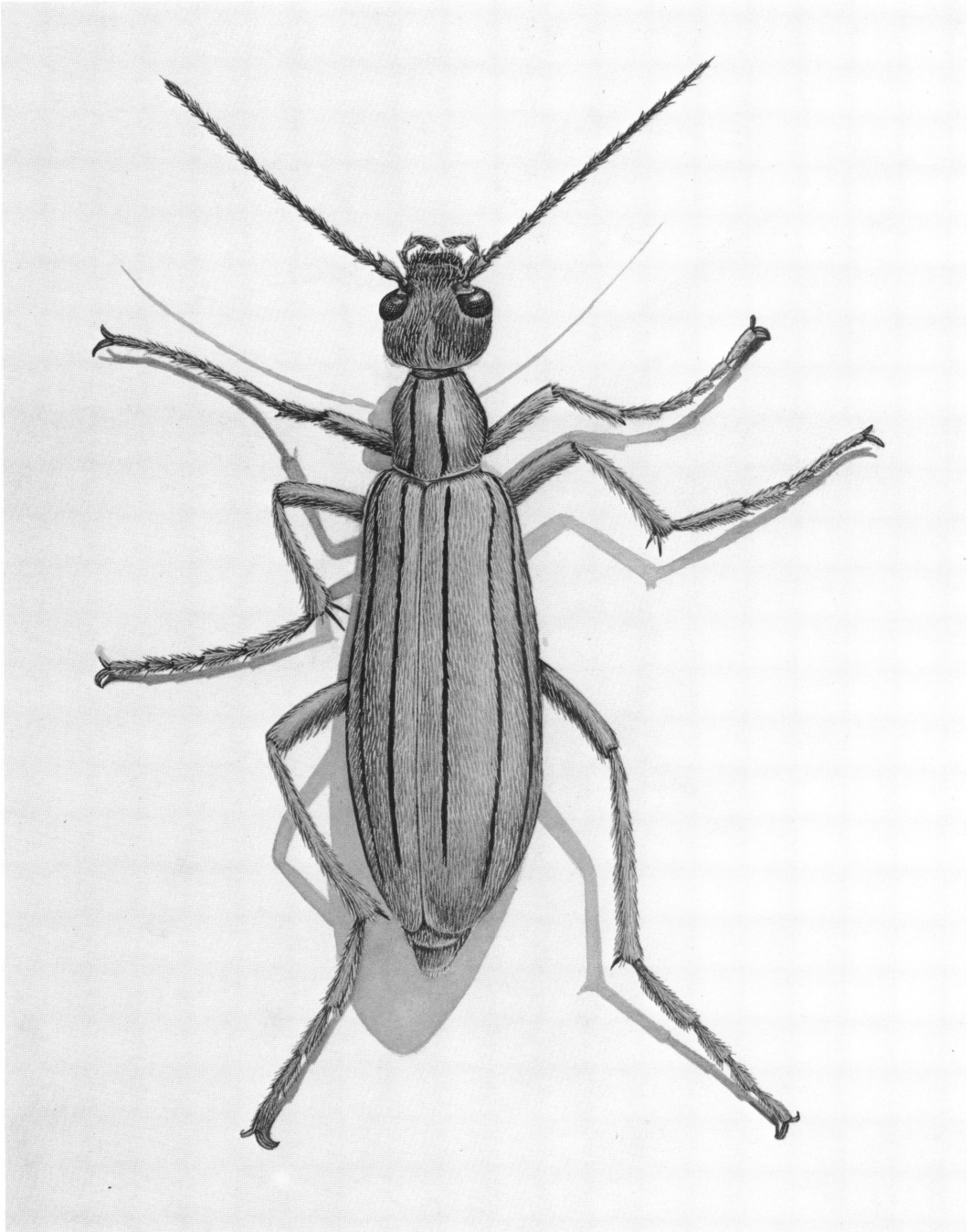


FIG. 61. *Epicauta monachica*, female.

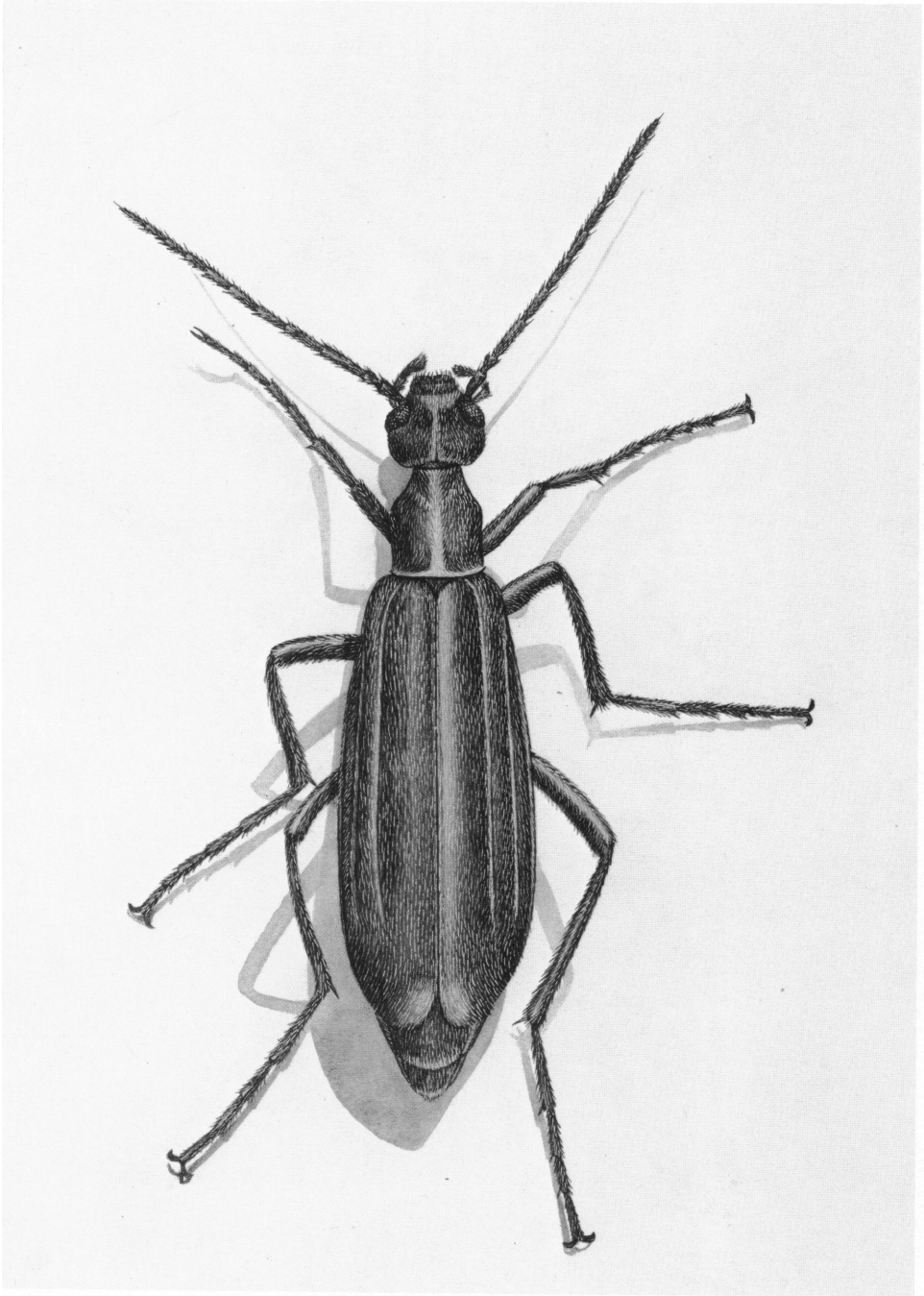


FIG. 62. *Epicauta luteolineata*, female.

[Syntypes from Córdoba, Argentina, in the Haag-Rutenberg Collection, Zoologisches Sammlung der Bayerischen Staates Munich].

*Cantharis leopardina*: Burmeister, 1881, p. 24. Berg, 1881, p. 304.

*Epicauta leopardina*: Bosq, 1934, p. 327; 1943, p. 11. Hayward, 1960, p. 22.

**REMARKS:** Superficially, the elytral color pattern appears to be formed by black fasciae or blotches, much as in many species of the genus *Pyrota* Dejean. However, on closer examination it is apparent that in *E. leopardina*, as in other species of the Vittata Group, there are actually three black vittae on each elytron (fig. 23). Both the inner vitta, which is much abbreviated, and the middle one are much broadened distally to form irregular blotches, with an additional blotch basally resulting from fusion of the middle and outer vittae. The pattern so formed, which is quite distinctive and permits immediate recognition of the species, is not basically different from the norm of the group and could have been derived, in fact, from one essentially like that of *E. monachica* (fig. 61).

#### LOCALITY RECORDS

**ARGENTINA:** *Buenos Aires*: (Bosq, 1934). *Catamarca*: Province label only, 1. *Chaco*: Villa Angela, 5. *Córdoba*: Arguello, 300 m. [not found]; Córdoba, 7; Villa María, 10. *Entre Rios*: La Paz, 2; Pronunciamento [not found], 1. *Mendoza*: (Bosq, 1943). *Misiones*: Eldorado, 1; San José, 10. *Neuquén*: (Bosq, 1943). *Salta*: Departamento de Auta, 1; province label only, 1. *Santa Fé*: Rosario, 3. *Santiago del Estero*: Fernández, 22; Icaño, 2; Río Salado, 1; Santiago del Estero and vicinity, 91; province label only, 1. *Tucumán*: San Pedro de Colalao, 2; Tucumán, 4.

**BRASIL:** *Río de Janeiro*: Muri, 1000 m., 4.

#### *Epicauta aemula* (Fischer)

*Cantharis aemula* Fischer, 1827, p. 20 [Type material from Brasil, originally in the Royal Museum of Munich; present location unknown].

*Lytta aemula*: Haag-Rutenberg, 1880, p. 53.

*Epicauta aemula*: Borchmann, 1917, p. 70.

**REMARKS:** Fischer (1827) described this species, possibly on the basis of a single specimen, simply from Brasil. A specimen in the Denier Collection, Museo de La Plata, is labeled as collected December 31, 1916, at São Paulo, Brasil. Denier's (1935) record of *E. aemula* from Coroico, Bolivia, was based on a misidentification of *E. yungana* Denier (Denier, 1940).

#### *Epicauta apure*, new species

**TYPE DESIGNATION:** Holotype, male, from San Fernando, Apure, Venezuela, July 31, 1975, at light, R. B. Selander and J. K. Bouseman, in the American Museum of Natural History.

**ETYMOLOGY:** *apure*, from the Venezuelan state, Apure.

**DESCRIPTION:** Head with antennae, palpi, labrum, and clypeus black and with a heavy black mark extending from clypeus along each side of front bordering eye; rest of head orange, unmarked; pronotum entirely black; elytra black, finely margined with orange and with two fine, longitudinal lines arising from humerus and extending to apical third; elytral pattern formed by enlargement and fusion of black vittae, as in *E. aragua*; inner and middle black vittae subequal in breadth, several times broader than orange line between them; outer black vitta much narrower than middle one, broadly fused with it basally and apically; orange line between middle and outer vittae very fine, tending to be marked in pale setae only at ends, generally less distinct than in *E. aragua*; venter and legs black except trochanters and basal fourth to third of femora orange. Clothing setae very fine, brown on disk of pronotum (except midline) and black areas of elytra, pale sericeous elsewhere, producing an overall brownish cast even though cuticle is black.

Eyes large. Antennae very slender, setaceous; segments III-XI at least four times as long as broad. Pronotum elongate, parallel-sided from base to apical third. Legs very slender; all tibial spurs slender, spiniform. Pygidium moderately deeply, narrowly excised. Length: 7-11 mm.

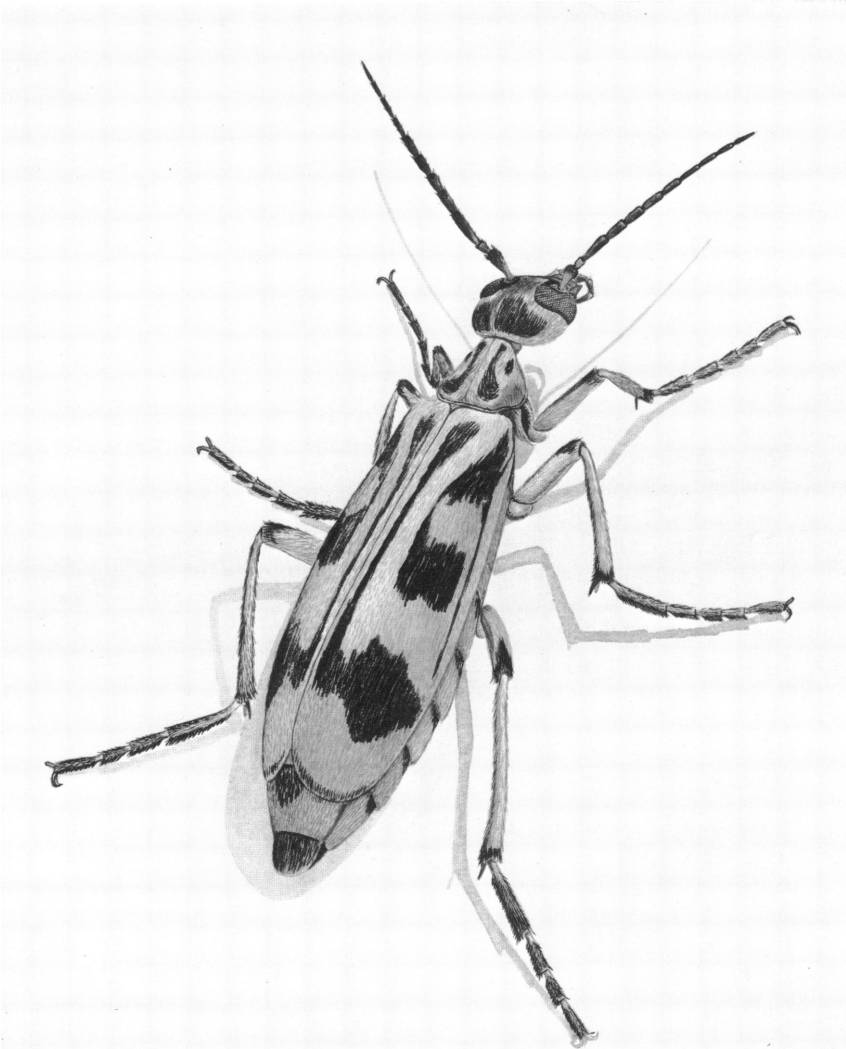


FIG. 63. *Epicauta leopardina*, male.

Male antennae not modified, as in female; fore tibial spurs not modified; fore and middle tarsal pads more densely padded than in female; first segment of fore tarsi a little elongated, weakly curved, not distorted; fifth visible abdominal sternum broadly, deeply emarginate; sixth deeply, triangularly emarginate.

REMARKS: Description of this species is necessitated by the need for a name for use in an article on behavior and ecology now in prepara-

tion. Possibly the species is the same as *E. grammica* (Fischer). However, the latter is unrecognizable on the basis of available information, and there seems to be little utility in continuing to assign the name *E. grammica* to any striped *Epicauta* that occurs in or near Brasil and whose color pattern does not differ greatly from Fischer's description.

*Epicauta apure* is largely allopatric with *E. aragua*, which it closely resembles in most characters. However, we took the two species

together at San Fernando, Apure, on *Kallstroemia* sp. As previously mentioned, *E. apure* appears to be more nocturnal than *E. aragua*. Limited data do not suggest inter-specific differences in feeding behavior or seasonal range of the adult stage.

Males of *E. apure* are easily distinguished from those of *E. aragua* by the lack of modification of the ventral edge of the flagellar segments of the antennae. This anatomical distinction is associated with pronounced inter-specific differences in the pattern of male courtship behavior (which will be described elsewhere). In both sexes *E. apure* is generally less extensively marked with orange than *E. aragua*; in addition, the clothing setae on the sides and midline of the pronotum tend to be less conspicuous in *E. apure*. There is, however, considerable overlap between the species in these last two characters. At present, we know of no way of distinguishing between females consistently.

#### LOCALITY RECORDS

TRINIDAD: *St. George*: Marval, 1; Port of Spain, 2. *District Unknown*: Coparo, 1; Warren, 1.

VENEZUELA: *Apure*: San Fernando, 81. *Guarico*: Calabozo, 14; Rio Guaiquito, 2. *Monagas*: 42 and 60 km. SE Maturia, 2.

#### *Epicauta borgmeieri* Denier

*Epicauta borgmeieri* Denier, 1935a, p. 153 [Holotype, male (?), from Campo Grande, Mato Grosso, Brasil, in the Museo de La Plata, examined].

REMARKS: This species was described from a holotype, allotype, and unspecified number of paratypes, all collected November 27-30, 1921, by Lane at Campo Grande. The holotype and allotype, dated November 30, are in the Denier Collection, Museo de La Plata; Paratypes are presumably in the collection of the Sección de Entomología Agrícola del Instituto Vegetal de Río de Janeiro.

#### *Epicauta bosqi* Denier

*Epicauta bosqi* Denier, 1935a, p. 153 [Holotype, female (?), from Rosario, Santa Fé, Argentina, in

the Museo de La Plata, examined]. Bosq, 1943, p. 11.

REMARKS: All the specimens examined are in the Denier Collection, Museo de La Plata, where they were determined as *E. bosqi* by Denier. The dates of collection range from January to May. According to Bosq (1943), the adults eat the leaves of alfalfa (*Medicago sativa*). We have seen none of Bosq's material.

#### LOCALITY RECORDS

ARGENTINA: *Buenos Aires*: (Bosq, 1943). *Chaco*: Colonia Castelli, 1; Cote Lai, 2; Puente La Plaza, 1; Villa Angela, 2. *Formosa*: Formosa, 2. *Salta*: (Bosq, 1943). *Santa Fé*: Rafaela (Denier, 1935a); Rosario, 2.

#### *Epicauta clericalis* (Berg)

*Cantharis clericalis* Berg, 1881, p. 308 [Holotype, sex not determined, from Misiones Province, Argentina, possibly in the Museo de La Plata].

*Epicauta clericalis*: Borchmann, 1917, p. 73. Denier, 1935, p. 23; 1935a, p. 154.

*Epicauta luteolineata* v[ar]. *brevebasalis* Pic, 1933, p. 26 [Type material from "Rio Salado," Argentina, presumably in the Museum National d'Historie Naturelle (Paris)].

*Epicauta luteolineata* v[ar]. *discolineata* Pic, 1933, p. 26 [Type material from "Rio Salado," Argentina, presumably in the Museum National d'Historie Naturelle (Paris)].

*Epicauta clericalis* var. *discolineata*: Denier, 1935a, p. 154.

REMARKS: In the Berg Collection in the Museo de La Plata there is a specimen from "Misiones" that is labeled as "*Lytta clericalis* Berg" and is perhaps the holotype. In the same museum, the Denier Collection contains a specimen from San Juan Province and another from Villa Ana, Santa Fé, labeled as compared with the type of *E. clericalis* by Denier. We found no significant differences among these three specimens.

On the basis of material in the Denier Collection from Rosario, Santa Fé, identified by Denier as representing *E. luteolineata* var. *brevebasalis* Pic and *E. l. discolineata* Pic, we concur with Denier's (1935) assignment of these names to the synonymy of *E. clericalis*. The latter variety is superficially distinctive in

that the pale strip of the elytron is not limited to the basal area but rather extends from the base to near the apex. No structural differences were detected in rather hurried comparisons of Denier's material of the Pic varieties with the Berg specimen of *E. clericalis* from Misiones mentioned above.

#### LOCALITY RECORDS

ARGENTINA: *Misiones*: Province label only, 1. *San Juan*: Province label only, 1. *Santa Fé*: Rosario, 3; Santa Ana, 1. *Province Unknown*: Río Salado (Pic, 1933).

#### *Epicauta floydwernerii* Martínez

*Epicauta floydwernerii* Martínez, 1955, p. 58 [New name for *E. rubriceps* (Blanchard, 1843), not *E. rubriceps* (Redtenbacher, 1942)].

*Lytta rubriceps* Blanchard, in Blanchard and Brullé, 1843, p. 200, pl. 15, fig. 8 [Type material from Santa Cruz Province, Bolivia, presumably in the Museum National d'Historie Naturelle (Paris)].

*Epicauta rubriceps*: Borchmann, 1917, p. 80. Denier, 1935, p. 24; 1935a, p. 159.

REMARKS: Haag-Rutenberg (1880) placed *Lytta rubriceps* as a junior synonym of *Lytta strigata* Gyllenhall (1817); both Borchmann (1917) and Denier (1935), p. 24; 1935a, p. 159 accepted the synonymy but inexplicably treated *rubriceps* as the senior synonym. In rejecting the synonym entirely Martínez (1955) renamed *E. rubriceps* (Blanchard) because of homonymy with the older name *E. rubriceps* (Redtenbacher), currently applied to an Old World species of *Epicauta*.

#### LOCALITY RECORDS

ARGENTINA: *Misiones*: San Ignacio, 1; province label only, 2.

BOLIVIA: *Santa Cruz*: (Blanchard, 1843).

#### *Epicauta franciscana* Denier

*Epicauta franciscana* Denier, 1935a, p. 155 [Holotype, male, from Rosario, Santa Fé, Argentina, in the Museo de La Plata, examined].

REMARKS: According to Denier (1935a), material from the type locality was collected in February and March of 1932 and that from

Uruguay on December 28, 1915. The holotype is labeled as collected by Denier on March 15.

#### LOCALITY RECORDS

ARGENTINA: *Buenos Aires*: (Denier, 1935a). *La Rioja*: (Denier, 1935a). *Santa Fé*: Rosario, 1.

URUGUAY: *Cerro Largo*: "cuchilla de" Melo (Denier, 1935a).

#### *Epicauta fuliginosa* (Olivier)

*Cantharis fuliginosa* Olivier, 1795, p. 14 (genus 46), pl. 2, fig. 20 [Type material from unspecified locality, possibly in the Museum National d'Historie Naturelle (Paris)]. Champion, 1899, p. 178.

*Epicauta fuliginosa*: Borchmann, 1917, p. 75.

REMARKS: Champion (1899) records this species from Colombia, presumably on the basis of information given by Mäklin ("Öfv. Finsk. Vet.-Soc. Förh. XVII, p. 81"). We have not been able to examine the reference cited by Champion.

#### *Epicauta grammica* (Fischer)

*Cantharis grammica* Fischer, 1827, p. 19 [Type material from Brasil, originally in the Royal Museum of Munich; present location unknown]. Haag-Rutenberg, 1880, p. 53 (in part?).

*Epicauta grammica*: Borchmann, 1917, p. 75 (in part). Denier, 1933, p. 39 (in part); 1935, p. 20 (in part); 1940, p. 420.

*Epicauta fidelis* Bréthes, 1925, p. 14 [Type (holotype?), sex unknown, from Santa Fé Province, Argentina, in the Museo de Historia Natural "Bernardino Rivadavia" (Buenos Aires), examined].

REMARKS: It has become apparent that the extensive geographical range recorded in the literature for this species (Central America to Argentina) is actually a composite of the ranges of several quite distinct species. In the present work we segregate *E. aragua*, ranging from El Salvador and Nicaragua to Venezuela and Colombia, and *E. apure*, of the Orinoco Basin of southern Venezuela, from *E. grammica*, thus restricting its recorded range to Brasil, Bolivia, Paraguay, and Argentina. Still, in our estimation, *E. grammica* represents more than a sin-

gle species, and additional segregation and naming of populations will be necessary. Unfortunately, there is considerable doubt as to which population the name *E. grammica* is ultimately assignable.

We have followed Denier (1935, p. 20) in listing *E. fidelis* Bréthes as a synonym of *E. grammica*. A specimen in the Bréthes Collection in Buenos Aires is marked as the type and labeled with the number "411." Despite repairs made on it by Dr. Viana in 1951, the specimen is in poor condition; it is mounted on a card, and we could not determine its sex.

"*Cantharis vittata*" of Olivier, recorded from Cayenne (1790-1791, p. 279) and "America" (1795, p. 13 (gen. 46), pl. 1, fig. 3), is perhaps referable to *E. grammica*. As noted by Staig (1940), Olivier's figure does not particularly resemble an adult of *E. vittata* (Fabricius).

#### *Epicauta kraussi* (Haag-Rutenberg)

*Lytta kraussi* Haag-Rutenberg, 1880, p. 25 [Type material from "Irisanga," Brasil, in the collections of the "Mus. Vind." and Haag-Rutenberg, the latter now part of the Zoologisches Sammlung der Bayerischen Staates, Munich].

*Epicauta kraussi*: Borchmann, 1917, p. 97.

**REMARKS:** This species is known only from the type locality, which we have not been able to find.

#### *Epicauta purpureiceps* (Berg), new status

*Lytta purpureiceps* Berg, 1889, p. 123 [Holotype, female (?), from Córdoba Province, Argentina, in the Museo de La Plata, examined].

*Cantharis purpureipennis* [sic]: Champion, 1899, p. 186.

*Epicauta purpureiceps*: Borchmann, 1917, p. 97.

*Epicauta kraussi* var. *purpureicens* [sic]: Denier, 1935a, p. 156.

*Epicauta kraussi* var. *purpureiceps*: Denier, 1940, p. 421.

**REMARKS:** It is difficult to explain why Denier regarded this species as a variety of *E. kraussi*. The original description of *E. kraussi* does not agree closely with either the type of *E. purpureiceps* or material identified as *E. kraussi* var. *purpureiceps* by Denier.

This species is known only from the type locality.

#### *Epicauta missionum* (Berg)

*Cantharis missionum* Berg, 1881, p. 306 [Holotype, female, from Misiones Province, Argentina, in the Museo de La Plata, examined].

*Cantharis* sp. #15, Burmeister, 1881, p. 28.

*Epicauta missionum*: Borchmann, 1917, p. 78.

**REMARKS:** In addition to the holotype, we have examined, in the Denier Collection, Museo de La Plata, a specimen collected February 23, 1934, by Hayward near Puerto Aguirre, Río Iguazú, Misiones, Argentina.

#### *Epicauta nattereri* (Haag-Rutenberg)

*Lytta nattereri* Haag-Rutenberg, 1880, p. 24 [Type material (apparently a single specimen) from "Irisanga," Brasil, in the "Mus. Vindob."].

*Epicauta nattereri*: Borchmann, 1917, p. 78.

**REMARKS:** On the basis of the distinctive color pattern described by Haag-Rutenberg, there should be no problem in recognizing this species. It is known only from the type locality.

#### *Epicauta philaemata* (Klug)

*Lytta philaemata* Klug, 1825, p. 434, pl. 41, fig. 6 [Syntypes from Brasil, presumably in the Zoological Museum, Humboldt University, Berlin]. Haag-Rutenberg, 1879, p. 412.

*Cantharis philaemata*: Fischer, 1827, p. 21.

*Lytta capitata* Castelnau, 1840, p. 275 [Type material from Brasil; present location unknown].

*Epicauta philaemata*: Borchmann, 1917, p. 80. Denier, 1935, p. 16. Guérin, 1953, p. 225.

#### LOCALITY RECORDS

There are eight records in December, two in November, and one each in September, October, and January.

**ARGENTINA:** *Formosa*: Province label only, 2. *Misiones*: Puerto Cazador, 1.

**BRASIL:** *Río de Janeiro*: Pico de Tijuca, 2. *Río de Janeiro* (D.F.): Corcovado, 1. *Santa Catarina*: Nova Bremen, 5; Nova Teutonia, 14; Tayo, 3. *São Paulo*: Cantareira, 1.

**REMARKS:** We believe that we have identi-

fied this species satisfactorily from the original description. The specimens cited above agree well with that description and also with the description of the synonym *capitata* Castelnau and a specimen in the Denier Collection, Museo de La Plata, identified as *E. philaemata*.

This species is included in the Vittata Group with considerable reservation since the male lacks erect setae on the abdominal sternum. In addition, the male is unusual for its extremely long antennae and the absence of the *anterior* fore tibial spur.

*Epicauta rutilifrons* Borchmann

*Epicauta rutilifrons* Borchmann, 1930, p. 91, pl. 4, fig. 5 [Syntypes from Ledesma and Senillosa, Jujuy Province, Argentina].

REMARKS: A specimen in the Denier Collection, Museo de La Plata, labeled "Argentina, Prov. Jujuy 190 C. Bruch," is apparently a syntype (although labeled as a "paratipo"). The present location of the rest of the type material is unknown to us.

*Epicauta strigata* (Gyllenhal)

*Lyta strigata* Gyllenhal, 1817, p. 18 [Type material questionably from Brasil, presumably in the Zoological Museum, University of Uppsala]. Haag-Rutenberg, 1880, p. 53.

*Cantharis strigata*: Fischer, 1827, p. 19.

*Epicauta strigata*: Borchmann, 1917, p. 83 [also listed, p. 80, as a junior synonym of *E. rubriceps* (Blanchard)]. Martínez, 1955, p. 58.

REMARKS: Haag-Rutenberg (1880) treated *E. floydwernerii* Martínez (as *Lyta rubriceps* Blanchard) as a junior synonym of *E. strigata* (Gyllenhal). Subsequent authors reversed the synonymy, despite the priority of Gyllenhal's name. Martínez (1955), who rejected the synonymy entirely, says that *E. strigata* is "very closely related" to *E. aemula*.

Gyllenhal indicated that it was questionable whether the type material came from Brasil. We are not aware of records subsequent to the original description.

*Epicauta subvittata* (Erichson)

*Lyta (Epicauta) subvittata* Erichson, 1848, p. 566 [Type material from Guyana (=British Guiana),

presumably in the Zoological Museum, Humboldt University, Berlin].

*Lyta sublineata* [sic]: Haag-Rutenberg, 1880, p. 53.  
*Epicauta subvittata*: Borchmann, 1917, p. 84.

REMARKS: According to Erichson, the type material was collected "in sunny woods, on bushes." We have seen no subsequent records.

*Epicauta xanthocephala* (Klug)

*Lyta xanthocephala* Klug, 1825, p. 434, pl. 41, fig. 5 [Type material from Brasil, presumably in the Zoological Museum, Humboldt University, Berlin].

*Cantharis xanthocephala*: Fischer, 1827, p. 20.

*Epicauta xanthocephala*: Borchmann, 1917, p. 85.

REMARKS: Three specimens in the Denier Collection, Museo de La Plata, from Jatahy, Goyaz, Brasil, agree with Klug's description except that the middle elytral vitta is not abbreviated but rather extends nearly the entire length of the elytron. All gray areas of the color pattern are densely pubescent and contrast strongly with the black areas.

*Epicauta yungana* Denier

*Epicauta yungana* Denier, 1935a, p. 160 [Holotype, male, from Coroico, 1300-1700 m., Nor-Yungas, Bolivia, in the Museo de La Plata, examined].

*Epicauta aemula*: Denier, 1935, p. 20.

REMARKS: According to Denier's description, the type material was collected April 10-25, 1931. In a previous reference to the material (misidentified as *E. aemula*), however, the month is given as May. There are several specimens from Coroico in the Denier Collection, Museo de La Plata, including the holotype.

*Epicauta zebra* (Dohrn)

*Cantharis zebra* Dohrn, 1876, p. 411 [Type material from Córdoba Province, Argentina; present location unknown].

*Lyta albovittata* Haag-Rutenberg, 1880, p. 29 [Syntypes from Córdoba Province, Argentina, presumably in the Haag-Rutenberg Collection, Zoologisches Sammlung der Bayerischen Staates, Munich].

*Epicauta somnolenta* Beaugard, 1889, p. ccxiii [New name for *Epicauta albovittata* (Haag-Ruten-



berg), not *E. albovittata* (Gestro, 1878)]. Bosq, 1943, p. 12.

*Epicauta zebra*: Denier, 1935a, p. 161; 1940, p. 422. Hayward, 1960, p. 23.

#### LOCALITY RECORDS

There are two records in December and one each in November, February, and March.

ARGENTINA: *Catamarca*: (Bosq, 1943). *Córdoba*: Arguello, 300 m., 24. *La Rioja*:

(Bosq, 1943). *Mendoza*: (Bosq, 1943). *Misiones*: Loreto, 6. *Salta*: Cafayate, 5. *Santiago del Estero*: (Bosq, 1943). *Tucumán*: Province label only, 2.

PARAGUAY: (Denier, 1940).

REMARKS: The type material of *E. zebra* was found on "retamo." Bosq (1943) recorded feeding on "pichanilla" (*Cassia aphylla*), a species of Leguminosae.

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